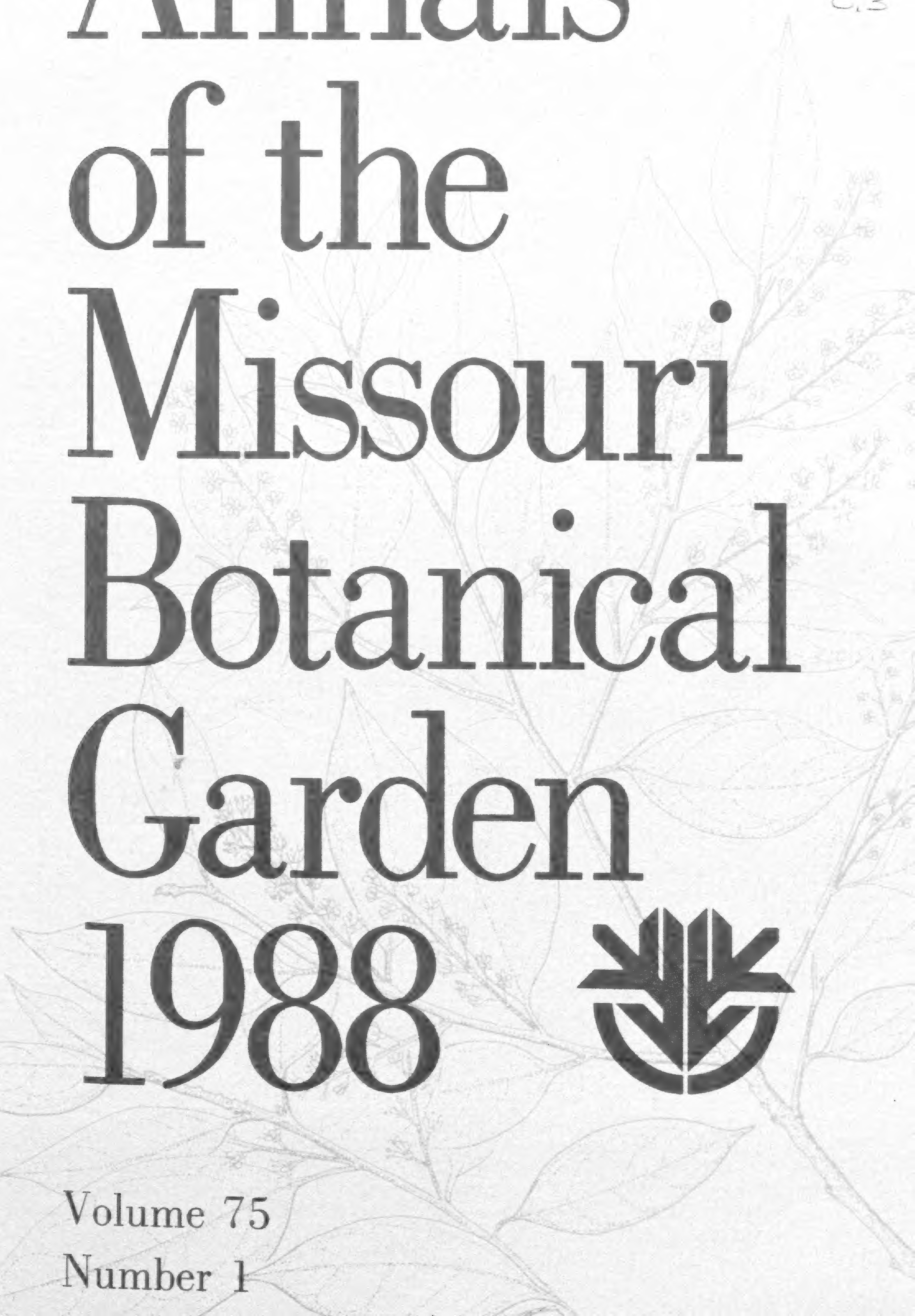
Annals of the Missouri Botanical Garden 1988



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CHANGES IN PLANT COMMUNITY DIVERSITY AND FLORISTIC COMPOSITION ON ENVIRONMENTAL AND GEOGRAPHICAL GRADIENTS[1,2]

Alwyn H. Gentry[3]

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[2] *I thank the National Geographic Society for a series of grants that supported much of the research summarized here. Collection of the Madagascar data set was funded by the World Wildlife Fund. The coastal Colombian and Ecuadorian data sets and some of the Amazonian Peru data were gathered incidental to floristic projects funded by the National Science Foundation. Additional Peruvian data sets were funded by USAID (DAN-5542-G-SS-1086-00) and the Mellon Foundation; study of the Tambopata tree plots was in part funded by a grant from the Smithsonian Institution to T. Erwin. The data sets from eastern Brazil and Paraguay were gathered as part of an NSF-sponsored monographic study of Bignoniaceae (BSR 83-05040, BSR 86-07113). The Osa Peninsula, Costa Rica, data were obtained as an OTS class project; the Los Tuxtlas, Mexico, data came from a similar class project for the Universidad Nacional Autónoma de México; parts of the Colombian data were gathered as a project of the Curso Pos-Grado de Botánica of the Universidad Nacional de Colombia. Among the many friends and colleagues who collaborated in gathering the data summarized here were R. Neumann, R. Palacios, C. Cristóbal, and A. Schinini (Argentina); K. Kubitzki, M. Fallen, H. Popppendieck, and W. Lippert (Germany); J. Miller, D. Faber-Langendoen, E. Zardini, and C. Burnett (U.S.A.); C. Ramírez (Chile); E. Lott (Mexico); D. Stevens, P. Moreno, and A. Grijalva (Nicaragua); H. Cuadros, E. Renteria, A. Cogollo, M. Monsalve, A. Juncosa, C. Restrepo, J. Ramos, P. Silverstone, and O. de Benavides (Colombia); C. Dodson (Ecuador); B. Stein, R. G. Troth-Ovrebo, and P. Berry (Venezuela); F. Ayala, C. Díaz, R. Vasquez, N. Jaramillo, D. Smith, R. Tredwell, K. Young, and D. Alfaro (Peru); A. Peixoto and O. Peixoto (Brazil); V. Vera, J. Dávalos, and S. Keel (Paraguay); G. Pilz (Nigeria); D. Thomas (Cameroon); L. Dorr, L. Barnett, and A. Rakotozafy (Madagascar); J. Connell and J. Tracy (Queensland); J. Tagai (Sarawak); G. McPherson (New Caledonia); and V. Kapos (Jamaica). Additional original data using the same or comparable techniques were made available by E. Lott (Mexico), D. Lorence (Mauritius), and J. Miller and P. White (U.S.A.). I also thank R. Perrozzi, S. McCaslin, G. Fulton, and especially J. Miller for computational and technical expertise, E. Zardini for help in the field and with the illustrations, and J. Hall and D. Thomas for providing African data. I thank S. Hubbell, T. Givnish, L. Emmons, P. Ashton, P. Raven, and D. Thomas for review comments.*

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ABSTRACT

Trends in community composition and diversity of neotropical forests as measured by a series of samples of (1) plants ≥ 2.5 cm dbh in 0.1 ha, (2) plants over 10 cm dbh in 1-ha plots, and (3) complete local florulas are analyzed as a function of various environmental parameters. These trends are also compared with those found in similar data sets from other continents. Altogether the basic 0.1-ha data sets are reported for 87 sites in 25 countries on six continents and several islands. New data from ten 1-ha tree plots in upper Amazonia are also compared with each other and with similar data from the literature. Some noteworthy trends include: (1) Lowland neotropical plant species richness is generally far more tightly correlated with precipitation than with edaphic factors. (2) The nearly linear increase of lowland neotropical plant species richness with precipitation reaches an asymptote (community saturation?) at about 4,000 mm of annual rainfall. (3) Although the species represented in adjacent forest types on different substrates may change dramatically, diversity tends to change relatively little in upper Amazonia. (4) The species present at different sites are very different but the families represented and their diversities are highly predictable from environmental parameters. (5) On an altitudinal gradient in the tropical Andes there is a sharp, essentially linear decrease in diversity from about 1,500 m to near the upper limit of forest above 3,000 m. (6) There is no indication of a "mid-elevation bulge" in diversity, at least not in the sampled habit groups. (7) Even near timberline, montane tropical forests are as diverse as the most diverse temperate forests. (8) Moist subtropical forests are markedly less diverse than their inner-tropical equivalents, but dry subtropical forests in Mexico are apparently richer in species than inner-tropical dry forests. (9) Central African forests are about as species rich as neotropical forests with similar amounts of precipitation, but forests in tropical West Africa are relatively depauperate. (10) Tropical Australasian forests are no more diverse than equivalent neotropical forests; the world's highest tree species diversity is in upper Amazonia, not Southeast Asia. (11) Contrary to accepted opinion, equivalent forests on the three continents are similar in plant species richness and (with a very few notable exceptions) floristic composition but are markedly different in structure. The predictability of the floristic compositions and diversities of tropical forest plant communities seems strong, albeit circumstantial, evidence that these communities are at ecological and perhaps evolutionary equilibrium, despite indications that certain aspects of their diversity are generated and maintained stochastically.

Comparisons of the species richness (or other facets) of different forests or different vegetation types are often difficult because of the dissimilarity of the available data. In tropical Asia there is a wealth of data for trees in large sample areas (Ashton, 1964, in press; Whitmore, 1984; Proctor et al., 1983; Kartawinata et al., 1981) but few published data on nontrees. In the Neotropics there are several local florulas (Croat, 1978; Dodson & Gentry, 1978; Janzen & Liesner, 1980; Dodson et al., 1985), but until recently there have been no tree-plot data from high diversity regions based on reliable identifications. Africa has far more extensive coverage by regional and country-wide floras but no local florulas nor large-plot data from high-diversity regions.

Recently, a series of 0.1-ha samples of many of the world's most diverse extra-tropical plant communities has been accumulating (e.g., Naveh & Whittaker, 1979; Cowling, 1983; Peet & Christensen, 1980; Rice & Westoby, 1983; Eiten, 1978). Elsewhere we have reported the first comparable data set for tropical forests (Gentry & Dodson, 1987a, b). A standardized sampling technique that includes only plants ≥ 2.5 cm in diameter in 0.1 ha has also been developed and applied to a series of tropical forests (Gentry, 1982b, 1986b; Lott et al., 1987; Stallings et al., in press; Lorence & Sussman, 1988); the methodology for obtaining these 0.1-ha samples, each the sum of ten 2 × 50 m belt transects, is discussed in detail elsewhere (Gentry, 1982b, in prep.). The primary data set on which this paper is based are these 0.1-ha samples, which are now available for 38 lowland neotropical sites, 11 montane neotropical sites, and 13 subtropical and 9 temperate-zone sites in the Americas. Similar data sets are available from 6 sites in tropical Africa, 3 sites in tropical Australasia, 2 sites in Europe, and from several tropical islands: New Caledonia, Madagascar, Mauritius, Jamaica (Tables 1, 2; Fig. 1). Supplementary data are taken from local florulas in the Neotropics (Dodson & Gentry, 1978, 1988; Croat, 1978;

FIGURE 1. *Locations of study sites. Dots = 0.1-ha samples (see Tables 1, 2). Arrows = local florulas. For location of 1-ha tree plots see Gentry, 1988.*

Janzen & Liesner, 1980; Dodson et al., 1985; Hammel, pers. comm. (La Selva, Costa Rica)) and from the Makokou region of northwestern Gabon (Halle, 1964, 1965; Halle & Le Thomas, 1967, 1970; Florence & Hladik, 1980; Hladik & Halle, 1973; Hladik & Gentry, in prep.). A supplemental data set is provided by a series of 1-ha tree plots in various parts of the Neotropics (Gentry, 1988; Prance et al., 1976; Campbell et al., 1986; see also Gentry, 1982b) and Paleotropics (e.g., Ashton, 1964, 1977, in press; Gartlan et al., 1986).

Here I first review how the species richness of plant communities changes on five different environmental gradients: latitudinal, precipitational, edaphic, altitudinal, and intercontinental. Observations on a few noteworthy trends in forest structure are also included. Second, I analyze some patterns of floristic change along the same environmental gradients. Finally, I use these analyses to examine briefly the question of why some plant communities have so many more species than others.

In all of these analyses I will use number of species as the simplest and most appropriate measure of diversity, as suggested by Whittaker (1977). Shannon-Wiener H′ values are reported in Tables 1 and 2, but are so tightly correlated ($R^2 = 0.93$) with the absolute number of species that their use would add little to the analysis. Moreover, the wet-forest H′ values of 7 to 8 are far above the levels at which H′ has been statistically analyzed (cf. May, 1975).

TEMPERATE-TROPICAL PATTERNS

Figure 2 summarizes the latitudinal trends in species richness, based on the 74 lowland (= < 1,000 m) 0.1-ha sites for which comparable samples are available. It is well known that tropical forests are generally far richer than temperate forests in species (e.g., see Richards, 1952; MacArthur, 1972). Figure 2 indicates that for vascular plants species-rich tropical forests are typically an order of magnitude more diverse. Also apparent in Figure 2 are several much less well-known corollaries to the general latitudinal diversity gradient. 1) The difference in species richness between different tropical forests is far greater than the difference between temperate zone and species-poor tropical forests. Whereas the temperate forest samples have 15–25 species and tropical dry forest ones mostly 50–60 species, the samples of moist and wet tropical forests average about 150 species and pluvial forests over 250 species (Gentry,

TABLE 1. *Site characteristics for 0.1-ha samples.*

Site	Grid Coordinates	Altitude (m)	Precipitation (mm)	Number of Families	Number of Species	H′	Reference
Temperate North America							
Burling Tract, Virginia	38°55′N 77°10′W	30	1,053	12	21	3.54	Givnish et al., unpubl.
Northwest Branch, Maryland	39°02′N 77°02′W	20	1,060	14	20	3.22	—
Tyson Reserve, Missouri (oak woods)	38°30′N 90°31′W	150	932	12	23	3.26	Zimmerman & Wagner, 1979
Tyson Reserve, Missouri (chert glade)	38°30′N 90°31′W	150	932	11	25	3.68	Zimmerman & Wagner, 1979
Babler State Park, Missouri	38°32′N 90°40′W	150	930	13	21	3.61	—
Cuivre River State Park, Missouri	39°01′N 91°00′W	140	930	15	26	3.46	—
Valley View Glades, Missouri	38°15′N 90°37′W	225	930	14	22	3.68	—
Indian Cave State Park, Nebraska	40°30′N 95°43′W	320	900	12	23	3.74	Tate, 1969
Great Smoky Mountains National Park, Tennessee/N.C.					21–30 (upper 5%)		White, 1983
Europe							
Süderhackstedt, West Germany	54°N 11°E	20	695	10	15	2.19	Walter & Lieth, 1960
Allacher Lohe, West Germany	48°04′N 11°30′E	530	866	11	20	3.41	Walter & Lieth, 1960
Temperate and Subtropical South America							
Rio Jejui-mi, Paraguay	24°42′S 55°30′W	150	1,800	31	85	5.40	S. Keel & V. Vera, pers. comm.
Parque El Rey, Argentina	24°45′S 64°40′W	1,000	1,500	27	40	4.18	Brown et al., 1985
Salta, Argentina	24°40′S 65°30′W	1,300	712	16	25	3.41	Walter & Lieth, 1960
Arroyo Riachuelo, Corrientes, Argentina	27°30′S 58°50′W	60	1,200	27	47	4.46	Walter & Lieth, 1960
Alto de Mirador, Chile	40°14′S 73°18′W	800	4,000	13	16	3.45	Ramírez & Riveros, 1975
Bosque de San Martín, Chile	39°30′S 73°10′W	30	2,316	14	18	3.25	Riveros & Ramírez, 1978
Puyehue National Park, Chile	40°43′S 72°18′W	500	3,000	13	16	2.41	Muñoz, 1980
"Subtropical" Central America							
Chamela, Mexico	19°30′N 105°03′W	50	733	37	92	5.76	Lott et al., 1987

TABLE 1. *Continued.*

Site	Grid Coordinates	Altitude (m)	Precipitation (mm)	Number of Families	Number of Species	H′	Reference
Chamela, Mexico	19°30′N 105°03′W	50	733	34	83	5.42	Lott et al., 1987
Chamela, Mexico	19°30′N 105°03′W	50	733	46	105	5.9	Lott et al., 1987
Los Tuxtlas, Mexico	18°35′N 95°08′W	200	4,953	40	108–109	4.52	Lot-Helgueras, 1976
Cerro Olumo, Nicaragua	12°18′N 85°24′W	750	2,000	36	97–98	5.8	—
Cerro El Picacho, Nicaragua	13°00′N 85°55′W	1,400	2,000	39	65	5.22	—
Lowland Neotropics (12°N to 12°S, ≤ 1,000 m)							
Corcovado, Costa Rica	8°30′N 83°35′W	30	3,800	46	132	6.56	Hartshorn, 1983
Guanacaste (upland) Costa Rica (700 m^2)	10°30′N ≈ 85°10′W	100	1,600	21+	53^a		Hartshorn, 1983
Guanacaste (gallery), Costa Rica (800 m^2)	10°30′N ≈ 85°10′W	50	1,600	33+	68^a		Hartshorn, 1983
Curundu, Panama	8°59′N 79°33′W	20	1,830	42	90	5.78	Gentry, 1982b
Madden Forest, Panama	9°66′N 79°36′W	50	2,433	45	126	6.34	Gentry, 1982b
Pipeline Road, Panama	9°10′N 79°45′W	300	3,000	58	167	6.77	Gentry & Emmons, 1987
Galerazamba, Colombia	10°48′N 75°15′W	10	500	21	55	5.05	—
Tayrona, Colombia	11°20′N 74°02′W	50	1,500	31	65	5.36	—
Bosque de la Cueva, Colombia	11°05′N 73°28′W	360	2,000	36	93	5.5	—
Tutunendo, Colombia	5°46′N 76°35′W	90	9,000	53	258	7.57	Gentry, 1986b
Bajo Calima, Colombia	3°55′N 77°02′W	100	7,470	58	265	7.74	Gentry, 1986b
Boca de Uchire, Venezuela	10°09′N 65°25′W	150	1,200	20	66	5.16	Gentry, 1982b
Blohm Ranch, Venezuela	8°34′N 67°35′W	100	1,400	31	68	5.38	Troth, 1979
Estación Biológico de los Llanos, Venezuela (500 m^2)	8°56′N 67°25′W	100	1,312	21+	59^a		Gentry, 1982b
Cerro Neblina, Venezuela (No. 1)	0°50′N 66°11′W	140	3,000	31	97	5.33	
Cerro Neblina, Venezuela (No. 2)	0°50′N 66°11′W	140	3,000	26	83	4.95	
Río Palenque, Ecuador (No. 1)	0°34′S 79°20′W	200	2,980	50	119	6.15	Dodson & Gentry, 1978

TABLE 1. *Continued.*

Site	Grid Coordinates	Altitude (m)	Precipitation (mm)	Number of Families	Number of Species	H′	Reference
Río Palenque, Ecuador (No. 2)	0°34′S 79°20′W	200	2,980	43	121	6.18	Dodson & Gentry, 1978
Centinela, Ecuador	0°34′S 79°18′W	550	3,000	55	140	4.78	Gentry, 1986b
Jauneche, Ecuador	1°16′S 79°42′W	60	1,855	38	96	5.39	Dodson et al., 1985
Capeira, Ecuador	2°00′S 79°58′W	50	804	26	60	5.41	Dodson & Gentry, 1988
INPA, Manaus, Brazil	3°S 60°W	75	1,995	34	101		Gentry, 1978
Mocambo, Belem, Brazil	1°30′S 47°59′W	30	2,760	39	131	6.42	Pires & Prance, 1977
Linhares, Espirito Santo, Brazil	19°18′S 40°04′W	50	1,403	53+	ca. 212	7.4	Peixoto & Gentry, in prep.
Jacarepagua, Rio de Janeiro, Brazil	23°05′S 43°25′W	200	1,500	45+	ca. 160		
Tarapoto, Peru	6°40′S 76°20′W	500	1,400	38	97	5.96	—
Sucursari, Peru	3°15′S 72°55′W	140	3,500	46+	ca. 240[a]	7.46	—
Yanamono, Peru (upland) (No. 1)	3°28′S 72°50′W	140	3,500	50	212	7.49	Gentry & Emmons, 1987
Yanamono, Peru (upland) (No. 2)	3°28′S 72°50′W	140	3,500	50	225	7.59	Gentry & Emmons, 1987
Yanamono, Peru (tahuampa)	3°28′S 72°50′W	130	3,500	51	163	6.67	
Mishana, Peru (floodplain)	3°47′S 73°30′W	130	3,500	58	249	7.63	Gentry & Emmons, 1987
Mishana, Peru (tahuampa)	3°47′S 73°30′W	130	3,500	40	168	6.44	
Mishana, Peru (upland white sand)	3°47′S 73°30′W	140	3,500	46	196	7.21	Gentry & Emmons, 1987
Bosque von Humboldt, Peru	8°50′S 75°00′W	270	2,500	44	154	6.37	
Cabeza de Mono, Peru	10°20′S 75°18′W	320	3,500(+)	42	147	6.82	Gentry, 1988
Cocha Cashu, Peru	11°51′S 71°19′W	400	2,000	49	162	6.78	Gentry & Terborgh, in press
Tambopata, Peru (lateritic terra firme)	12°50′S 69°17′W	260	2,000	48	149	6.7	Erwin, 1985
Tambopata, Peru (sandy terra firme)	12°50′S 69°17′W	260	2,000	43	130	6.44	Erwin, 1985
Africa							
Makokou, Gabon (No. 1)	0°34′N 12°52′E	500	1,755	39	135	6.44	Hladik, 1978
Makokou, Gabon (No. 2)	0°34′N 12°52′E	500	1,755	32	116	6.25	Hladik, 1978

TABLE 1. *Continued.*

Site	Grid Coordinates	Altitude (m)	Precipitation (mm)	Number of Families	Number of Species	H′	Reference
Omo Forest, Nigeria	7°N 5°E	50	1,800	29	73	4.42	Richards, 1939
Oban Forest, Nigeria (200 m^2)	5°10′N 8°28′E	50	4,000	?	(53++)		
Mt. Cameroon, Cameroon	4°N 9°E	230	8,000	37	129	6.31	Richards, 1963
Korup National Park, Cameroon	5°N 8°31′E	50	5,460	43	139	6.34	Gartlan et al., 1986
Belinga, Gabon (500 m^2)	1°N 14°E	750	1,800	26(+)	115		Aubreville, 1967
Perinet, Madagascar	18°55′S 48°25′E	950	1,200	52+	ca. 199		
Australia							
Davies River State Park, Queensland	17°05′S 145°34′E	800	2,300	41	115	6.29	Connell et al., 1984
Asia							
Semengoh Forest, Sarawak	1°50′N 110°05′E	20	4,000	47	243	7.39	Walter & Lieth, 1960
Bako National Park, Sarawak	1°52′N 110°06′E	30	4,000	39	143	6.5	Ashton, in press
Tropical Islands							
Rivière des Pirogues, New Caledonia	22°10′S 166°50′E	360	2,200	47	151	6.31	
Round Hill, Jamaica	17°50′N 77°15′W	40	1,200	31	58	3.96 (4.47)	Kapos, 1982
Brise Fer, Mauritius	20°30′S 57°30′E	600	2,400	26	61		Lorence & Sussman, 1988

[a] Extrapolated from number of species in sample of < 1,000 m^2.

1986b). 2) The latitudinal decrease in species richness seems to be asymmetrical about the equator; in the Southern Hemisphere it begins near the Tropic of Capricorn, but in the north it begins well inside the Tropic of Cancer, apparently near 12°N latitude. 3) Temperate zone forests are very similar in species richness of woody plants, compared with the massive differences in species richness between temperate and tropical forests or between different tropical forests. Temperate zone forests are so massively depauperate that even if boreal forests with two or three species ≥ 2.5 cm dbh in 0.1 ha were included in Figure 2, they would not significantly change it, even though the reported values are for some of the reputedly richest temperate zone forests. 4) Species-poor tropical forests with single-species dominance are generally still much more diverse than any temperate-zone forest. 5) South temperate forests, at least in Chile, where data sets are available, have fewer species than temperate forests in North America, contrary to the popular perception of the "rich" Valdivian forest; a major reason for this diffference is that Valdivian forests do not have sympatric congeners like the up to seven *Quercus* and four *Carya* species typical of 0.1-ha samples of eastern North American forests. 6) Subtropical dry forests can have more species than do full-tropical dry forests, even though wet or moist forests usually have fewer species in the subtropics than in the inner tropics.

TABLE 2. *Site characteristics for 0.1-ha samples from upland Neotropics (≥ 1,000 m, 12°N to 12°S). Parentheses indicate sites too incompletely sampled for a meaningful estimate of number of species in 0.1 ha.*

Site	Grid Coordinates	Median Altitude (m)	Number of Families	Number of Species	H′
(Monteverde, Costa Rica (200 m^2))	10°48′N 84°50′W	1,550	(33+)	(61+)	
Cerro Kennedy, Colombia (500 m^2)	11°05′N 74°01′W	2,600	26	50[a]	4.92
(Cuchillo de San Antonio, Colombia (200 m^2))	10°58′N 73°30′W	1,710	(15+)	(24+)	
Finca Zungara, Colombia (600 m^2)	3°32′N 76°35′W	1,990	37+	100[a]	
Farallones de Cali, Colombia	3°30′N 76°35′W	1,950	55	134–135	6.48
Finca Mehrenberg, Colombia	2°16′N 76°12′W	2,290	40	107	4.46
La Planada, Colombia	1°10′N 77°58′W	1,800	38	116	5.14
Pasochoa, Ecuador (400 m^2)	0°28′S 78°25′W	3,010	21	28[a]	3.03
Venceremos, Peru	5°45′S 77°40′W	1,850	46	159	6.65
Incahuara, Bolivia	15°55′S 67°35′W	1,540	45	130	6.71
Sacramento, Bolivia	16°18′S 67°48′W	2,450	32	93	4.89

[a] Extrapolated from number of species in sample of < 1,000 m^2.

There are also latitudinal differences in forest structure. In general, tropical forests, far from being open and cathedral-like, are denser than temperate forests. This difference is almost entirely due to small-diameter plants, lianas, and trees less than 10 cm dbh (also see Gentry, 1982b). Biomass (as extrapolated from basal area) is roughly equivalent among different tropical forests ($\bar{X}$ = 34.9 m^2/ha, N = 36 (excluding Africa; $\bar{X}$ = 70.7 m^2/ha, N = 6)) and north temperate deciduous forests ($\bar{X}$ = 29.6 m^2/ha, N = 5) but markedly greater in the Valdivian forests ($\bar{X}$ = 155.7 m^2/ha, N = 3) as well as in their north temperate equivalent, the northwestern coniferous forests (Waring & Franklin, 1979).

DIVERSITY VS. PRECIPITATION

In the Neotropics, plant species richness is strongly correlated with absolute annual precipitation (Gentry, 1982b). However, this relationship is more complex than originally suggested (Gentry, 1982b), and the correlation may not exist at all in the Paleotropics. In tropical Asia, high rainfall areas such as Mt. Cherrapunji, Assam, often have relatively low plant species richness (Ashton, in press). In tropical Africa, two high rainfall sites (> 5,000 mm per year) in southwestern Cameroon (Korup, Mt. Cameroon) have only marginally more species in 0.1-ha samples than do samples from northeastern Gabon that receive < 2,000 mm of annual rainfall. Moreover, a more monsoonal climate site in Nigeria (Omo Forest) had many fewer species than the Gabon sites despite having similar precipitation values. Thus, it seems likely that the generalization that diversity increases linearly with precipitation (Gentry, 1982b) applies only in the special case of the Neotropics, where total annual rainfall and strength of

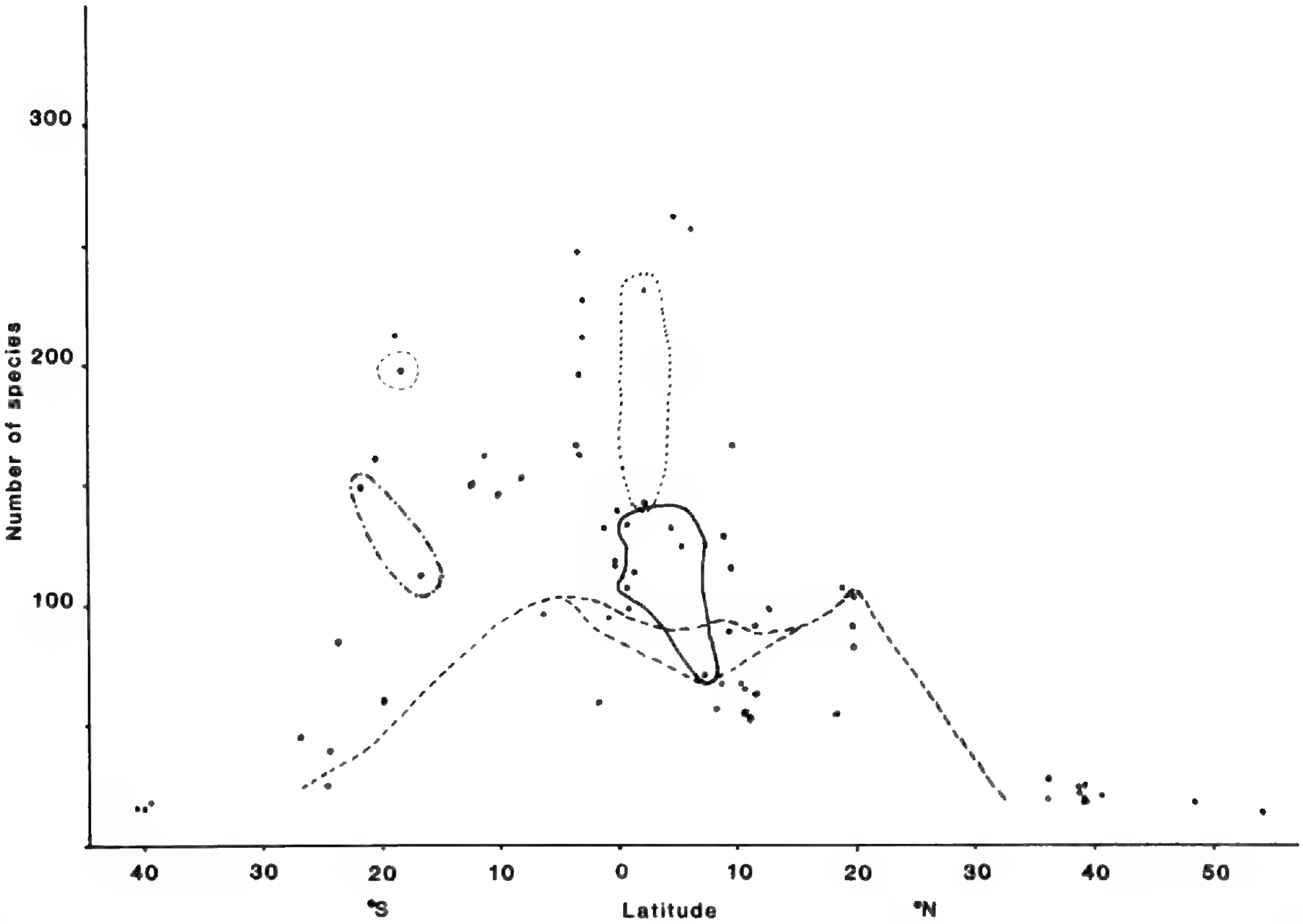

FIGURE 2. *Species richness of 1,000 m² samples of lowland (< 1,000 m) forest as a function of latitude. Closed line encloses continental African points; dotted line encloses Asian points; dash-dot line encloses Australian and New Caledonian samples; other tropical and subtropical points all neotropical except anomalously high diversity Madagascar point at 19°S, (circled). Dashed line separates dry forest (bottom) from moist and wet forest (top) with three intermediate sites (moist forest physiognomy despite relatively strong dry season) indicated by alternate lines.*

the dry season are strongly correlated. A potential test of the relative importance of distribution and amount of precipitation comes from a single 0.1-ha site in coastal Brazil (Linhares), which has the unusual (for the Neotropics) condition of low, evenly distributed annual rainfall. Although analysis of the Linhares diversity data is not completed (Peixoto & Gentry, in prep.) and the site is thus not included in Figure 3, it is obvious that its estimated 212 species in 0.1 ha are far more than would be expected from its 1,400 mm of annual precipitation.

While the many additional 0.1-ha samples now available from the lowland Neotropics generally strengthen the previously reported relationship between neotropical plant species richness and precipitation (Gentry, 1982b), additional data sets at the upper end of the precipitation scale strongly indicate that the relationship becomes nonlinear, reaching a marked asymptote at around 4,000–4,500 mm of annual precipitation (Fig. 3). The relationship is significantly curvilinear ($F = 4.299$, $P < 0.05$). From 4,000 mm to near the wettest place in the world (Tutunendo, Colombia) there is little or no change in the species richness of neotropical plant communities as measured by the 0.1-ha sampling protocol. The regularity of species richness patterns, and especially the apparent lid on community richness suggested by this asymptote, seem strong circumstantial evidence of the kind that zoologists (e.g., MacArthur, 1965, 1969) have construed as representing niche saturation and community equilibrium.

It is also possible that part of the apparent lid on plant community richness merely reflects the intrinsic limitations of the sampling technique. Figure 4 compares the accumulation of species with sample area for several representative sites. In low-diversity forests the species area curves level off below 500 m² indicating that most of the species present

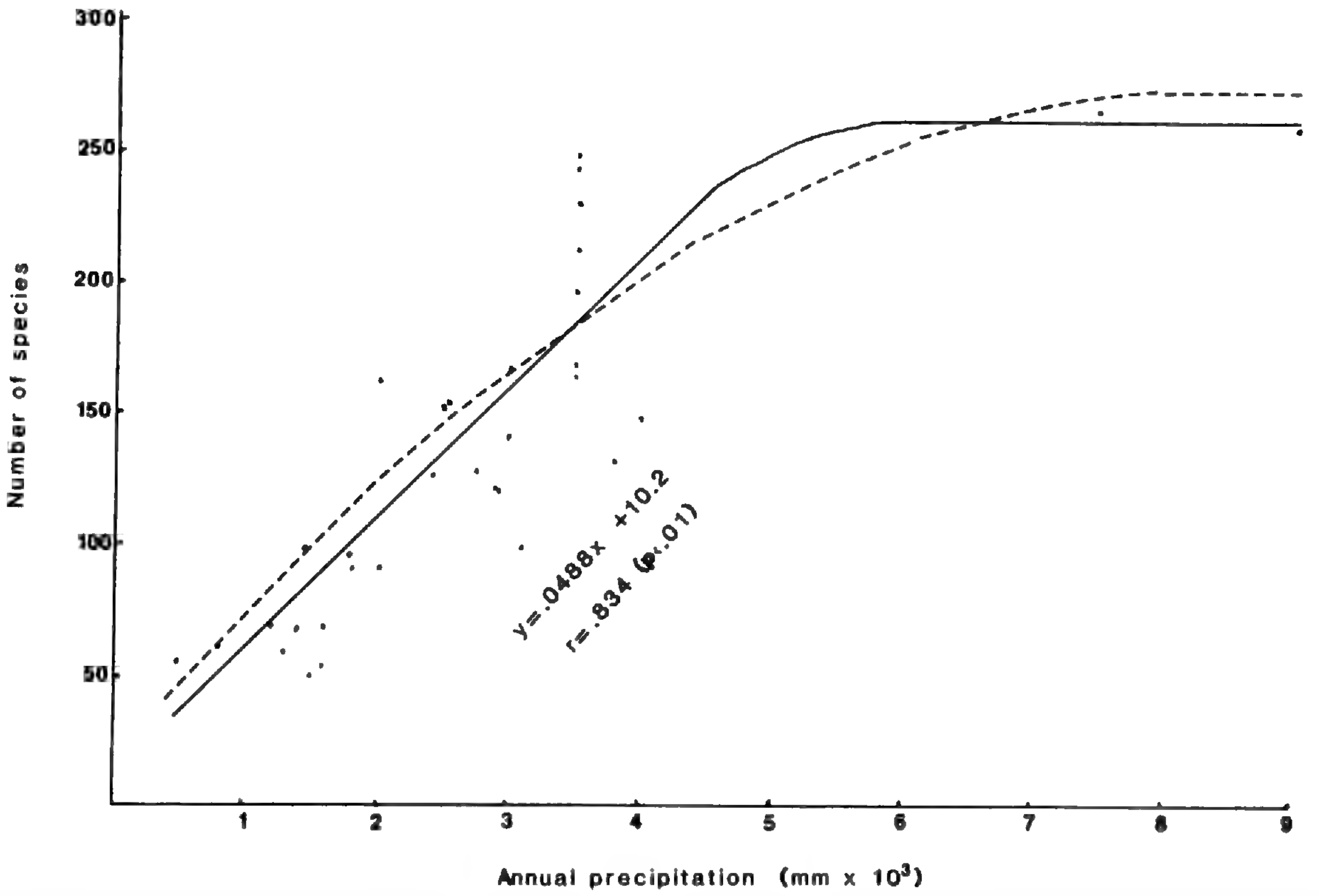

FIGURE 3. *Numbers of species in 0.1-ha samples of lowland neotropical forest vs. annual precipitation. Solid line = straight line regression for sites with < 5,000 mm annual precipitation with visually estimated asymptote. Dashed line = computer generated curve:* $y = 12.37 + 0.0613x - 0.000003598x^2$. *The curve is displaced slightly upward from the data points, since questionable morphospecies and lost specimens are treated as distinct species by the computer while the data points represent best estimates of species numbers. Data from Table 1 with subtropical sites excluded.*

in a given community have been sampled, but in species-rich vegetations the species–area curves show little sign of leveling off. To what extent a larger sampling area might reveal significant diversity differences between the different high rainfall sites remains unknown.

The strong relationship of species richness to precipitation in neotropical forests is further supported by preliminary data from 1-ha tree plots in upper Amazonia (Gentry, 1988). In these samples only trees and large lianas ≥ 10 cm in diameter were censused (Fig. 5). The two most species-rich sites are from the everwet high rainfall (3,000–4,000 mm) Iquitos area of northern Amazonian Peru, where diversity reaches almost ridiculous ex-

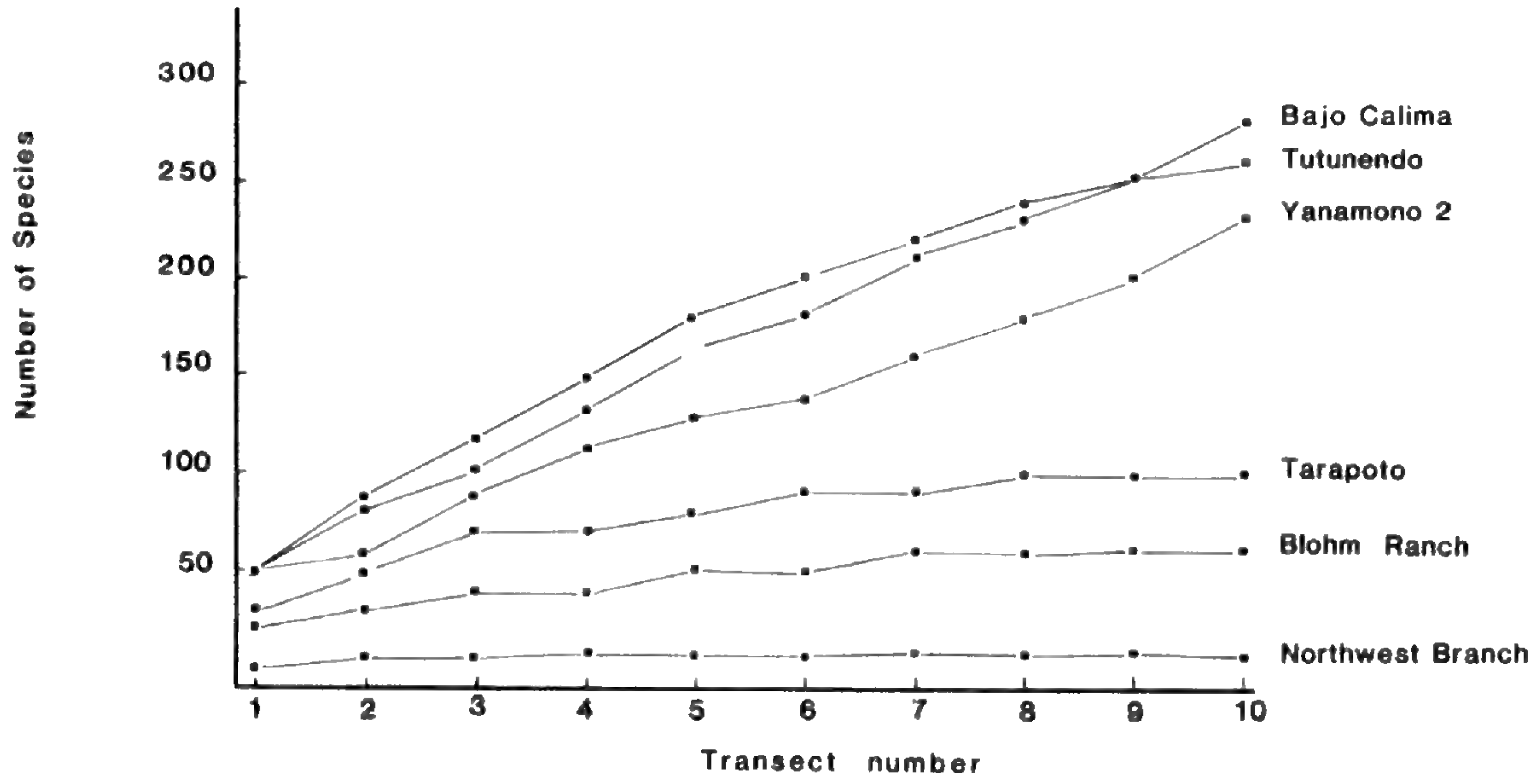

FIGURE 4. *Species–area curve for 100 m² subsamples of representative high- and low-diversity 0.1-ha samples.*

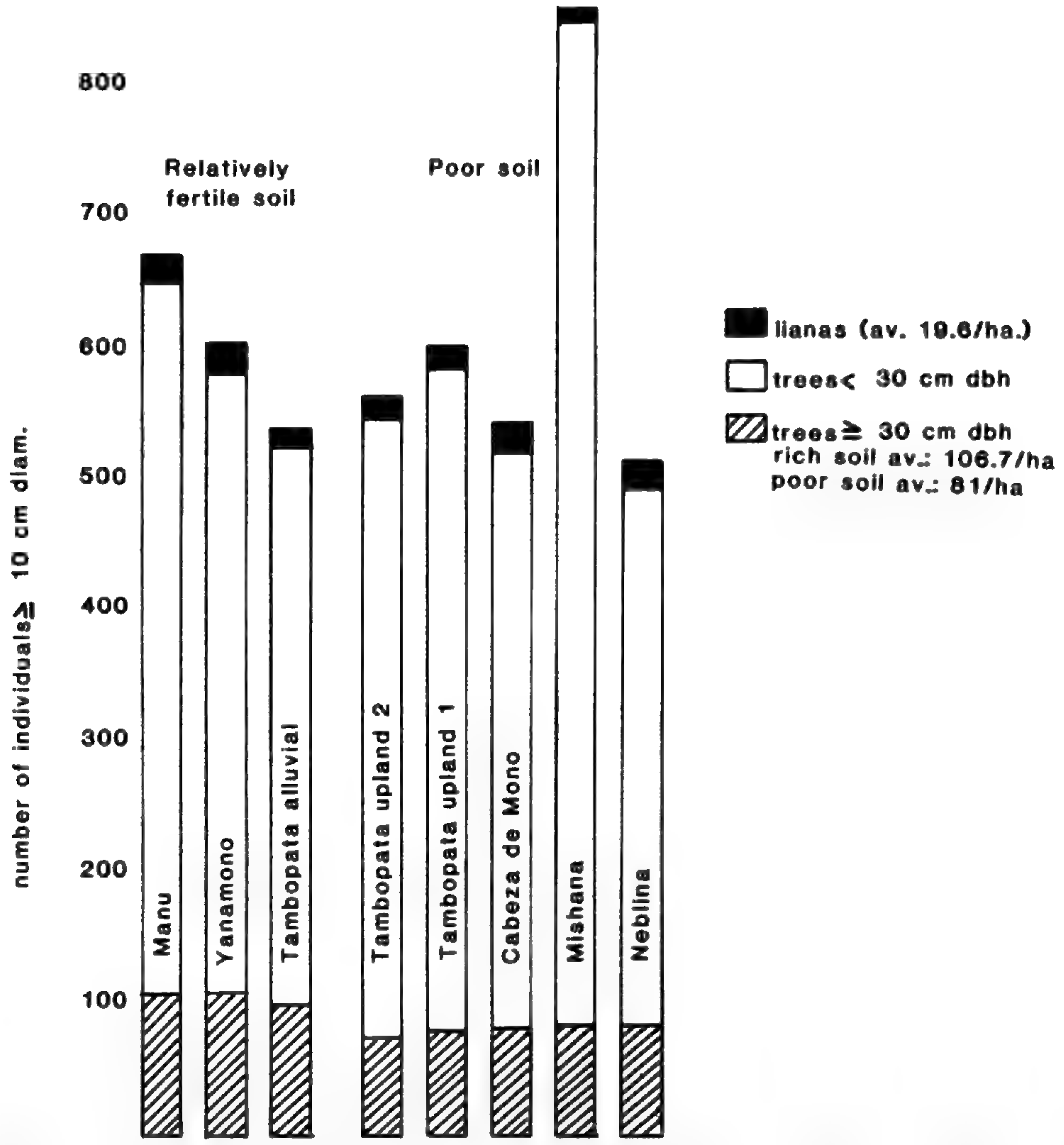

FIGURE 5. *Density of trees and large lianas in 1-ha Amazonian plots. Black = lianas; hatched = trees > 30 cm dbh; white = trees 10–30 cm dbh.*

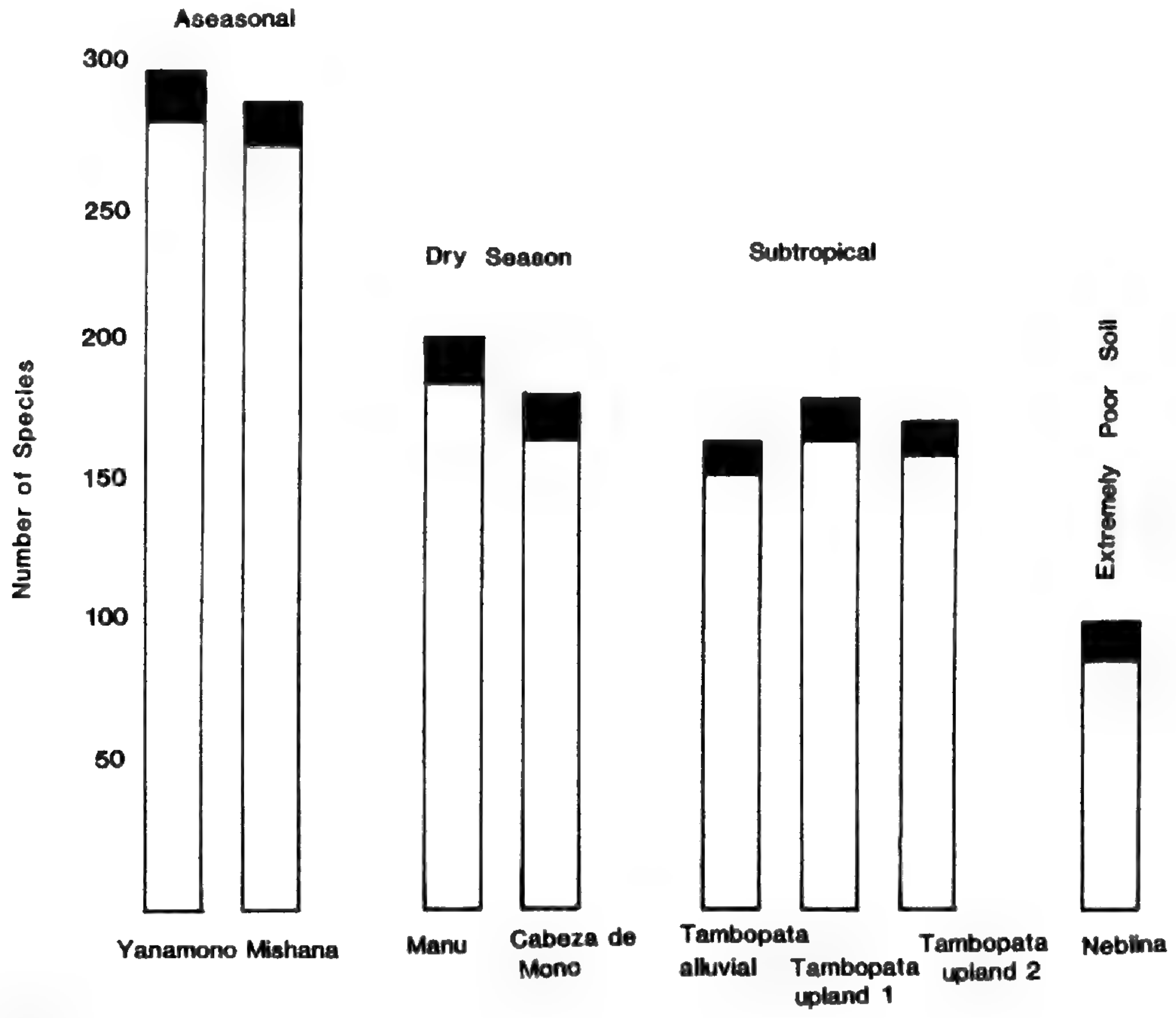

FIGURE 6. *Number of species in 1-ha Amazonian tree plots (plants ≥ 10 cm dbh). Black area = lianas ≥ 10 cm greatest diameter.*

tremes (Fig. 6). At Yanamono there are 300 species ≥ 10 cm in diameter out of the 606 individual plants in a hectare plot! The other 1-ha plots in Amazonian Peru are in areas with generally greater dry season stress and less overall precipitation. Two sites between 10° and 12°S latitude have about 200 species ≥ 10 cm dbh, while several 1-ha plots in different habitat types at Tambopata Reserve in southeastern Madre de Dios (12°50′S) have between 153 and 181 species. Thus tree species richness also appears to be greatest in aseasonal high rainfall areas, at least within Amazonia.

Epiphyte diversity likewise increases in wetter areas. While epiphytes can be well represented in areas with high atmospheric humidity but relatively low rainfall, our data indicate that absolute precipitation is generally a remarkably good predictor of epiphyte diversity (Gentry & Dodson, 1987b). We have data sets from a series of local florulas in western Ecuador and southern Central America; epiphytes vary from 9–24 species (2–4% of the total flora) in dry-forest sites to 72–216 species (12–16% of the total flora) in moist-forest sites to 238–368 species (23–24% of the total flora) in wet-forest sites (Gentry & Dodson, 1987a, b). For a series of 1,000 m^2 samples in which all plant species were identified and tabulated in three western Ecuadorian forests, 3 epiphytes constituted 2% of the species in a dry forest, 13 epiphytes constituted 8% of the species in a moist forest, and 127 epiphytes constituted 35% of the species in a wet forest (Gentry & Dodson, 1987b). The wet forest at Rio Palenque is so diverse in plant species that, even excluding tree species, it has more species of herbs (including herbaceous epiphytes) or of shrubs in 0.1 ha than any nontropical plant community in the world (Gentry & Dodson, 1987a).

DIVERSITY VS. SOIL NUTRIENTS

There has been much recent interest in the relationships between tropical soil nutrient levels and plant community richness (Ashton, 1977, in press; Gartlan et al., 1986). These authors suggest that phosphorus, magnesium, and potassium are among the nutrients whose levels are most strongly correlated with tropical plant community diversity. Nevertheless, at least in the Neotropics, soil nutrients are far less important than biogeographic factors or precipitation in determining plant species richness (Gentry, 1982b; Stark et al., submitted ms.). Multiple regression of a series of 31 lowland neotropical sites for which we have both soil and species richness data for 0.1-ha samples produced the equation: Species Richness = 84.48 + 0.025(mean annual precipitation) − 0.100(extractable soil K). $R^2 = 0.76$, N = 31 (Stark et al., submitted ms.).

Thus our data indicate that the nutrient most closely correlated with neotropical species richness is K. The importance of K agrees with what Ashton (1977, in press) found for a large series of tree plots in Borneo, Gartlan et al. (1986) also found available K to be highly and significantly correlated with floristic diversity in a series of sites in Cameroon. Our data contrast with those of Ashton (1977, in press) and Gartlan et al. (1986) in that we do not find phosphorus to be strongly correlated with diversity. This may be due in part to different techniques of nutrient extraction (ammonium acetate vs. HCl). It is also related to the fact that the most species-rich 0.1-ha sample (Bajo Calima, Colombia) comes from a peculiar white clay soil with 0 phosphorus as measured by our technique.

Whereas Ashton's (in press) data sets indicate greatest diversity at intermediate nutrient values, a "humped" nutrient/diversity curve that fits the model proposed by Tilman (1982, 1984), I see no indication in my data of a general decrease in diversity on richer soils in the Neotropics. Quite the contrary, the most species-rich tree plot in the world at Yanamono, Peru, is on relatively rich soil (Gentry, 1988; Stark et al., submitted ms.); further south, in an area with a strong dry season, the 0.1-ha Cocha Cashu sample on unusually rich alluvial soil is farther above the precipitation–diversity regression line than

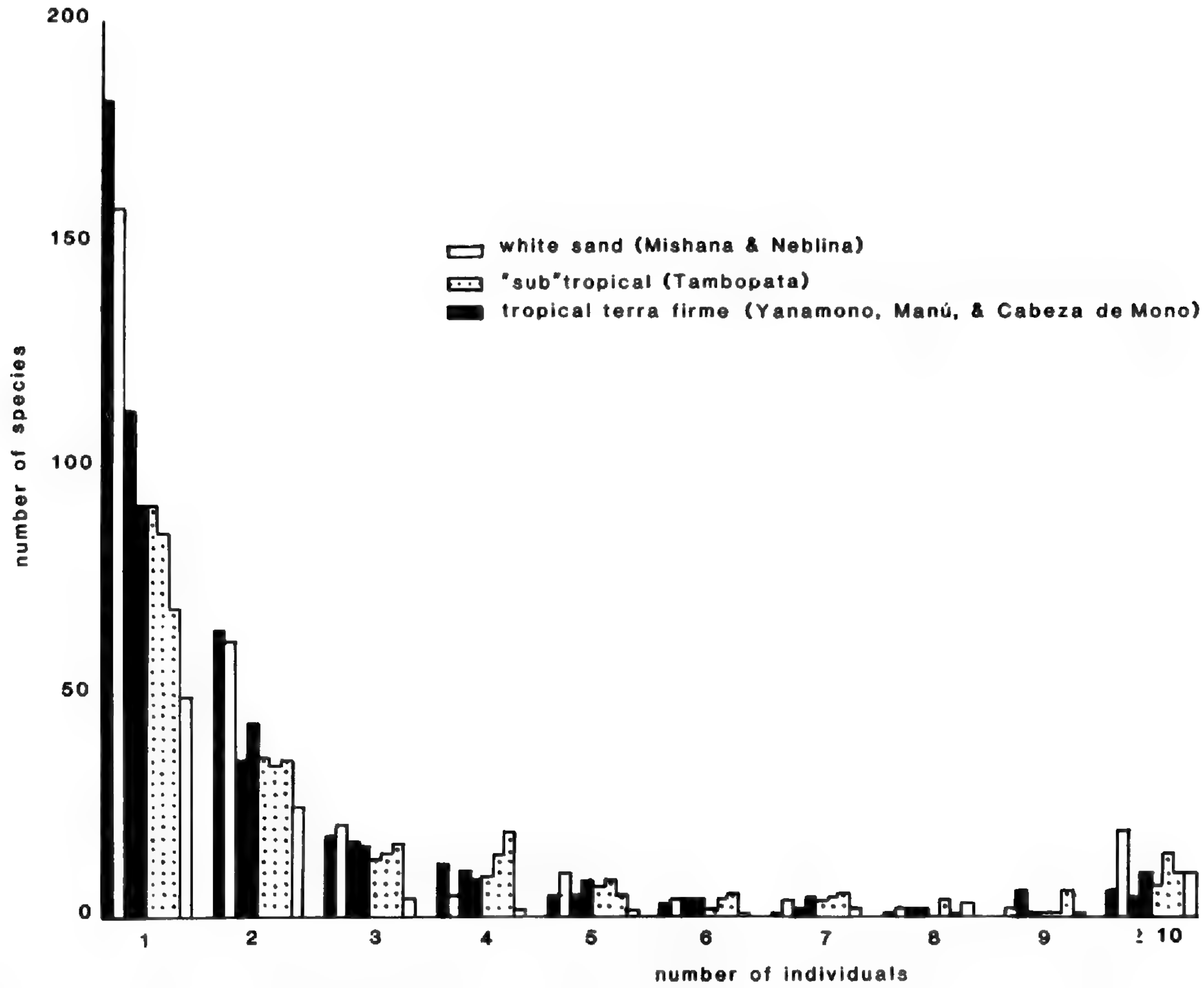

FIGURE 7. *Number of individuals/species in 1-ha Amazonian tree plots (plants ≥ 10 cm diam.).*

any other site (Gentry, 1985a). My data do fit well with Ashton's along the low nutrient end of the diversity–soil nutrient gradient, where there is a general increase in species richness from nutrient-poor to intermediate sites, contrary to the suggestions of Huston (1979, 1980).

Another way of comparing the effects of soil fertility on diversity is by comparing otherwise approximately matched site pairs on fertile and poor soils. The series of six tree plots in Amazonian Peru fall into three natural groups based on latitude and strength of the dry season (Gentry, 1988). Of the two plots in the everwet Iquitos area, one on rich soil has (marginally) more species than a nearby site on white sand; on a species per individual basis the difference would be much stronger (Figs. 7, 8). Of two sites from central Peru, the one on rich alluvial soil (Manú Park) has more species than one on poor soil (Iscozacin). Several plots at Tambopata south of the Holdridge system tropical–subtropical demarcation have fewer species than the full-tropical ones on either rich or poor soils. Moreover, the site with the most nutrient-poor soil of all, Cerro Neblina, on pure white sand, has many fewer species than do any of the other sites. Thus the Amazonian tree plot data generally support the idea that relatively rich soil correlates with relative richness in tree species.

Especially noteworthy in the context of the relative importance of soil nutrients and precipitation as determinants of species richness is the series of 0.1-ha samples from different substrates in the Iquitos area (Table 3). All of the sites have the high species richness (168–212 species) that would be expected (Gentry, 1982b) in a region with high rainfall and no dry season. While samples from the forests subjectively judged likely to be subjected to greater stress (i.e., seasonally inundated tahuampa or white-sand campinarana) have slightly lower species richness, all

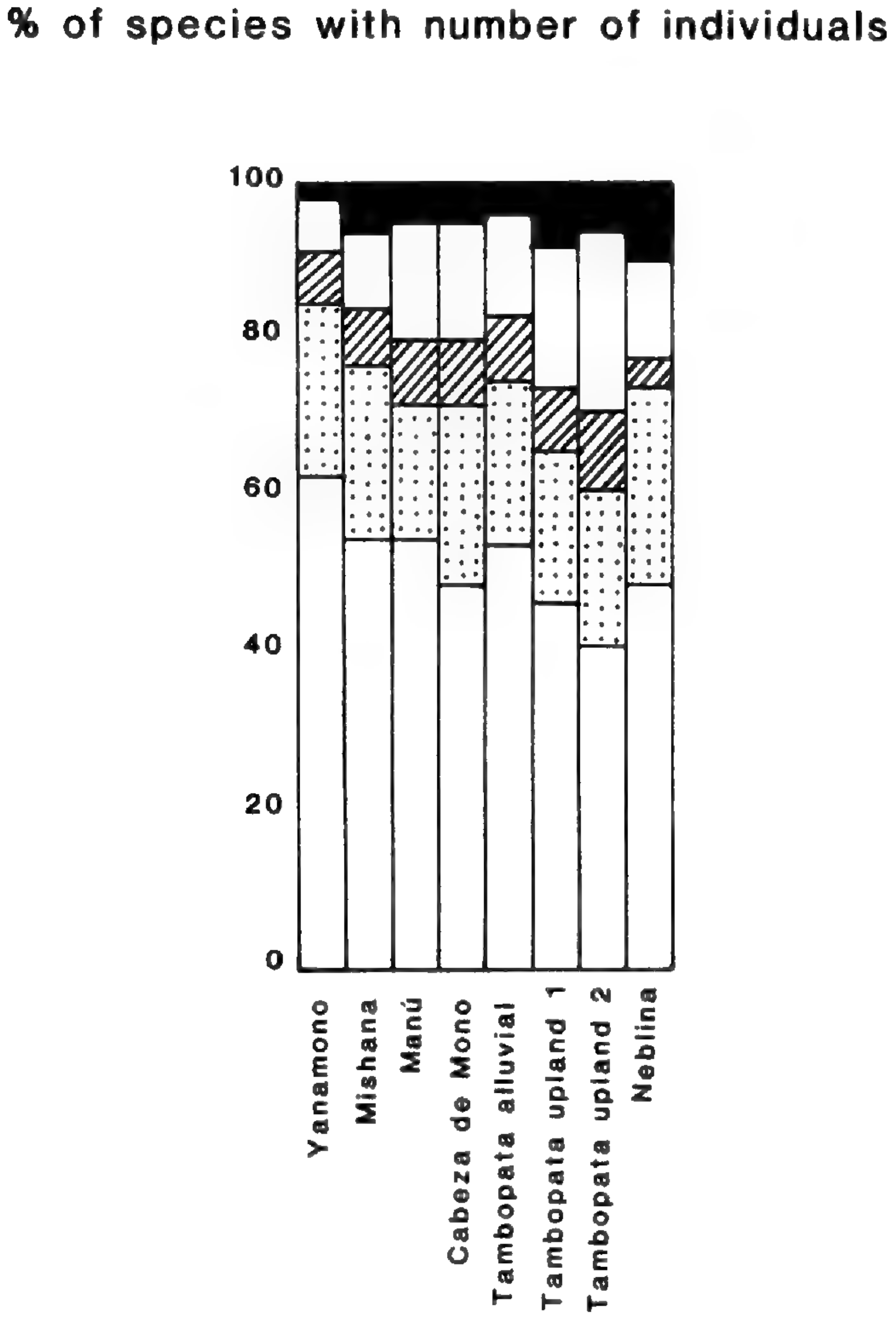

FIGURE 8. *Percent of species with different numbers of individuals in Amazonian tree plots (plants ≥ 10 cm diam.). Lower white bar = 1 individual; dotted bar = 2 individuals; hatched bar = 3 individuals; black bar = 10 or more individuals. Note that an average across all plots of 50% of the species are represented by single individuals.*

sites are very diverse compared with moisture-stressed sites with a strong dry season or low annual precipitation.

I conclude that the species richness of neotropical plant communities generally increases with soil fertility and with precipitation, when such broader-scale biogeographic factors as latitude and altitude are controlled. This relationship would predict that the highest neotropical α-diversities should be found in upper Amazonia, where the soils are relatively rich, compared with those of comparably high rainfall areas of the Guayana Shield. My data for 0.1-ha samples and for 1-ha tree plots both appear to fit this prediction. Moreover, many other kinds of organisms, including birds, reptiles and amphibians, butterflies, and bats, appear to show excactly the same pattern of greatest diversity in areas with relatively fertile soils near the base of the Andes, suggesting that this relationship is a general biogeographic trend (Gentry, 1988). It is possible that increased productivity on the generally richer soils of this region makes possible finer niche partitioning and specialization in otherwise marginal habitats (cf. Emmons, 1984; Gentry & Emmons, 1987).

Even though the effect of soil nutrients on α-diversity may be relatively minor, soil nutrients undoubtedly do play a major role in contributing to the high overall diversity of Amazonian forests through their effect on β-diversity (e.g., Gentry, 1981, 1986a, c). Much of upper Amazonia, probably more than any other part of the lowland Neotropics, constitutes a conspicuous habitat mosaic, with very different sets of plant species occurring in adjacent communities on different substrates (Salo et al., 1986; Gentry, 1986a, c). Table 3 shows how little overlap in species there is between different, more or less equally diverse plant communities on different substrates in the Iquitos area. Only 3–24 species

TABLE 3. *Number of species shared by 1,000 m² samples of Iquitos area forest types.*

	Yanamono No. 1	Yanamono No. 2	Yanamono Tahuampa	Mishana Lowland	Mishana Campinarana	Mishana Tahuampa
Yanamono						
Terra firme No. 1	212	91	20	24	12	14
Terra firme No. 2		230	20–21	19	9	8
White-water tahuampa			163	9	5	ca. 19
Mishana						
Lowland noninundated				249	55	17
Campinarana (white sand)					196	3
Black-water tahuampa						168

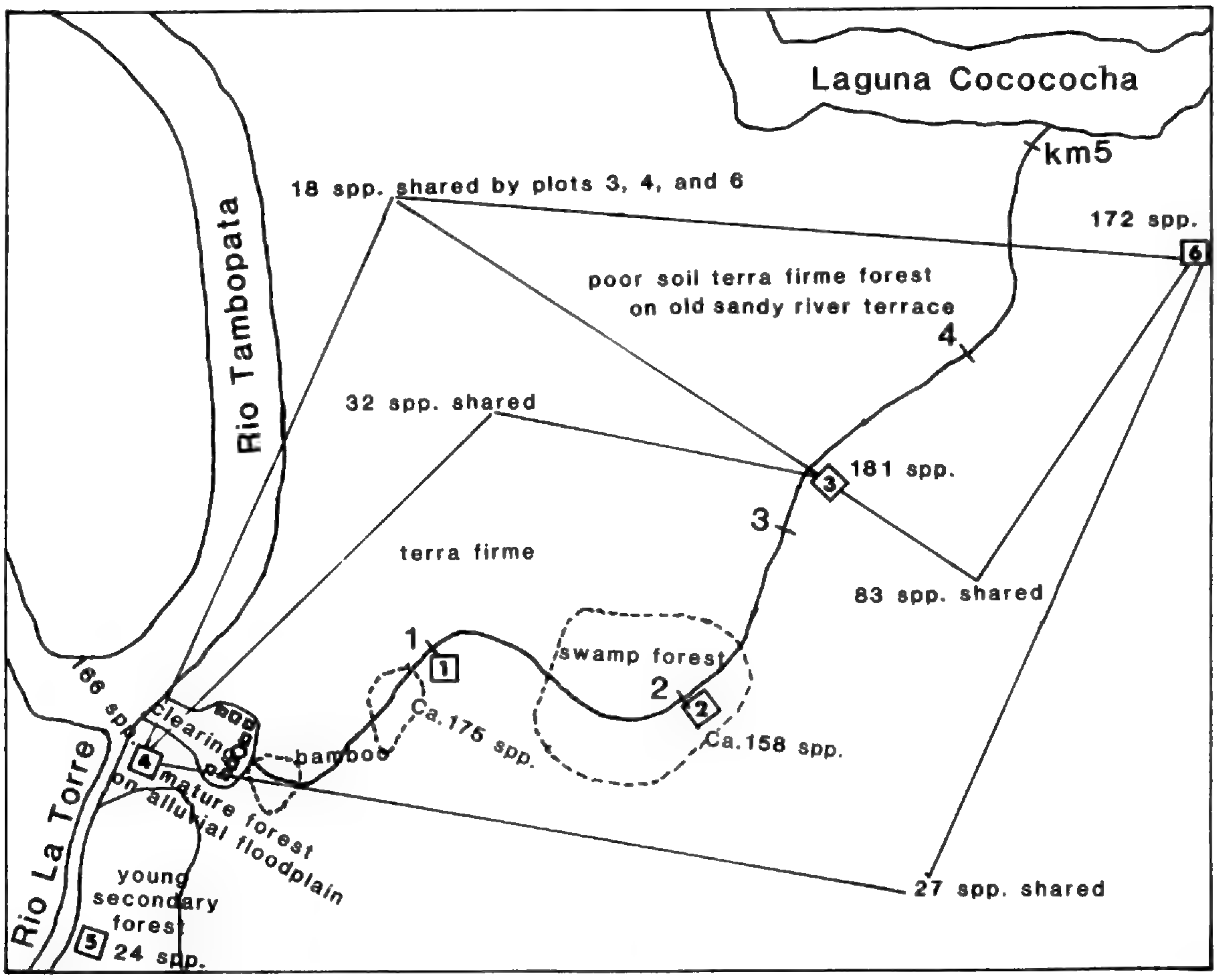

FIGURE 9. *Location of 1-ha tree plots in the Tambopata Wildlife Reserve, Madre de Dios, Peru. Indicated species numbers for plots 2 and 5 are approximate since sampling is not yet complete. Plot 1 data in part based on field identifications of Gary Hartshorn (pers. comm.), and the actual number of species will undoubtedly be higher as well. Shared species indicated only for plots (3, 4, 6) completely sampled and identified by me.*

out of the ca. 200 species sampled for any habitat are shared by a different adjacent habitat. The one exception is the Mishana white-sand and floodplain samples (55 species overlap), but these two vegetation types have similar substrates and are not very well differentiated. While some of this lack of overlap might be due to inadequacy of the sampling technique in such diverse plant communities, a repeat sample of the same forest at Yanamono gave a much greater, almost 50% overlap in species; in other species-rich moist and wet forests similar repeat samples of the same vegetation always give the same ca. 50% overlap in sampled species (Gentry, 1982b), contrasting strongly with the ≤ 20% overlaps between different communities. Similarly, for two 1-ha tree plots on terra firme forest on poor sandy soil at Tambopata, 83 species (46% of the 181 species in plot 1 and 48% of the 172 species in plot 2) were shared with the other plot, for a coefficient of association of 44%. Only 16–18% of the species of either poor soil plot were shared with a nearby tree plot on rich alluvial soil (coefficients of correlation of 10–11%) (Fig. 9). Incompletely analyzed data for additional plots in other forest types at Tambopata indicate that they, too, will show little overlap in species with sandy soil or alluvial forests. The uniquely high species richness of the Tambopata reserve for such well-known groups as birds (Donahue et al., in press) and butterflies (Lamas, 1985) has been suggested as largely due to the reserve's habitat diversity, a conclusion that clearly accords with the botanical evidence.

Thus the high species richness of woody plants in Amazonia as compared with the rest of the Neotropics (Gentry, 1982a) is largely β-diversity due to habitat specialization. Typically, related species may fill similar niches in forests on different upper Amazonian substrates (Gentry, 1981, 1986c). Dramatic differences in specific composition, though not intracommunity diversity, accompany spe-

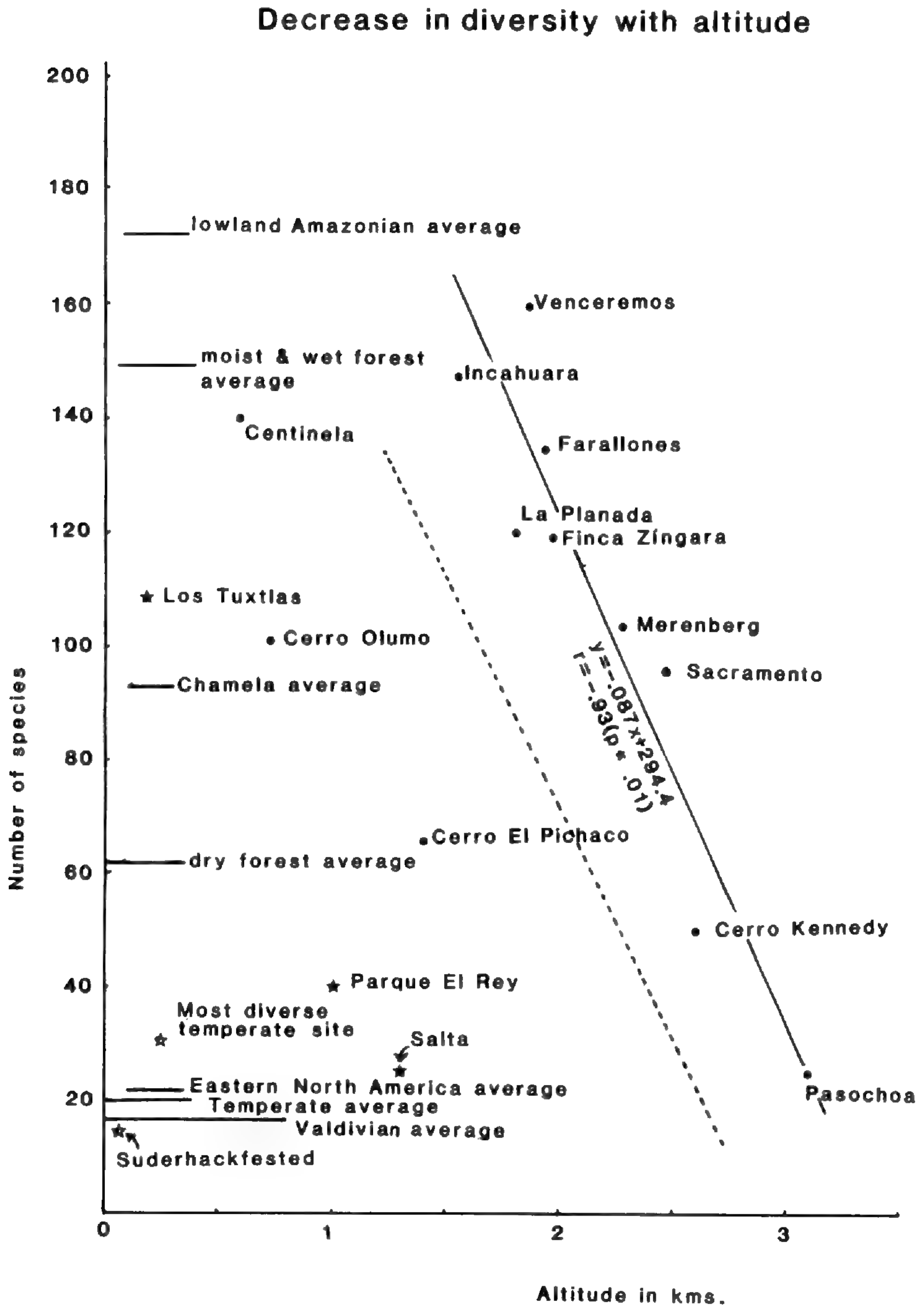

FIGURE 10. *Species richness of 0.1-ha samples vs. altitude. Points to right of dashed line and the calculated regression are for Andean sites. Comparative data from other selected sites to left of dashed line. Stars are for individual temperate and subtropical sites: Süderhackfestedt is in Germany; Salta and Parque El Rey are in northwest Argentina; Los Tuxtlas is in Veracruz, Mexico; Cerro Olumo and Cerro El Pichaco are in Nicaragua; Centinela is an isolated ridge west of the Andean Cordillera Occidental in Ecuador. Average species richness for other site-series indicated by lines spanning appropriate altitudinal range; Chamela is western Mexican dry forest. Several of the Andean values are preliminary, being based only on field identifications with herbarium comparison of vouchers still pending or on samples of less than 1,000 m² (see Table 2).*

cializations for different edaphic conditions, often related to different soil-nutrient availability in different Amazonian habitats.

ALTITUDINAL TRENDS

Eleven sites in tropical forests between 1,500 and 3,100 m altitude, mostly in the Andes, are included in Table 2. Although the available data set for upland sites is very incomplete, the trend of decreasing diversity with increasing altitude is clear. At least within the Andes, this inverse correlation is linear (Fig. 10), but the relatively low diversity of two Central American lower montane sites suggests that the extra-Andean decrease in diversity with altitude may not follow the same rules; certainly Central American montane forests have very different floristic compositions as well. Although there has been much

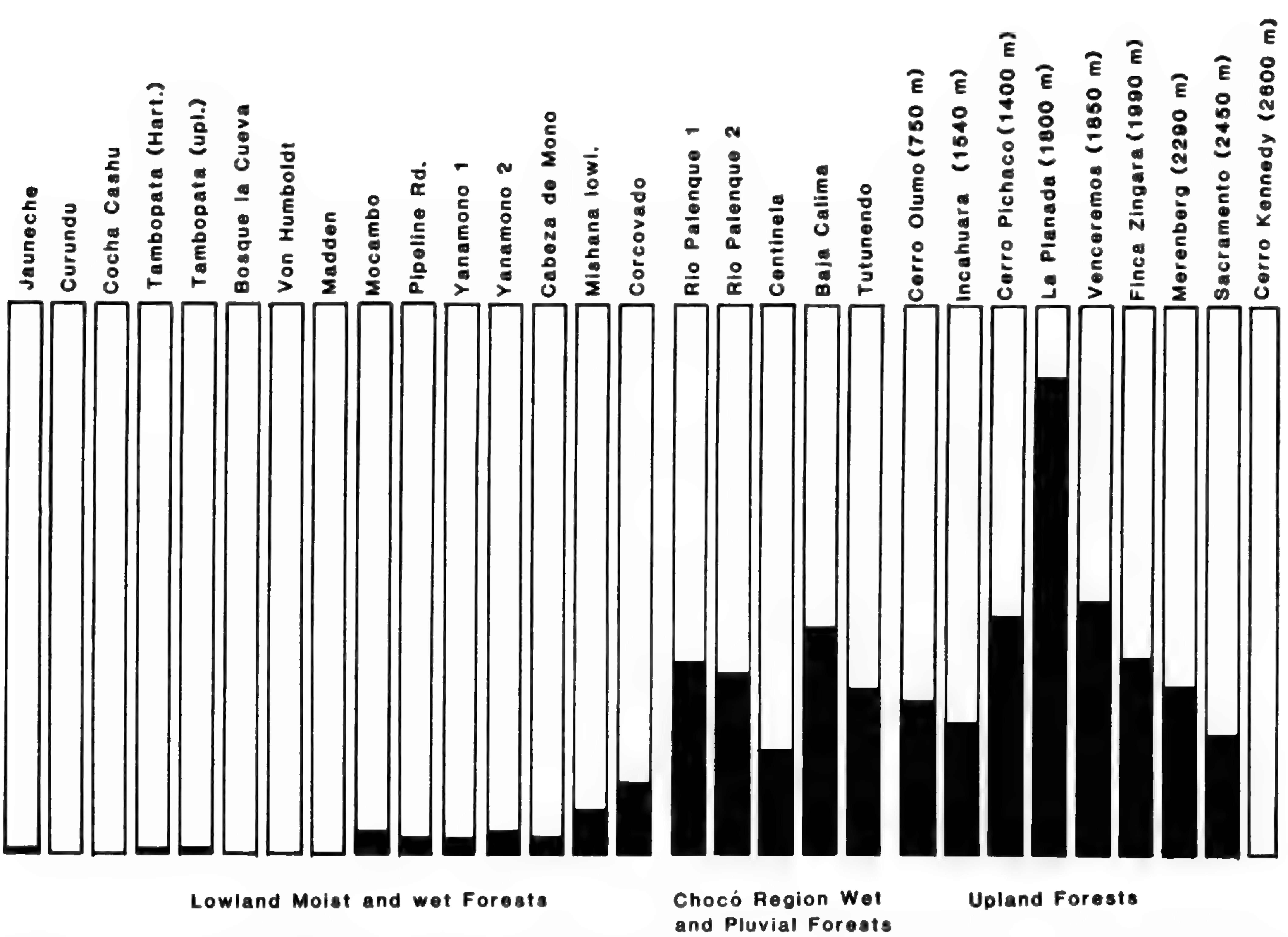

FIGURE 11. *Percent of hemiepiphytes (black portion of bar) in sampled climbers for 0.1-ha samples of upland forests (in altitudinal sequence) compared with lowland Chocó area and non-Chocó area samples. Note apparent peak in hemiepiphytes at 1,800 m.*

speculation in the literature about a "mid-altitude bulge" in diversity (Janzen, 1973; Janzen et al., 1976; Scott, 1976; Gentry & Dodson, 1987b), there is no hint of such a phenomenon in the data of Figure 10. Instead, there seems to be a constant rate of decreasing species richness in moist Andean forests from the lowland tropics to near tree line. Unfortunately, no sites have been sampled from the Andean foothill region between 600 and 1,500 m, making it difficult to judge at what altitude the decrease in diversity begins. Clearly there is no altitudinal effect up to at least 500 m (Cocha Cashu, Peru; see Gentry, 1985a). Since samples from sites at 1,700 m would be near the average value for lowland wet- and moist-forest sites (Fig. 10), we can assume that there is little or no decrease in diversity up to that altitude.

Although there is no increase in diversity at middle elevations, there are some noteworthy physiognomic changes. One of the most striking is the increase in sampled hemiepiphytes around 1,800 m (Fig. 11). However, since increased numbers of hemiepiphytic species (and individuals) are concomitant with decreased numbers of free-climbing liana species and individuals, there is no net change in community diversity. Also noteworthy is the relative abundance of hemiepiphytic climbers in wet lowland sites in the Chocó area, a typical example of the tendency of the forests of this region to have features and taxa more characteristic of upland forests (Fig. 11; Gentry, 1986b). At higher altitudes free-climbing lianas take over again, so that at 2,500 m and above, hemiepiphytes have completely dropped out.

Even near the tree line above 3,000 m, Andean forests are more species rich than are temperate forests. Our highest-altitude sample, from 3,010 m at Pasochoa in the Ecuadorian Andes, has 25 species compared with only 21–30 species in the richest 5% of

TABLE 4. *Representation of different habits in local florulas (from Gentry & Dodson, 1987b).*

Habit	Capeira		Santa Rosa		Jauneche		Barro Colorado	
	Number	%	Number	%	Number	%	Number	%
Epiphyte (including stranglers)	8	2	19	3	72	12	216	16
Parasites + saprophytes	4	1	6	1	4	1	12	1
Climbers	112	24	115	18	136	22	258	20
Trees ≥ 10 cm dbh	69	15	142	21	112	19	290	22
Terrestrial herbs, shrubs, treelets	270	58	381	58	280	47	540	41
Total species	463		667		604		1,316	

[a] Data from B. Hammel (pers. comm.).

some 312 Great Smokies Mountains samples (White, pers. comm.) and 15–26 ($\bar{X} = 20.5$) for the 13 other temperate-zone forests listed in Table 1.

SOME INTERCONTINENTAL DIVERSITY TRENDS

At a continental level, the Neotropics have many more species of plants than do either the Asian or Australasian tropics (Raven, 1976; Prance, 1977; Gentry, 1982a). Elsewhere, I have suggested that the "excess" neotropical species are mostly in herbaceous, epiphytic, and shrub taxa that have speciated explosively along the lower slope of the Andes and in southern Central America. To what extent, if any, does higher α-diversity of neotropical forests contribute to the continental pattern?

While I have relatively few comparable paleotropical data sets, a few general trends seem evident. One surprising indication from the available African data is that Central African forests ($\bar{X}$ = 127 spp., N = 5) may be as diverse in species ≥ 2.5 cm dbh as their neotropical equivalents ($\bar{X}$ = 105 spp., N = 9) for sites with 1,600–2,000 mm of precipitation. Even though the two high-rainfall sites in Cameroon do not show the increases in species richness that might be expected in the Neotropics, they are still very diverse, and the drier Gabon samples actually have more species than would be expected for similar rainfall values in the Neotropics. Moreover, one of the high rainfall sites with anomalously low diversity (Mt. Cameroon) is on the slopes of an active volcano, and the other (Korup) is on an unusually poor, highly leached skeletal soil (Thomas, pers. comm.).

West African forests, including Nigeria's Omo Forest in my data set and the Ghana forests studied by Hall & Swaine (1981), may be poorer in species for historical reasons since there are suggestions that most West African forests may have been extensively altered by Bantu populations prior to the first European colonization (Keay, 1953; Jones, 1956). Even though my anomalously low diversity Omo Forest site was in a plot of protected forest considered to be climax (though surrounded by a mosaic of other plots subjected to varying degrees of degradation historically) (G. Pilz, pers. comm.), a number of its constituent species, such as *Pausinystalia macroceras*, *Spathodea campanulata*, *Markhamia lutea*, and *Musanga cecropioides*, seem more characteristic of late secondary than of primary forest.

Nor is the high diversity of Central African forests restricted to woody plants. Data comparable to a complete local florula are available for one African forest site at Makokou, Gabon (Hladik & Halle, 1973; Florence & Hladik, 1980; Hladik & Gentry, in prep.). Comparison of these data with local florulas from the Neotropics indicates that Makokou is not only as species rich as equivalent neotropical local florulas, but it also has a similar habit composition (Table 4; Gentry & Dodson, 1987b). Similarly, data from 1-ha tree plots indicate that African forests may be almost as rich in tree species as comparable neotropical and Southeast Asian forests (Gartlan et al., 1986; Thomas, pers. comm.: 138

TABLE 4. *Continued.*

Río Palenque		La Selva[a]		Makokou	
Number	%	Number	%	Number	%
238	23	368	25	66+	6+
6	1	8	1	9	1
171	16	182	12	259	23
165	16	310	21	389	34
475	45	622	42	418	37
1,055		1,490		1,140	

spp. in 0.64 ha on transect S, Korup National Park, Cameroon; Gentry, in press).

On the other hand, it is noteworthy that my single Madagascar site is richer in species than any of the continental African sites, which might be anticipated from the now widely accepted hypothesis that Africa's low continent-wide plant (and bird) species richness stems largely from extinctions associated with climatic deterioration during the Pleistocene or late Tertiary, whereas Madagascar was protected by being an island (Raven & Axelrod, 1974; Axelrod & Raven, 1978).

Quite the opposite of Africa, Asian forests have been widely thought to have more tree species than neotropical forests (e.g., Ashton, 1977; Whitmore, 1984). This conclusion was based on comparison of extant neotropical data for 1-ha tree plots with similar Asian data sets. However, the previously available neotropical tree plots were all from areas that would be anticipated on biogeographical or ecological grounds to have species-poor forests (Gentry, 1988). Hectare plots in upper Amazonia consistently have more tree species than in most Asian forests (Gentry, 1988), and the most species-rich 1-ha plots are in upper Amazonia. Indeed, these plots are so diverse—up to 300 species out of 606 individuals ≥ 10 cm diameter at Yanamono, Peru—that it is hard to imagine how a forest could be much more diverse.

I conclude that plant community diversity, at least of woody plants in plots of 1 ha or

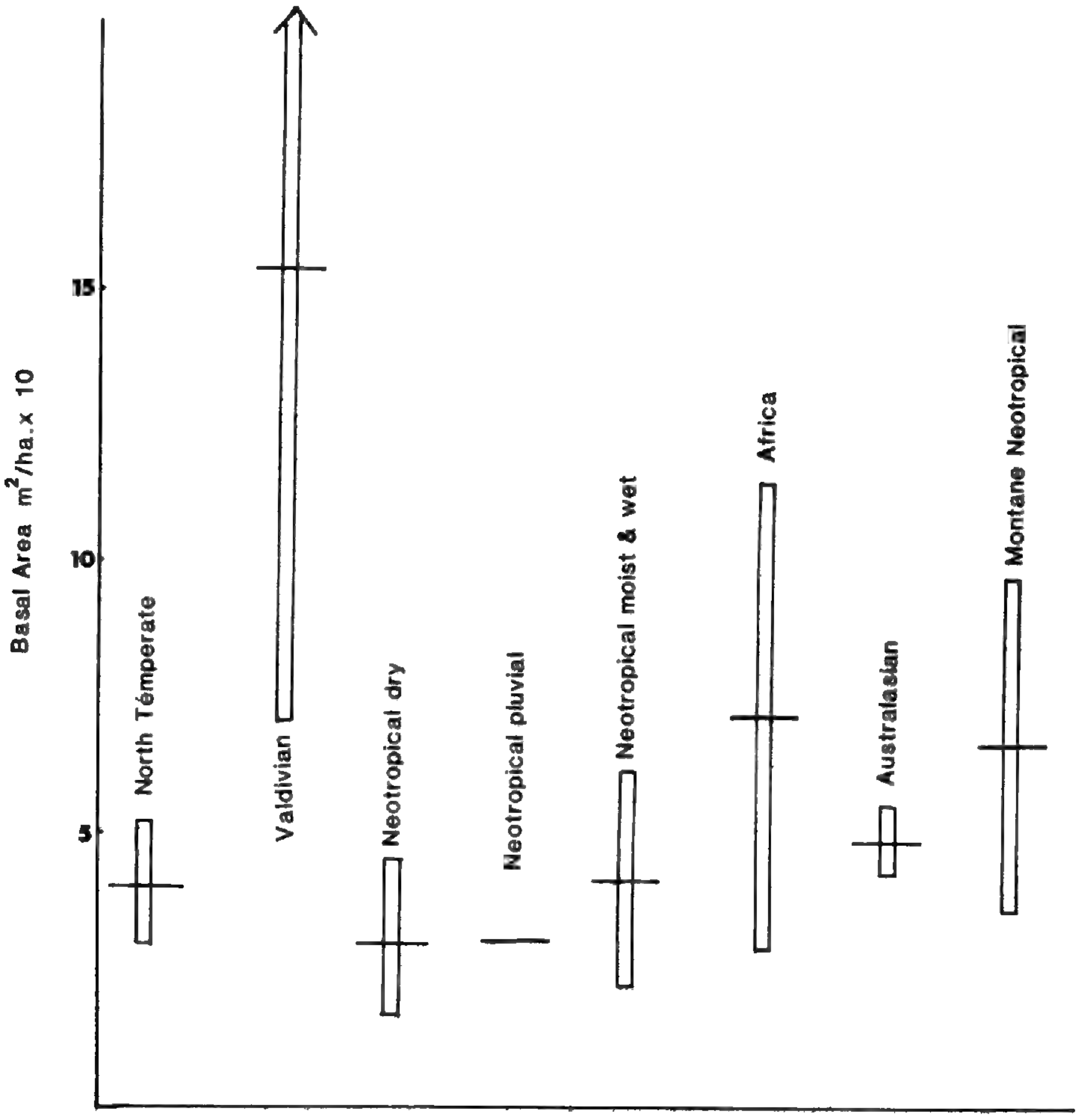

FIGURE 12. *Basal areas for 0.1-ha samples of some different forest types. Line = average basal area for forest type; bar = ± 1 s.d.*

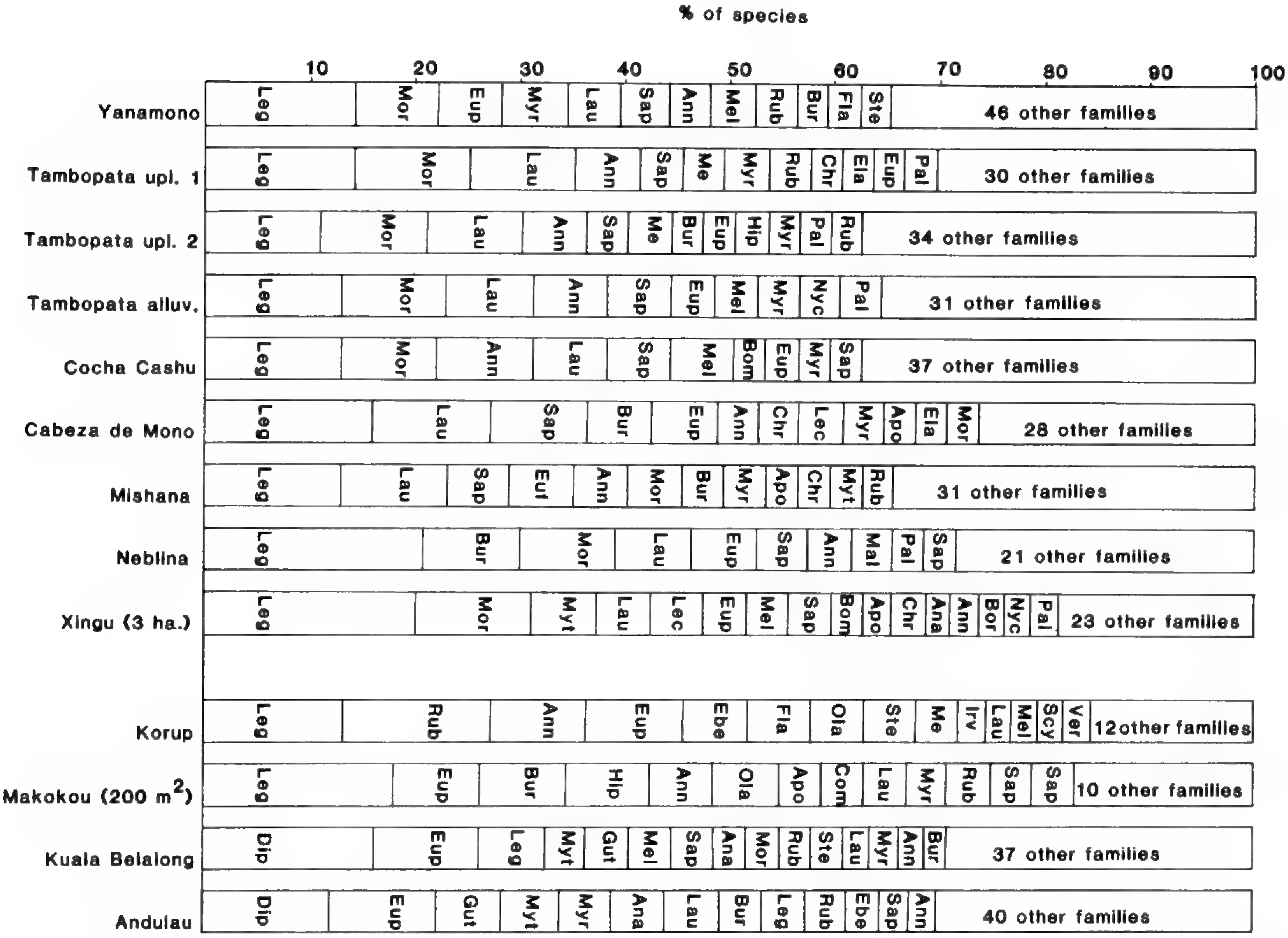

FIGURE 13. *Familial compositions of some tropical forest tree plots (plants ≥ 10 cm dbh) in Amazonia (Yanamono to Xingu), Central Africa (Korup and Makokou), and Southeast Asia (Kuala Belalong, Andulao). South American sites are from original data except Xingu (Campbell et al., 1986); Korup is from D. Thomas (pers. comm.); the Makokou data are the total for the ≥ 10 cm dbh subset for the two 0.1-ha plots listed in Table 1 combined. The two Asian sites are from Ashton (1964): the data are for a total sample area of 20 ha at each site, composited from 50 individual acre plots on different types of terrain. The other data are for 1-ha plots except as otherwise noted. Family codes are the first letters of the familial names, self-evident except me = Melastomataceae, mel = Meliaceae, sap = Sapotaceae (the second, if present, = Sapindaceae), myr = Myristicaceae, myt = Myrtaceae. Note that Leguminosae, the dominant family in all neotropical and African tree plots, is just as speciose as is Dipterocarpaceae in Southeast Asia. Also note that, except for dipterocarps, the forests on all three continents are mostly composed of species belonging to the same few woody families.*

less, has a similar range of variation according to local environmental conditions in all three of the world's main tropical regions; what happens at larger spatial scales remains an open question.

Although tropical forest α-diversity may be similar on different continents, its structure is not. For example, lowland neotropical forests have fewer lianas than African forests and more lianas than Asian forests (Emmons & Gentry, 1983). Large palms as a major and characteristic canopy element of lowland terra firme forest seem largely restricted to the Neotropics (Gentry & Emmons, 1987), Madagascar (20 palms ≥ 10 cm dbh/ha at Perinet), and a few other islands (e.g., New Caledonia: 20 palms ≥ 10 cm dbh/ha at Rivière des Pirogues). While stem densities of trees ≥ 10 cm dbh may be similar from continent to continent (Dawkins, 1959), tropical African forests tend to have more large trees and higher basal areas (and presumably biomasses) (70.7 m^2/ha vs. 34.9 m^2/ha) than do neotropical or Australasian forests (Fig. 12). On the other hand, Asian dipterocarp forests may have uniquely high densities of small polelike trees. Such structural differences, only beginning to be discovered, may be critical to forest organisms. For example, the intercontinental difference in liana density

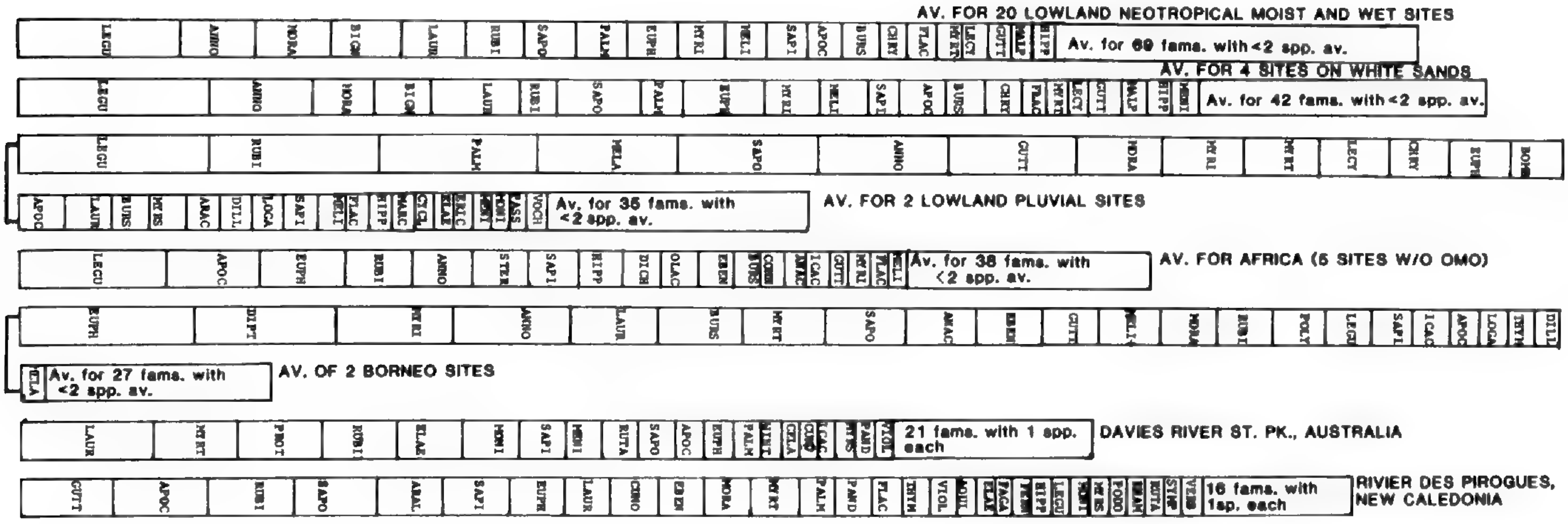

FIGURE 14. *Comparison of average number of species per family for 0.1-ha samples from subsets of different lowland neotropical forest types with equivalent paleotropical data. From top to bottom the columns represent: 1) average for 20 lowland neotropical moist and wet sites; 2) average for 4 neotropical sites on white sand; 3) average for 2 pluvial-forest sites in Chocó; 4) continuation of 3; 5) average for 5 central African sites (i.e., excluding Omo); 6) average for 2 Bornean sites; 7) continuation of 6; 8) Davies River State Park, Queensland, Australia; 9) Rivière des Pirogues, New Caledonia. Shortest column segments are two species tall.*

may have been the critical factor selecting for different locomotor adaptations among canopy vertebrates on the three continents (Emmons & Gentry, 1983).

FLORISTICS

Neotropical plant communities are put together in decidedly nonrandom ways. Thus community-level frequency of different seed dispersal and pollination syndromes is generally predictable from environmental parameters (Gentry, 1982b, 1983). Similarly, the floristic composition of different plant communities is remarkably consistent, at least at the familial level. Legumes are virtually always the dominant family in neotropical and African lowland primary forests. The only neotropical exceptions are on extremely rich soils where Moraceae become very diverse and are occasionally as species-rich as Leguminosae in 0.1-ha plots (Gentry, 1986b, c). Of the 43 continental neotropical lowland 0.1-ha samples between 23.5°N and S latitudes, 39 had Leguminosae as the most species-rich family. The dominance of legumes in the Neotropics and Africa is equally apparent when only trees ≥ 10 cm dbh are considered (Fig. 13). Indeed, legumes contribute almost exactly as much to the diversity of neotropical and African forests as dipterocarps do in Southeast Asia. Similarly, in Africa, on the rich volcanic soil of the Mt. Cameroon plot, several families, especially Rubiaceae, Apocynaceae, and Euphorbiaceae have more species than legumes, but this forest, on the lower slopes of an active volcano, may not be strictly primary.

The other families that contribute most to species richness of different plant communities are also predictable. In the Neotropics the same 11 families—Leguminosae, Lauraceae, Annonaceae, Rubiaceae, Moraceae, Myristicaceae, Sapotaceae, Meliaceae, Palmae, Euphorbiaceae, and Bignoniaceae—contribute about half (38%–73%; $\bar{X} = 52\%$) of the species richness to 0.1-ha samples of any lowland forest. At least eight of these families are always among the ten most species-rich families in any lowland neotropical moist or wet forest (Fig. 14; Gentry, 1987b). Similarly, in 0.1-ha samples of lowland neotropical dry forests, Bignoniaceae, the preeminent liana family, is always second only to Leguminosae in its contribution to species richness (Fig. 15).

Somewhat surprisingly, the dominant families in neotropical forests also tend to be the most speciose on other continents. Rubiaceae, Annonaceae, and Euphorbiaceae are always among the ten most species-rich families in Africa and Asia, just as they are in the Neotropics. The rest of the 11 most species-rich neotropical families (Lauraceae, Moraceae,

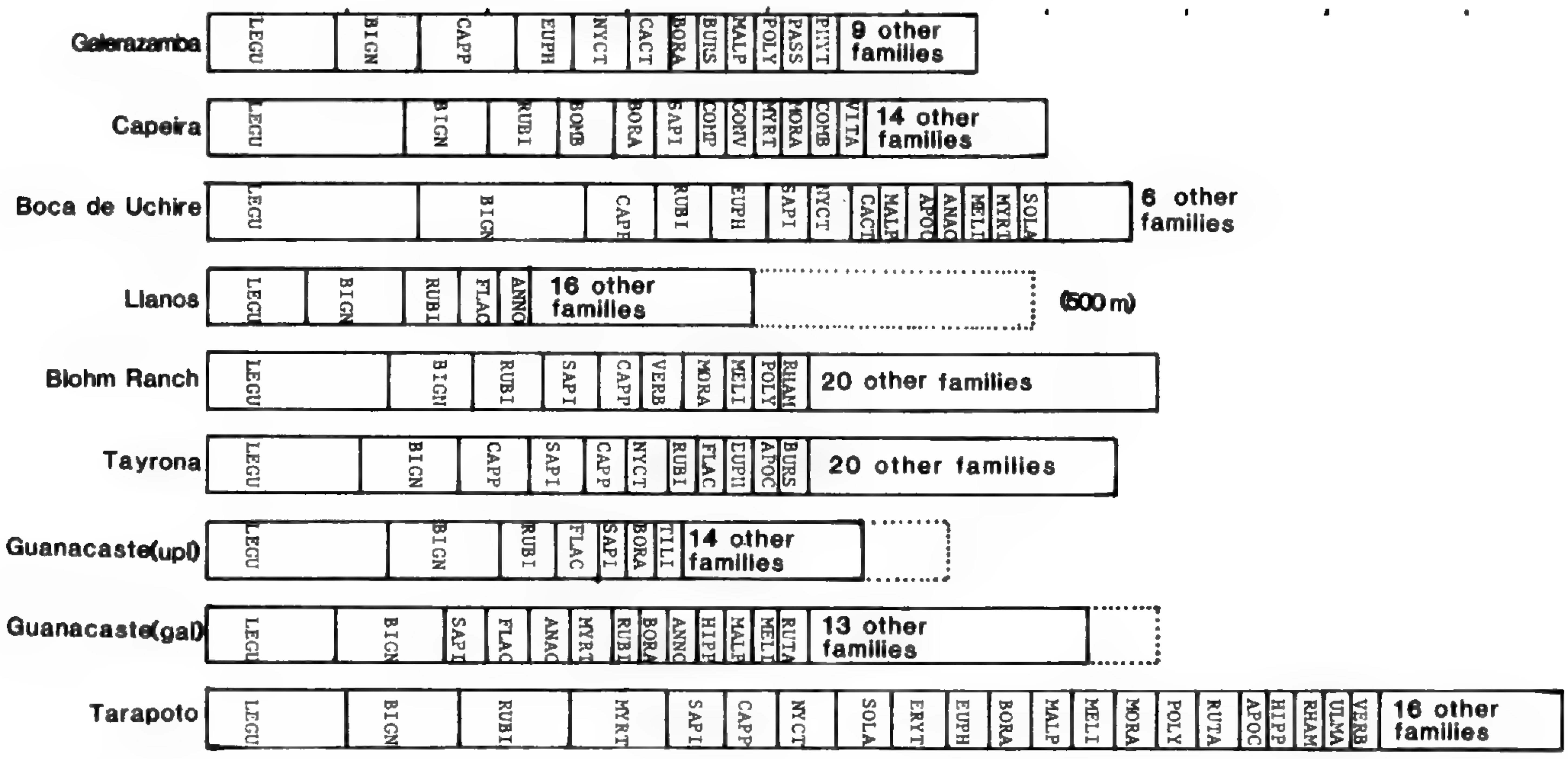

FIGURE 15. *Number of species per family for 0.1-ha samples of lowland neotropical dry forests. For three sites with sample areas of < 1,000 m²—Llanos, Guanacaste (upland) and Guanacaste (gallery), with 500 m², 700 m², and 800 m² of sample area, respectively—the actual values are inside the solid outlines with the anticipated number of species in 1,000 m² indicated by the dotted outline. Shortest column segments are two species tall.*

Sapotaceae, Palmae, Myristicaceae, Meliaceae, and Bignoniaceae) are all represented in at least some samples from both Africa and Asia and, except for Bignoniaceae and Palmae, are among the ten most species-rich families in at least one African or Asian sample. Thus, with the exception of the substitution of Dipterocarpaceae for Leguminosae as the most species-rich woody family in Southeast Asian forests, pantropical familial composition of lowland forests is remarkably similar.

Other minor differences include Ebenaceae (almost always present in Africa and Asia and among the ten most species-rich families in about half the samples from those continents but only occasionally represented in the neotropical samples, never by more than a single species), Olacaceae (usually represented on all continents but generally among the ten most species-rich families in Africa, never so in Asia or the Neotropics), and Sterculiaceae (always among the ten most species-rich families in Africa; represented by 1–3 species in almost all neotropical and Asian samples, although among the ten most species-rich families only in Cocha Cashu, Peru). Dichapetalaceae are almost always among the ten most species-rich families in African samples but are only occasionally represented by one or two species in the Neotropics and are absent from my Asian samples. Apocynaceae and Sapindaceae almost always turn up in samples from any continent but are generally among the ten most species-rich families in Africa (always in the case of Apocynaceae) but only rarely elsewhere. Disproportionately represented in Asia, besides Dipterocarpaceae, are Myrtaceae (always among the most species-rich families vs. almost always present but only rarely among the most species-rich families in the Neotropics and represented by a single species in a single sample on continental Africa). Other noteworthy anomalies include 9 species of Proteaceae, 7 of Elaeocarpaceae, and 6 of Monimiaceae in the Queensland sample (these three families ranking 3rd, 5th, and 6th in diversity after Lauraceae, Myrtaceae, and Rubiaceae), 7 Araliaceae species and 5 of Cunoniaceae in the New Caledonia sample (ranking 5th and 8th, respectively, in familial diversity), and 8 and 3 species, respectively, of *Xanthophyllum* (Polygalaceae) at Semengoh and Bako, Borneo.

Put another way, all of the paleotropical forests sampled were constituted almost entirely of the same plant families encountered in equivalent samples of neotropical forests.

Although 13 families not represented in the Neotropics were included in the paleotropical samples, and although each African and Asian sample included 1–3 families not represented in the Neotropics, with two exceptions, the sum contribution of all of these to species richness of the Asian and African forests is negligible. The two exceptions are Dipterocarpaceae in tropical Asia and Pandanaceae in Madagascar (3 spp.), Queensland (2 spp.), and New Caledonia (4 spp.). Excluding these two families, an average of 2 species (and ca. 3 individuals) per sample was contributed to paleotropical community diversity by families not included in the equivalent neotropical samples. At this level New Caledonia was the most distinctive, with one species each of Balanopaceae, Epacridaceae, Oncothecaceae, and Pittosporaceae, plus 4 of Pandanaceae. The Madagascar sample included, besides 3 Pandanaceae, a species of Sarcolaenaceae and two of Pittosporaceae, the Queensland sample a species of Balanopaceae and 2 of Pandanaceae (plus one of the sometimes Cunoniaceae segregate Davidsoniaceae). In Africa, Ancistrocladaceae was represented by one individual at one site, Medusandraceae by one individual at one site, and Scytopetalaceae by two species at one site. Only in the latter case did an endemic family contribute significantly to a site's diversity, with *Ouabangia alata* the 5th most common species (13 individuals) at Korup and *Rhaptopetalum* cf. *coriaceum* represented by three individuals at the same site. It is perhaps worth noting that several of the endemic families included in the above total are somewhat dubious segregates—Pandaceae (from Euphorbiaceae), Irvingiaceae (from Simaroubaceae), and Ixonanthaceae (from Linaceae). Lowland tropical forests throughout the world are overwhelmingly made up of the same plant families, with the exception of the Dipterocarpaceae for Leguminosae substitution in Southeast Asia.

Even at the generic level, there are striking floristic similarities between the compositions of lowland tropical forests on different continents. The generic similarity is especially marked between Africa and South America. An average of 30% (with extremes of 25% at Korup to 34% at Belinga) of the genera at the six continental African sites are neotropical genera, nearly all also included in the neotropical samples. When complete local floras are compared, generic concordance between tropical Africa and the Neotropics remains equally high. Thus 30% of the genera represented at Makokou Gabon also occur in the Neotropics. Both sets of figures would be much higher if such tenuously differentiated genera as *Pycnanthus* and *Virola* (Myristicaceae) or *Macrolobium* and its segregates (Leguminosae) were considered to be congeneric.

Generic overlap between tropical Asia and the Neotropics is less, averaging 23%, and between Australasia and the Neotropics intermediate (25% neotropical genera in the Queensland sample, 26% in the New Caledonia one). These relationships might be predictable from Cretaceous and Tertiary plate tectonic history and the timetable of Gondwanan breakup. In this light, it is especially interesting that about 36% of the genera sampled at Perinet, Madagascar, are shared with the Neotropics, the highest value for any paleotropical site.

There are also consistent and predictable floristic changes along environmental gradients, at least in the Neotropics. On poorer soils families like Burseraceae, Lauraceae, and Sapotaceae become more prevalent, whereas on the richest soils palms and Moraceae are disproportionately speciose.

In neotropical areas with a strong dry season, floristic composition is likewise predictable. Leguminosae are always the most species-rich family, with Bignoniaceae, represented mostly by wind-dispersed lianas, always second (Fig. 15).

On an altitudinal gradient in the Andes, Lauraceae consistently replace Leguminosae as the most species-rich family at intermediate elevations (Fig. 16). Other families that contribute to the diversity of middle elevation forests are Rubiaceae, Melastomataceae, Euphorbiaceae, Moraceae, Guttiferae, tree ferns, (hemiepiphytic) Araceae, and Palmae. Fam-

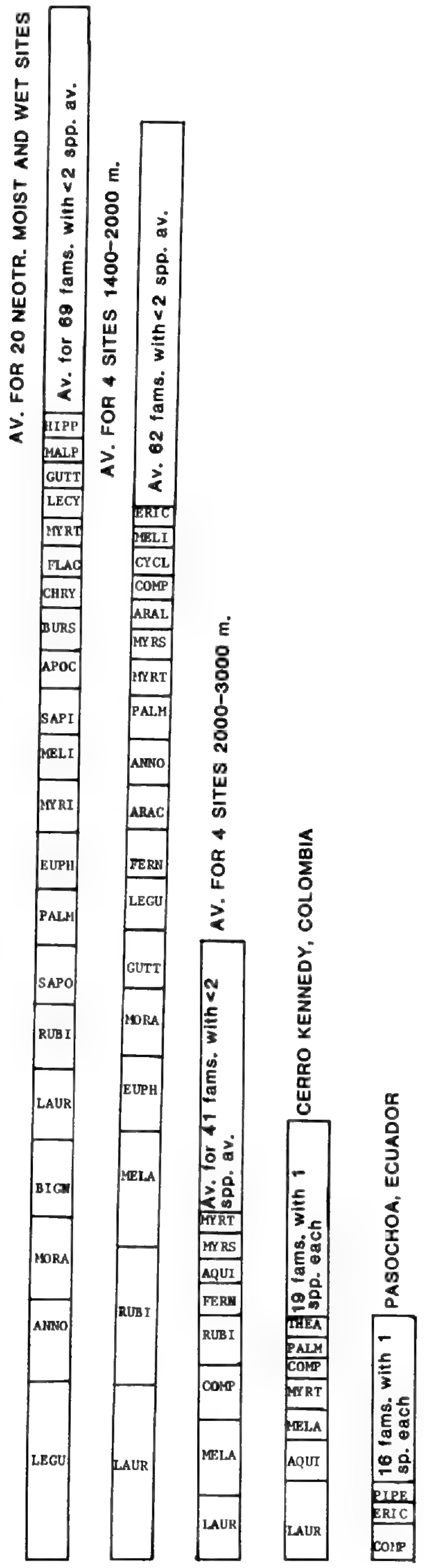

FIGURE 16. *Number of species per family for 0.1-ha samples at different altitudes in the Neotropics. From left to right columns are 1) average for 20 lowland neotropical moist- and wet-forest samples; 2) average for 4 sites between 1,400–2,000 m (Cerro Pichaco, Incahuara, Venceremos, Farrallones de Cali); 3) average for 4 sites at 2,000–3,000 m (Sacramento, Finca Mehrenberg, Cerro Kennedy, Finca Zungara); 4) Cerro Kennedy, Colombia (2,600 m, 500 m² of sample area);* ← *5) Pasochoa, Ecuador (3,010 m, 200 m² of sample area). Site data from Table 2. Shortest column segments are two species tall.*

ilies like Bignoniaceae, Sapotaceae, Myristicaceae, Meliaceae, Sapindaceae, Burseraceae, and Chrysobalanaceae are especially noteworthy as absent or much more poorly represented than in lowland forests. At higher elevations (> 2,000 m), Melastomataceae, Compositae, Rubiaceae, and tree ferns become more prevalent, although of these only Compositae increase in absolute number of species. At even higher altitudes, Aquifoliaceae, Myrtaceae, and Theaceae become relatively more important, while near timberline Compositae and Ericaceae predominate.

Curiously, the site at 1,000 m altitude at Perinet, Madagascar, had virtually an identical familial composition to the middle-elevation neotropical site; in addition to Lauraceae being the most speciose family, Rubiaceae, Euphorbiaceae, Moraceae, and Guttiferae followed in species richness; the only substantial differences are a transposition of the roles of Melastomataceae (more species in the Andes) and Myrtaceae (more species at Perinet), the presence of several species of Monimiaceae and Oleaceae in Madagascar, and the frequency of hemiepiphytic Araceae in the Neotropics (Fig. 17). A Queensland, Australia, site from 850 m was also rather similar in familial composition to the Andean middle-elevation sites, again with Lauraceae dominating, closely followed by Rubiaceae, though with greater prevalence of such southern families as Proteaceae, Elaeocarpaceae, and Myrtaceae. Such strikingly repeated patterns in parts of the world so widely separated today can hardly be due to chance.

Many of the major latitudinal changes in floristic composition are well known, with families such as Fagaceae and Juglandaceae replacing the tropical taxa in North America (Fig. 18). Perhaps less emphasized are how remarkably similar in familial composition different eastern North American forests are. While species, and to some extent genera, do change from place to place, from a world

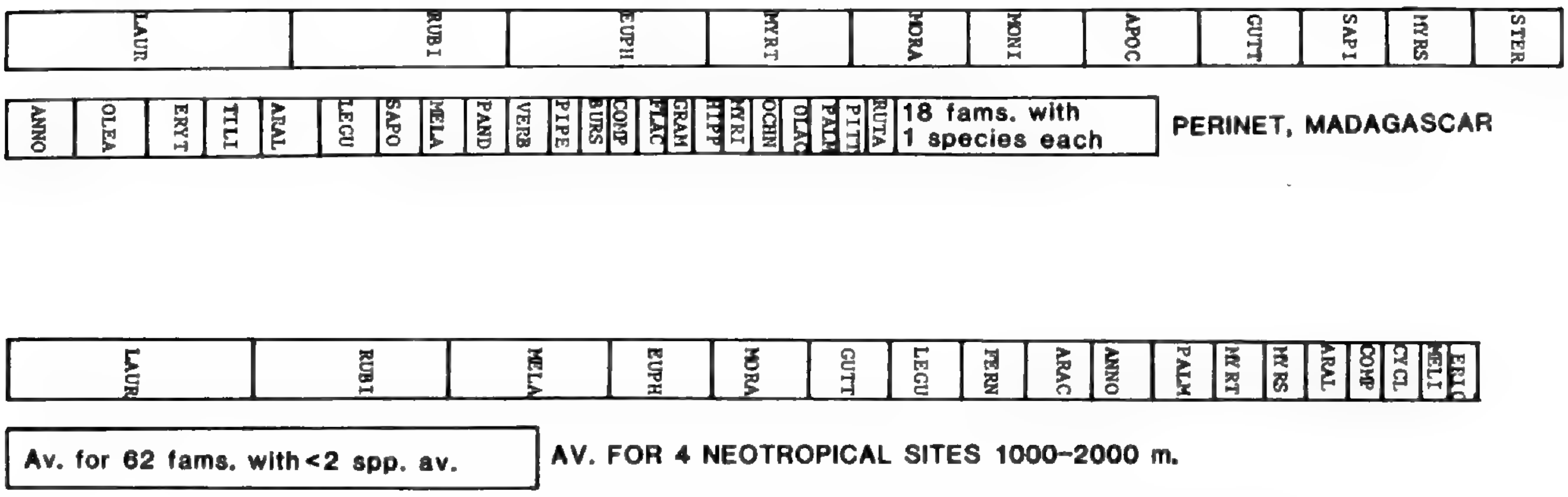

FIGURE 17. *Number of species per family for 0.1-ha sample at Perinet, Madagascar (950 m) (top two columns) compared with average for four mid-elevation neotropical sites (1,000–2,000 m) (bottom two columns). Note the remarkable similarity of familial composition. Perinet data based only on field identifications pending herbarium comparison of vouchers. Shortest column segments are two species tall.*

perspective the overall floristic composition of most of these forests is as similar as is their diversity. The contrastingly austral composition of the Valdivian flora is also well known. There are also floristic similarities between the austral and north temperate ones. For example, gymnosperms and Fagaceae become more prevalent in both north temperate and south temperate areas. One interesting and previously unremarked floristic difference between the Valdivian forests and their northern equivalents is that the former lack sympatric congeners. The difference in diversity between eastern North American and Valdivian forests (as well as between the North American forests and my two European samples) is almost entirely accounted for by this lack of sympatric species in genera like *Quercus* and *Carya*. Why Chilean *Nothofagus* species, unlike their northern cousins, should be almost entirely allopatric is unclear, but the effect of this pattern on the diversity of the south temperate forests is obvious.

DISCUSSION

To this point I have attempted to present a series of observations of changes in diversity and floristic composition on various gradients. I now focus briefly on some theoretical generalizations that would seem to derive from these data.

The overall message is that plant communities are put together in decidedly nonrandom ways. Diversity and floristic composition are highly predictable from environmental and geographical factors, with maximum plant community diversity occurring in full-tropical lowland areas with rich to intermediately infertile soils and high annual precipitation and/or little dry-season stress. Such patterns are often taken as evidence of niche saturation and community equilibrium (MacArthur, 1965, 1969; Cody, 1975; see also Whittaker, 1977).

Much of the controversy about equilibrium vs. nonequilibrium communities has focused on the role of niche specificity vs. stochastic generation or maintenance of diversity (e.g., Hubbell, 1984; Hubbell & Foster, 1986; Ashton, 1969; Connell, 1978). My data suggest that even though tropical forests contain many different plant species, they are far from random assemblages. Can these data and conclusions be reconciled with the very different ones of Hubbell (1979; Hubbell & Foster, 1986, 1987)? Below I will focus on several points that may be relevant to this debate.

From a somewhat different perspective, some authors (e.g., Federov, 1966) have argued that the exceedingly high diversity of tropical forests is too great to be accounted for by niche specificity; therefore, some kind of nonselective or stochastic mechanism must be invoked. However, it seems to me that it is stochastically most unlikely that the extreme species richness of forests like that at Yanamono, Peru, with 300 species out of 606 individuals in a hectare, would result

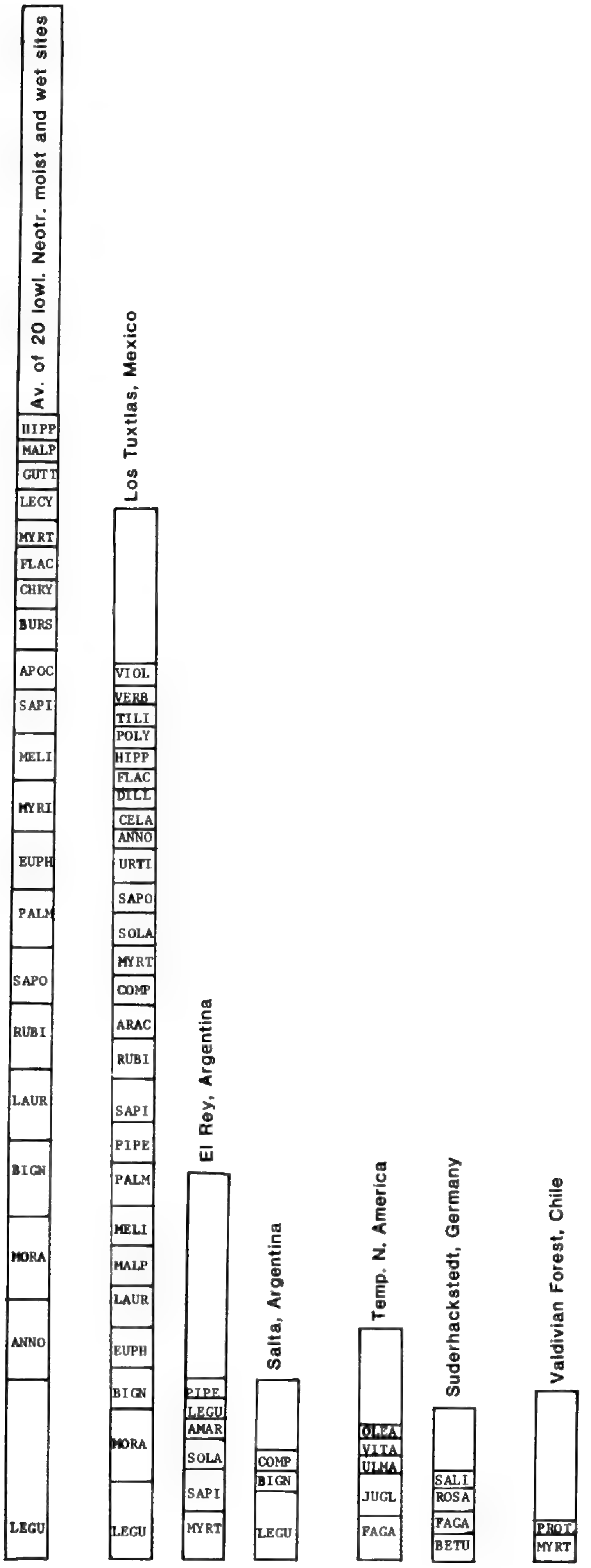

FIGURE 18. *Number of species per family for some 0.1-ha samples at different latitudes. From left to right, columns are: 1) average for 20 lowland neotropical moist- and wet-forest samples; 2) Los Tuxtlas, Mexico (wet forest, 18°35′N, 200 m alt.); 3) Parque El Rey, Argentina (moist forest, 24°45′S, 1,000 m alt.); 4) Salta, Argentina (dry forest, 24°40′S, 1,300 m); 5) average for seven temperate North American sites (28°15′N–39°2′N); 6) Suderhackstedt, Germany* ← *(54°N); 7) average for three Valdivian, Chile, sites (39°30′S–40°43′S).*

from random processes, unless there is a potential sample universe of many thousands of tree species. Forty-eight species are represented in the first 50 individuals sampled at Yanamono, and the 65 individuals in the first Yanamono 0.1-ha subplot constitute 58 species. Such high levels of diversity, far from indicating stochasticity, would seem to indicate very strong ecological pressures resulting in phenomenally low densities of the individual species (and high community diversity).

The striking regularities in the patterns discussed above clearly indicate that at some levels both community composition and diversity are highly predictable. How this relates to community equilibrium remains clouded, however, in part because of definitional problems. Hubbell & Foster (1986) defined an equilibrium community as one in which a particular combination of *species* maintains itself against outside perturbations, whereas the predictable diversities of different tropical forests with similar environments but different assemblages of species is more akin to the "equilibrium" theory of island biogeography (MacArthur & Wilson, 1967), considered by Hubbell as a nonequilibrium theory because of the taxonomic randomness involved. Many Amazonian forests are clearly richer in tree species than equivalent Central American forests (Gentry, 1988). They also have much greater habitat differentiation and β-diversity (Gentry, 1986a). Thus some of the higher diversity of the Amazonian forests may be due to the "mass effect" phenomenon of Shmida & Wilson (1985), with accidental immigrants adapted to other environments contributing significantly to the α-diversity of an individual Amazonian forest. Arguing along similar lines from the nonequilibrium viewpoint, Hubbell & Foster (1986) suggested that biogeographical pattern plays a major role in tropical forest α-diversity: if the regional diversity is greater, as it certainly is in Amazonia, more species, on the average, should occur in individual forests due purely to phenomena associated with patch dynamics and local immigrations. But there are also problems with such interpretations. That the families and genera represented in these different samples are so predictable strongly suggests that at least some kind of familial-specific niches may be involved. Moreover, the apparent partitioning of the species of each family into different sets of species specialized for different substrates in Amazonia seems strong circumstantial support for selectionist interpretations (Gentry, 1985b).

Data from several 1-ha tree plots in the Tambopata Reserve, Madre de Dios, Peru, can be used to document the effect of substrate specificity on species composition. Data are available from two completely identified 1-ha samples from similar poor-soil terra firme forest separated by about 1.5 km, a completely identified plot in mature forest on rich alluvial soil, and from as yet incompletely identified plots in young riverside secondary forest, in swamp forest, and in forest in a transitional area between the rich floodplain and poor-soil uplands (see Fig. 8). As is usually the case in species-rich tropical forests, most of the species sampled were represented by one or two individuals on a single plot and are inadequately sampled to draw any conclusions about habitat specificity. Table 5 lists the species that occur in all three completely sampled plots plus all species that are common (i.e., > 10 individuals) in at least one of the plots plus a few other selected species.

At one extreme are 13 species that occur both in the two poor-soil plots and in the fertile-soil alluvial plot. These might be classed as ecologically insensitive; none of them occurs in the secondary forest, six of them (and possibly more) in the swamp plot, and most (perhaps all) of them on the intermediate plot. All of these are essentially uniformly dispersed with similar numbers of individuals in each hectare. *Bertholettia excelsa*, which has 1–2 large emergent trees per hectare throughout the Tambopata Reserve (except in secondary forest), is a good example of this pattern. Other good examples include the subcanopy tree *Leonia glycicarpa*, which has 6–19 individuals per hectare, and the canopy tree *Symphonia globulifera* with 1–4 individuals per hectare, again excluding the second growth plot.

At the opposite extreme are the 21 habitat specialists listed in Table 5, locally common, but occurring in only a single habitat: good soil, poor soil, swamp, or second growth. The extreme case is *Lueheopsis hoehnei*, the absolute dominant in the swamp plot with 265 trees, but completely absent elsewhere; that this is only the second record of such a locally common species from Peru is instructive as to the state of Amazonian Peruvian floristic knowledge. Another example worth mentioning is *Sparrea schippii*, previously unreported from Peru (or indeed from Amazonia), which is the fourth most common species in the alluvial plot. The large number of species that are completely faithful to a single habitat (presumably also including many additional less common species not listed in Table 5) is a good example of the importance of niche specificity in maintaining overall Amazonian species diversity. Each community is rich in large part because it has many species uniquely adapted to a specific substrate.

Perhaps more interesting from the viewpoint of ecological theory are the other two distributional categories indicated in Table 5. The first are species that are common in one habitat but also have a few individuals in one or more of the other habitats. Some of these may represent cases of "mass effect" (Shmida & Wilson, 1985), with an occasional individual surviving but not reproducing outside its normal ecological range. The second pattern is species of the poor soil forest that are common in one of the two sample plots but absent from the other. These may be examples of "ecological equivalents" (Shmida & Wilson, 1985), where due to some accident of dispersal or establishment, a given species occurs at one site but not at another where it would be equally well adapted. The ecological equivalent hypothesis seems especially germane to *Cordia*, where *Cordia mexiana* and *C. panamensis* occur in one upland plot while *C.*

TABLE 5. *Differences in occurrence and abundance in different 1-ha tree plots of some common Tambopata species (all species occurring in all three complete plots or with 10 or more individuals in any one plot plus a few others). Plot 1 is relatively fertile terra firme; plot 2 is swamp forest; plots 3 and 6 are on poor sandy, upland terra firme; plot 4 is on rich alluvial soil; and plot 5 is in young riverside secondary forest.*

	Plot Number					
	1	2	3	4	5	6
Ecologically insensitive, ± uniformly dispersed						
Bertholettia excelsa	2	(1)	2	1	—	2
Eschweilera coriacea	6?	?	4	2	—	9
Glycidendron amazonica	1	(1)	1	2	—	1
Leonia glycicarpa	19	(1)	12	12	—	6
Lindackeria paludosa	4	(1)	10	1	—	4
Minquartia guianensis	1	—	3	1	—	2
Nectandra cissiflora	?	?	1	1	—	4
Neea divaricata	X	?	2	5	—	4
Ocotea rubrinervis	?	?	7	7	—	7
Oenocarpus mapora	1	(1)	4	3 (4)	—	3
Symphonia globulifera	1	(3)	3	3	—	4
Tapirira guianensis	1	—	—	1	—	2
Clarisia racemosa	1	—	3	2	—	2
Ecologically sensitive but widespread						
Amaioua corymbosa	1	(1?)	11	1	—	6
Euterpe precatoria	17	4	2	2	—	4
Iriartea deltoides	106	(15)	7	86	—	—
Iryanthera juruensis	5	(3)	19	5	—	22
Iryanthera laevis	17	(2)	13	2	—	31
Mabea	—	(1)	1?	11	—	—
Pourouma minor	18	(6)	17	1	—	44
Pseudolmedia laevis	14	(5)	4	7	–	1
Siparuna decipiens	13	3	8	1		9
Socratea exorrhiza	10	5	1	38	7+	2
Tetragastris altissima	1	(2+)	7	1		22
Ecologically restricted						
Cecropia membranacea	—	—	—	—	46+	—
Ficus insipida	—	—	—	—	13	—
Citharexylum poeppigii	—	—	—	—	9+	—
Sparrea schippii	—	—	—	17	—	—
Rinorea viridifolia	X	—	—	27	—	—
Astrocaryum murumuru	—	—	—	16	—	—
Myroxylon balsamum	1	?	—	6	—	—
Cordia lomatoloba	—	—	—	2	—	—
Cordia nodosa	X	—	—	1	—	—
Mauritia flexuosa	—	41	—	—	—	—
Lueheopsis hoehnei	—	265	—	—	—	—
Pithecellobium latifolium	—	12	—	—	1	—
Rouchera punctata	1	(2)	19	—	—	15
Virola sebifera	1	(1)	18	—	—	15
Ouratea	—	—	14	—	—	14
Euceraea nitida	—	(1)	6	—	—	8
Cedrelinga cateniformis	—	—	3	—	—	5
Cordia mexiana	—	—	10	—	—	—
Cordia panamensis	—	?	4	—	—	—
Cordia toqueve	—	?	—	—	—	4
Cordia ucayaliensis	—	—	—	—	—	7

TABLE 5. *Continued.*

	Plot Number					
	1	2	3	4	5	6
Major density differences not explainable by ecology						
Bixa arborea	—	—	15	—	—	—
Hevea guianensis	1	—	15	—	—	—
Pseudolmedia laevigata	1	—	23	—	—	4
Ocotea (*domatia*)	?	—	1	—	—	10
Arrabidaea tuberculata	—	—	—	—	—	4

X = present in Hartshorn plot but number of individuals not known.
? = presence or absence not known due to incomplete identifications (plot 1) or sampling not yet completed (plot 2).
( ) = species occurring in plot 2 only in corner on higher ground.

toqueve and *C. ucayaliensis* occur in the other. Both of the latter situations represent the pattern thought to be prevalent on Barro Colorado Island (Hubbell & Foster, 1986), with high diversity of a given community due in large part to nonequilibrium fluctuations in its species.

At a different level, my data on plant community composition also seem much less predictable and much more in accordance with the nondeterministic, nonequilibrium viewpoint. In the nine 1-ha tree plots that have been analyzed, there was not a single repetition of a most-dominant species. Although one (or a few) species is always much more common, there is a different "dominant" species in each plot. Even if the several most-dominant species in each plot are compared, there is little overlap. Considering only those species with 10 or more individuals per hectare in at least one tree plot generates a list of 54 species documented to be relatively common locally somewhere in upper Amazonia. But of these, only five species are abundant on two different plots. The shared abundant species include *Astrocaryum murumura*, common on all three rich-soil plots (Yanamono, Cocha Cashu, Tambopata alluvial), and *Hevea guianensis*, common on three poor-soil plots. The other shared abundant species are *Otoba parviflora* on two of the three rich-soil sites (Yanamono and Cocha Cashu) and *Iriartea deltoidea* on a different pair of rich-soil sites (Cocha Cashu and Tambopata alluvial). But even though the same species are generally not abundant at different sites with similar ecology, they are usually *present*. If we take the three rich-soil tree plots as an example, all the abundant Tambopata alluvial-plot species are present in the Yanamono plot, and all the abundant Yanamono species, except *Otoba glycicarpa* and *Carapa guianensis*, are present at Tambopata. All of the abundant Cocha Cashu species are at Yanamono, and all but four of the abundant Yanamono species are at Cocha Cashu. If we compare the sandy-soil plots from Mishana and Cabeza de Mono, there is only one species abundant at both sites (*Hevea guianensis*), but all the common Cabeza de Mono species are present at Mishana, and most of the common Mishana species are at Cabeza de Mono. In contrast, only four species that are abundant at any poor-soil site are present at all in any rich-soil site, all at Yanamono, which has an intermediate level of soil fertility. The relevant point is that although the species present at a site may be predictable, the frequency of a particular species in different forests seems entirely unpredictable and is likely determined stochastically. This is similar to the concept that Shmida & Wilson (1985) have termed "ecological equivalency," i.e., the coexistence of species with effectively identical niche and habitat requirements for largely stochastic reasons. It is also the pattern that would be predicted by Hubbell's (1979; Hubbell & Foster, 1986) community drift theory. Indeed, Grubb (1986) generalized that the relatively sparse or rare species that of necessity constitute the bulk of the species of species-rich communities should interact so infrequently with each other that niche differentiation becomes largely irrelevant.

The same conclusion arises from the 0.1-ha samples. There are almost always a few very common species in any sample. One of these is usually much more common than all the others; at 11 sites the most common species was between two and seven times more common than the second most common species. Yet the only repeat of a "most dominant" species among 25 moist- and wet-forest sites is *Catoblastus velutinus*, shared between Rio Palenque and immediately adjacent Centinela in western Ecuador. For 12 dry-forest sites there was not a single repeat of a "most dominant" species.

Even if all 213 species that are dominant or subdominant in any of these samples (i.e., among the most common 5–10 species) are considered, only 38 are repeated in two or more different samples; ten of these repeated common species (13 if Rio Palenque and Centinela are considered part of the same site) are in repeat samples of the same forest. Thus, only 24 species are abundant at more than one site. One species, *Socratea exorrhiza*, is abundant at four sites, and three species—*Jessenia bataua*, *Arrabidaea oxycarpa*, and *Arrabidaea pubescens*—are abundant at three sites. Ten of the 24 species abundant at more than one site are shared between different dry forests, twelve are shared between different moist forests (typically between Central America and Amazonia), and one (*Mansoa verrucifera*) is abundant in one dry-forest and in one moist-forest site.

A major part of the debate on whether tropical-forest ecosystems are at equilibrium or nonequilibrium may be a by-product of the scale of a particular study or the focus of a particular author. The "rare" species that "random walk" through a 50-ha plot on Barro Colorado Island are mostly common understory or second growth species that would be regarded as permanent and continuous members of the more comprehensive moist-forest plant community that a biogeographer might define. The numerous microhabitat specialists suggested by a casual glance at a series of the Hubbell-Foster Barro Colorado Island distribution maps become nonspecialists if the relatively few individuals that occur away from a favored habitat are emphasized. I suspect that differences in taxonomic focus may also relate to the interpretational differences. Hubbell focused entirely on a particular combination of *species* in addressing the question of community equilibrium. My data suggest that while the species that make up different communities may be very inconstant from place to place, at the same time the different families (and perhaps genera) that contribute to community floristic diversity are very consistent. Perhaps the family is the basic unit on which selection for low population densities (and thus indirectly for high species richness) occurs. For example, many seed predators and leaf-eating insects are host-specific at the generic or familial, as well as the specific, level (Janzen, 1975, 1980, 1984). If family-specific predators and/or family-specific competition are added to the scenario of dynamic forests with some niche differentiation, an explanation pleasing to selectionists and nonselectionists alike could begin to take shape. As indicated in Table 1, the familial diversity of tropical moist and wet forests, unlike the species richness, is both high and remarkably constant. It is certainly within the realm of possibility that this is due to ca. 50 family-specific niches in a given forest, whereas the differing species richness of different forests could be largely stochastically generated by factors relating to higher turnover in the more species-rich sites on better soils and with higher productivities.

A different type of reconciliation, especially of the differences between upper Amazonian and Central American species richness, their causes, and the equilibrium status of the forests involved, might come from a different approach to the data. Hubbell & Foster (1986) emphasized that niche differentiation among Barro Colorado Island species seems to consist mostly of separation into about a dozen generalized multi-species guilds based on degree of shade tolerance and preference for edaphic or topographic microsites. Indeed they suggest that *lack* of niche differentiation might make possible the co-occurrence of many potential competitors which are forced to share the same generalized niche. But by and large the lowland forests of Central America are composed of the same species that in Amazonia would be regarded as the most widespread and weediest species of their respective families or genera (Gentry, 1982a, 1986c). A relatively depauperate Central American forest made up of species adapted for weedy generalized strategies might have little in common with an upper Amazonian forest composed mostly of narrow-habitat specialists. Given a few million more years of evolution, perhaps Central American forests might seem much closer to ecological equilibrium than they do today.

It is no accident that many tropical biologists who have considered the question of why tropical forests are so rich in plant species have greatly modified their original views, no matter on which side of the equilibrium/nonequilibrium question they began (Ashton, 1969 vs. 1984; Hubbell, 1979 vs. Hubbell & Foster, in press; Gentry, 1982b vs. 1982a and Gentry & Dodson, 1987b). We still know so little about tropical forests that generalizations elude us. Almost certainly there are elements of truth on both sides of the question. Quite possibly different forests and the different taxa that make them up will often prove to be doing things quite differently. Although we have not yet reached anything like a consensus on how different factors, or even which factors, interact to determine diversity, it seems abundantly clear from the data presented here that there are discernible and surely deterministic patterns in the species richness of different plant communities. I conclude that which families, how many species, and possibly what individual species make up a tropical plant community are to a large extent deterministic and predictable from simple environmental parameters; how common the species are and how they are put together into different communities may be completely random.

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PATTERNS OF VASCULAR PLANT DIVERSIFICATION IN THE FOSSIL RECORD: PROOF AND CONJECTURE

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ABSTRACT

An analysis of historical trends in diversification can suffer from a variety of defects and limitations. Among these is the potential failure of genus and family compilations to yield sufficient information on biological events, such as mass species extinctions. Another is the inadequacy of taxonomically based estimates of diversification to reveal patterns in changing community structure and morphology, which are important in evaluating adaptive evolution. These deficiencies are examined for the plant fossil record and by means of computer simulations of mass extinction events. Comparisons among species, genus, and family diversification patterns reveal qualitative differences sufficient to warrant caution in the use of taxonomic ranks above the species level. However, genus tabulations appear to be an adequate surrogate database for inferring patterns of species origination. Computer simulations revealing patterns of family extinctions may be inadequate for evaluating mass species extinction events since peaks in species and family extinctions rarely, if ever, coincide. A pluralistic approach to evaluating diversification is advocated involving the examination of biotic changes within assemblages and trends in morphological, anatomical, and reproductive evolution.

The notion of *diversity* in paleontology differs little from its use in ecological studies (Raup & Stanley, 1971; Whittaker, 1977). Diversity can be defined as the number of taxa in a community or as the synthetic characteristic of taxonomic richness and equitability, i.e., the relative evenness of the importance values of taxa within a sample (Lloyd & Ghelardi, 1964). However, the nature of the fossil record precludes a direct comparison of diversity between past and present biotas (Krassilov, 1975; Padian & Clemens, 1985). In ecology, taxonomic richness reflects the number of species in a sample of standard size, while measures of equitability involve some gauge of the abundance or productivity of one species divided by the importance values of all other species within the sample (Pielou, 1977). By contrast, fossil assemblages usually reflect time-averaged samples of a geographically ill-defined area. Further, terrestrial organisms are preserved where they were buried, not generally where they lived, and most often after significant periods of decomposition (cf. Niklas et al., 1980; Padian & Clemens, 1985). Frequently, transport to sites of burial results in the disarticulation of land plants and animals, and in deposition of parts in sedimentologically different microenvironments (cf. Kidwell, 1986). Consequently, there is great difficulty (1) in recognizing a species from its parts, (2) reassembling the components of a community, and thereby (3) arriving at a measure of diversity that is comparable to contemporary ecological studies (Raup, 1976, 1979; Niklas et al., 1980; Knoll, 1984; Benton, 1985).

Despite its limitations, the fossil record provides a potentially valuable perspective on a number of evolutionary issues. The paleontologist can compare patterns of diversification over billions of years of Earth's history and can track the origin, radiation, and eventual taxonomic diminution of organisms that no longer exist or are rare in present biotas. Although the nature of paleontological data defines the temporal and taxonomic resolution with which evolutionary issues can be ad-

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dressed, recognition of large-scale patterns that develop, change, and disappear over long intervals of time confers a perspective that augments neontological studies.

This paper is concerned with changes in tracheophyte diversity over the last 400 million years of the Phanerozoic. The fossil record of terrestrial vascular plants is reviewed and discussed within the context of large-scale patterns in composition and taxonomic richness of assemblages through time. The bulk of the data to be discussed has been presented elsewhere in a variety of forms (Niklas et al., 1980, 1985; Tiffney, 1981; Knoll, 1984, 1986; Knoll et al., 1984). Consequently, many facets of tracheophyte diversification will be referenced but not discussed in detail. The principal focus of this paper will be on the limitations of the data and on the qualitative statements about plant evolution that can be made from an inherently imperfect fossil record.

LARGE-SCALE CHANGES AND TAXONOMIC LEVEL

The species is the taxonomic level of choice for determining changes in diversity through geologic time. However, species-level compilations present a variety of procedural difficulties, the most significant of which involve sampling errors (Signor & Lipps, 1982; see also Pease, 1985). Comparisons of global patterns in species diversification with higher taxonomic levels are desirable, because they provide insights into the information to be gained or lost by each type of compilation.

The upper panel of Figure 1 shows a plot of the total species-richness of vascular plants through the Phanerozoic. The data are taken from primary paleobotanical citations tabulated by Niklas et al. (1985) and are segregated into three major categories of tracheophytes: pteridophytes, gymnosperms, and angiosperms. The plot shows a Silurian to mid-Devonian radiation of primitive pteridophytes followed by a Carboniferous proliferation of more advanced or derived pteridophytes and early gymnosperms. A Permo-Triassic decrease in overall diversity precedes a more or less constant level of species number until the middle of the Cretaceous when angiosperms begin to radiate. Diversity of pteridophytes decreased during the Permo-Triassic and reached a relatively constant level throughout much of the Mesozoic and Cenozoic. With the advent and proliferation of angiosperms, the number of gymnosperm species decreased significantly through much of the late Cenozoic.

The lower panel in Figure 1 shows large-scale temporal patterns in diversity at the family level. These data (from Knoll, 1984) were compiled independently from the data on species from Niklas et al. (1980). Data for pteridophytes and gymnosperms are not segregated, thus providing for direct comparisons between species- and family-level diversity for nonangiosperms and for angiosperms. Differences in the diversity between Devonian and Carboniferous families are less pronounced than those seen in the top panel. As Knoll (1984) noted, the number of species in late Paleozoic families is higher than in early Paleozoic families, presumably due to the appearance of more complex or numerous morphological and anatomical features upon which species can be based. Ordinal changes in plant diversity compiled by Knoll (1984) conform in large measure to the trends seen in the family diversity plot.

Despite the differences between species and family diversity, it is evident that the number of vascular plant taxa increased throughout much of the Paleozoic and has accelerated during the Cenozoic with the advent of angiospermy.

The value of comparing diversity among different taxonomic levels can be further illustrated by examining data for a specific group rather than the entire domain of tracheophytes. The selected group ought to have a fossil history that spans the Phanerozoic and thus obviates any idiosyncratic feature of a geologic period. Three major groups of vascular plants have a virtually continuous fossil record since the Upper Devonian: lycopods, sphenopsids, and ferns (Stewart, 1983). Of these three groups, the ferns are the most abundant through time. Hence, they

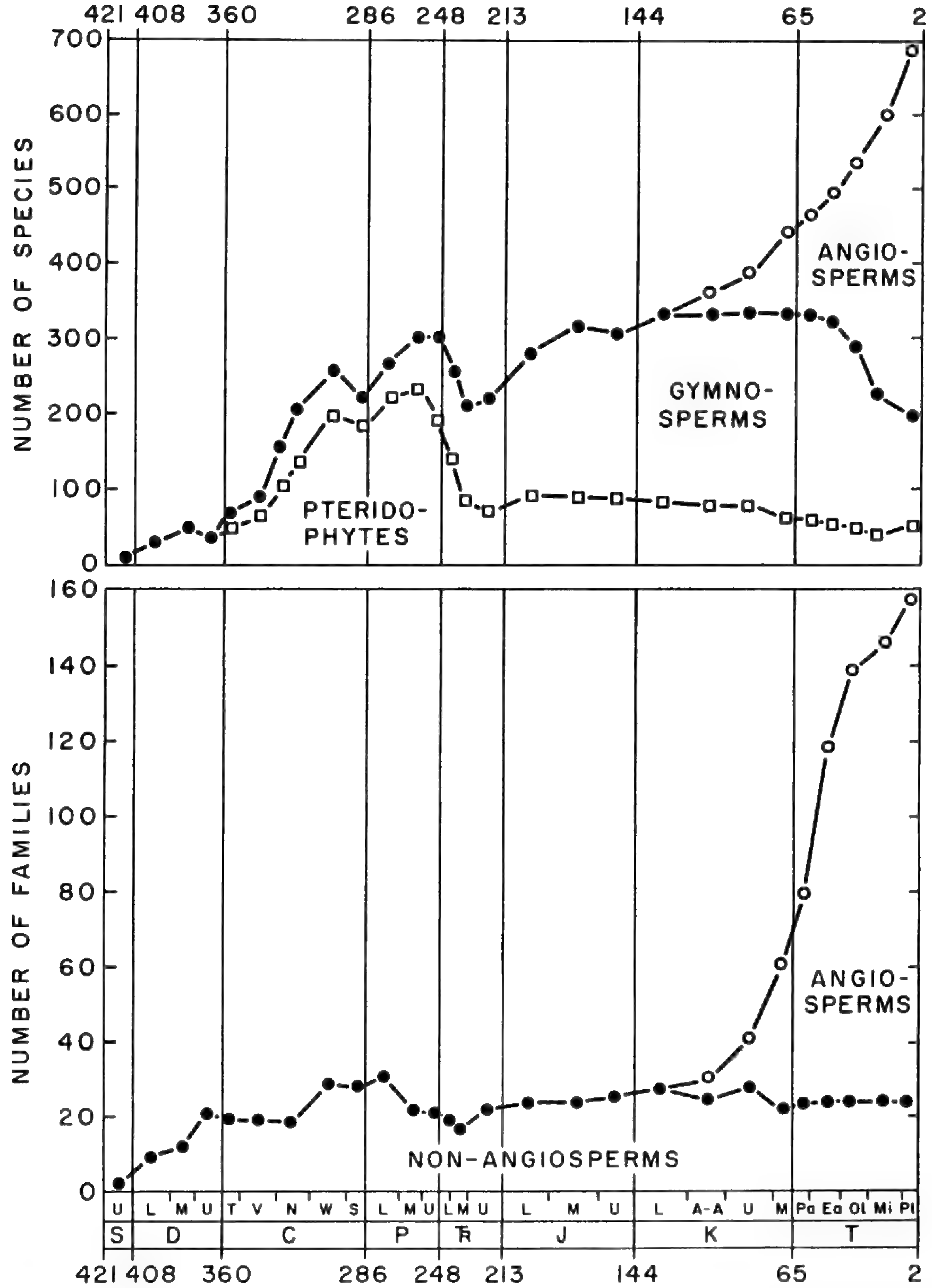

FIGURE 1. *Large-scale changes in diversity of tracheophytes at the species- and family-level (upper and lower panels, respectively) recorded per epoch through the Phanerozoic. Species global diversity data were taken from Niklas et al. (1980, 1985); family diversity data are redrawn from Knoll (1984). The time-scale is that of Harland et al. (1982): For the Carboniferous (C), T = Tournaisian, V = Visean, N = Namurian, W = Westphalian, S = Stephanian; for the Cretaceous (K), L = Berriasian-Barremian, A-A = Aptian-Albian, U = Cenomanian-Campanian, and M = Maastrichtian.*

are convenient for comparing differences in diversity based on compilations of species, genera, and families. The most complete treatment of fossil ferns is that of Boureau (1970). Unfortunately, this does not reflect recent advances in taxonomy nor does it present a critical evaluation of stratigraphic occurrences (see for example Phillips, 1974; Stewart, 1983). Nonetheless, the data contained within this volume are useful because they are easily accessible and reflect the state of paleobotanical knowledge as compiled in a single reference. Accordingly, the data for fossil ferns are dealt with here solely for the

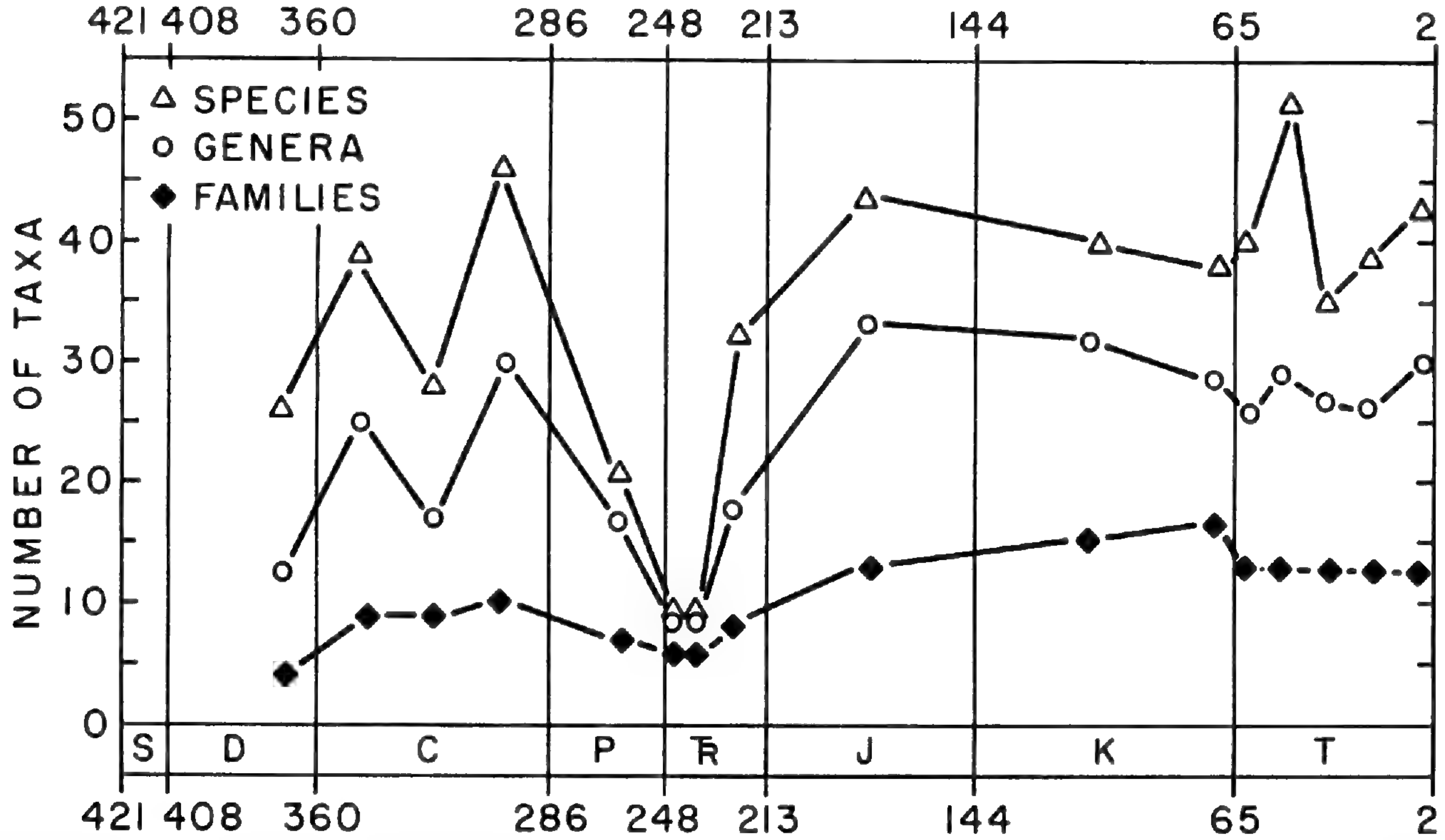

FIGURE 2. *Taxonomic diversification of ferns based on data compiled by Boureau (1970). Stratigraphic resolution of species, genus, and family occurrences from the source is coarser than that of species diversity plotted in Figure 1. Consequently, the time-scale of this figure is less precise than desirable.*

purpose of comparing the qualitative diversity measurements made at different taxonomic levels within a major plant group.

Figure 2 shows the total diversity of fossil ferns based on species, genus, and family compilations. Since the citations given in the data sets are rarely more specific with regard to stratigraphy than lower or upper, middle, and lower divisions of each period, the resolution of the geologic scale is necessarily more crude than desirable and not directly comparable to those given in Figure 1.

Peaks in the species diversity of ferns occur in the Lower and Upper Carboniferous, the Middle Jurassic, and in the Eocene. The maximum number of fossil fern species is recorded in the Eocene. Species numbers significantly decrease in the Middle Carboniferous, Lower and Middle Triassic, and in the Oligocene. Generic tabulations reveal similar peaks and valleys in diversity as those seen in the species data; however, the overall diversity maximum in the Lower Eocene is less pronounced in the generic data set than in the species compilation. Family diversification is muted throughout much of the Phanerozoic. Nonetheless, the Triassic decrease in diversity (from ten families in the Upper Carboniferous to six families in the Middle Triassic) occurs in both the species and generic plots.

What then is the appropriate taxonomic level for gauging long-term patterns in diversification? Large-scale changes in tracheophyte diversification at the species and family levels are poorly correlated (Fig. 1). This is not surprising given the diversity of lineages that comprise the tracheophytes. The diversification of tracheophyte species may show episodes of increase due to the radiation of a few families even if the majority of the remaining families dwindle in species numbers or go to extinction. Even for a particular group of plants, such as the ferns, there appears to be only a loose correlation between changes over geologic time in species or genus and family numbers, presumably for much the same reason—"taxonomic stacking."

The family may not be the appropriate taxonomic level for analysis for many types of evolutionary questions, as, for example, the identification of mass-extinction events (see next section). A family is eliminated from the fossil record with the extinction of its last surviving species. This terminal extinction event may occur well after the major period of species-attrition within a family. Thus, there is a double-edged effect in the use of higher taxa for determining unusual perturbations in overall diversity. A "mass-extinction event" may be due to the geologically synchronous elimination of the relic species of numerous, species-depauperate families. On the other hand, many species-rich families could undergo a geologically sudden and severe depauperation in species without the total disappearance of these families from the fossil record. A dramatic reduction in taxonomic diversity below the family level would reflect a significant event in the history of life that could go undetected in family tabulations of diversity. Similar arguments could be made concerning the effectiveness of genus tabulations in detecting intense episodes of species extinction.

Species compilations comprise the most biologically relevant database for paleontology. However, a paleospecies is not operationally defined or identified at the same level of taxonomic scrutiny or with the same body of information and experimental format as a species of living organism. This severely limits the application of conventional species concepts to fossil material.

Recognition of a fossil plant species is perhaps even more difficult than that of a fossil animal species. Plants are phenotypically more plastic than many major groups of animals (Cahn & Harper, 1976; Harper & Bell, 1979; Harper, 1985; White, 1979). The recognition of ecotypes or taxonomic varieties of living plants is notoriously difficult and requires detailed transplant experiments, cytological and electrophoretic examination, and field observations of population dynamics across environmental gradients (Harper, 1977, and references therein). Fossil plants are most frequently found as disarticulated organs which, for many plants, have been previously assigned to separate taxa (Knoll & Rothwell, 1981; Stewart, 1983). Only when found in organic connection can organ genera be placed in synonymy. Consequently, the recognition of genus as an "organ" can only be done on an ad hoc basis. Since whole plant reconstructions are still rare in the paleobotanical literature, the inflation of species richness due to the effects of dealing with fragmented parts is a serious limitation to assessing the true taxonomic diversity in a fossil assemblage.

Perhaps the only reasonable solution to the choice of taxonomic level is to deal with species and genus tabulations for each family. Correlations in the patterns of diversification among all three taxonomic levels for particular groups of plants could then be used to estimate long-term trends or geologically sudden changes in taxonomic richness. As yet this suggested type of multiple-level analysis has not been undertaken for any group of organisms.

MASS EXTINCTIONS: AN ARTIFACT OF HIERARCHY?

Measurements of diversity based on taxa above the species level have been used to determine large-scale evolutionary patterns. Perhaps the best example of this approach comes from the use of family-level data on marine animals to determine major diversification and extinction patterns (Sepkoski, 1980, 1981a, b, 1984; Raup & Sepkoski, 1982, 1984). Sepkoski (1981a, b, 1984, and elsewhere) has argued that family data represent a good proxy for estimating diversity of species (cf. Sepkoski et al., 1981). In addition, comprehensive data with good stratigraphic resolution do not exist for marine animal species or even genera (e.g., Sepkoski, 1984: 247–248). However, as will be shown in this section, the behavior of families as evolutionary "units," and in particular the pattern of family extinction rates, is dependent upon the frequency distribution of species within families.

Raup & Sepkoski (1982, 1984) identified five statistically significant "mass extinction" events in the Phanerozoic record of marine animal families: late Ordovician (Ashgillian), late Devonian (Frasnian), late Permian (Guadalupian-Dzhulfian), late Triassic (Norian), and late Cretaceous (Maastrichtian). Although the magnitudes of species-extinctions are hard to

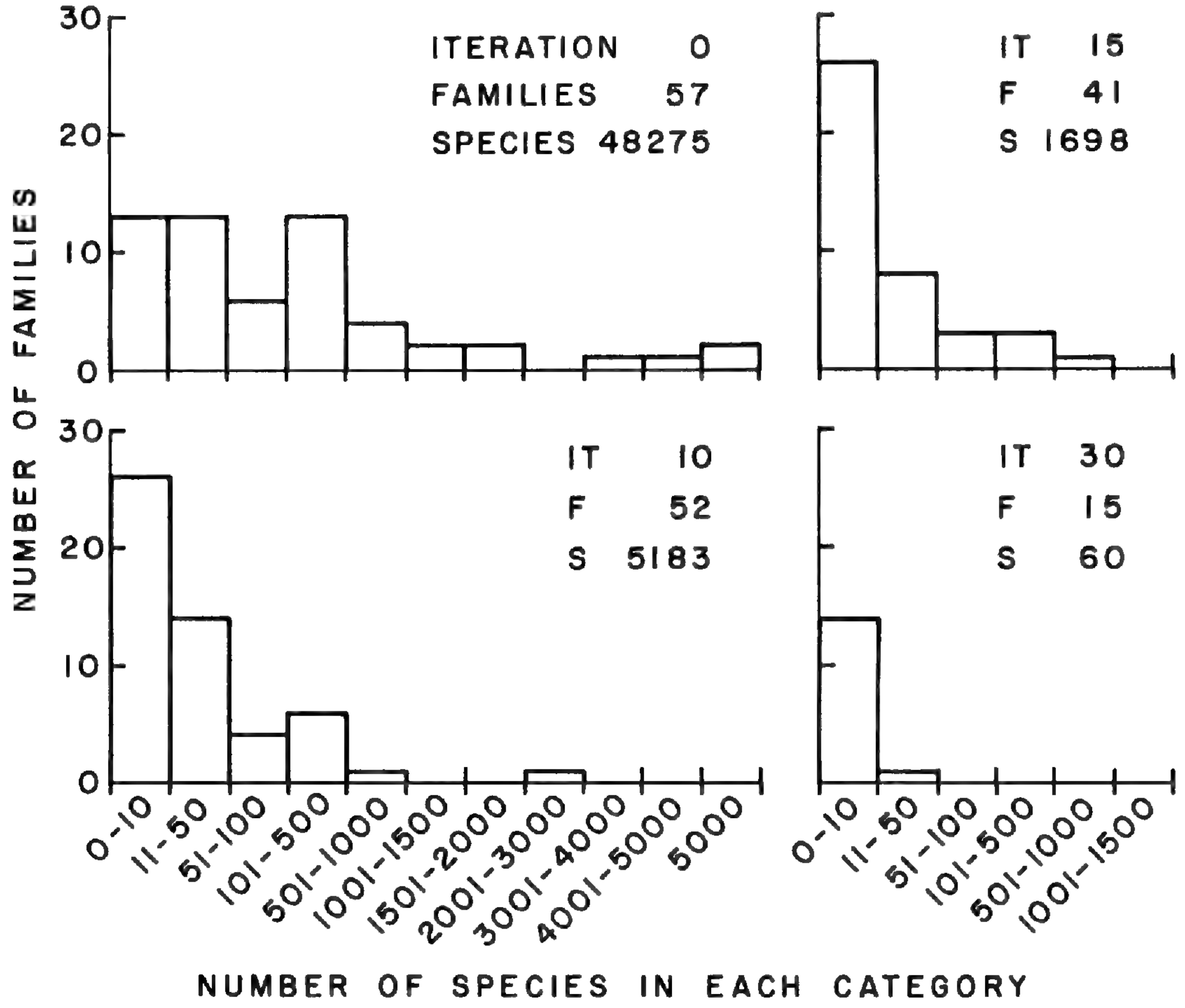

FIGURE 3. *Changes in the species frequency distribution of monocotyledon families predicted from a computer simulation of random species extinction. Data from Cronquist (1968, 1981) were used to construct an initial histogram (= iteration 0) representing 57 families and 48,275 species. Random species extinction (20% reduction of species number every iteration) results in a "mass species-extinction event" at iteration 1. Sequential extinction events (which withdraw fewer and fewer absolute numbers of species with each successive iteration) result in shifts of the histogram (cf. Figs. 5, 6).*

estimate from the family data, Raup (1979) suggested that the late Permian "mass extinction" event involved a reduction of as many as 96% of marine animal species. Significantly, Raup's regression of family background extinction rates against time yields a negative slope (a long-term decline in family extinction rates), which Raup & Sepkoski (1982) interpreted as reflecting a "fitness-optimization" in which surviving marine taxa become more resistant to extinction through geologic time (but see Kitchell & Pena, 1984). More recently, Sepkoski (1984) modeled the total rate of background extinction (with constant extinction parameters) and suggested that the decline in rates resulted from differential expansion and replacement of evolutionary faunas. Sepkoski's model involves lag phases in the evolutionary behavior of clades within each evolutionary fauna.

A continuous and constant rate of species extinction can produce discontinuous and abrupt increases in rates of family extinction provided blocks of species go to extinction. This can be illustrated by modeling family extinction rates based on the species frequency distributions of angiosperms.

Data on the approximate numbers of species per family in the major groups of angiosperms are provided by Cronquist (1968, 1981). Histograms of the species frequency distributions in the families of monocotyledons and dicotyledons are shown in Figures 3 and 4. In both cases, the majority of families have fewer than 500 species per family; however, both monocots and dicots have families with species numbers in excess of 5,000. (The Compositae with 19,000 species is not shown in the data set for dicotyledons.) These distributions are similar to those constructed by Clayton (1972, 1974) for the generic frequency distribution in angiosperm families, which conforms to a

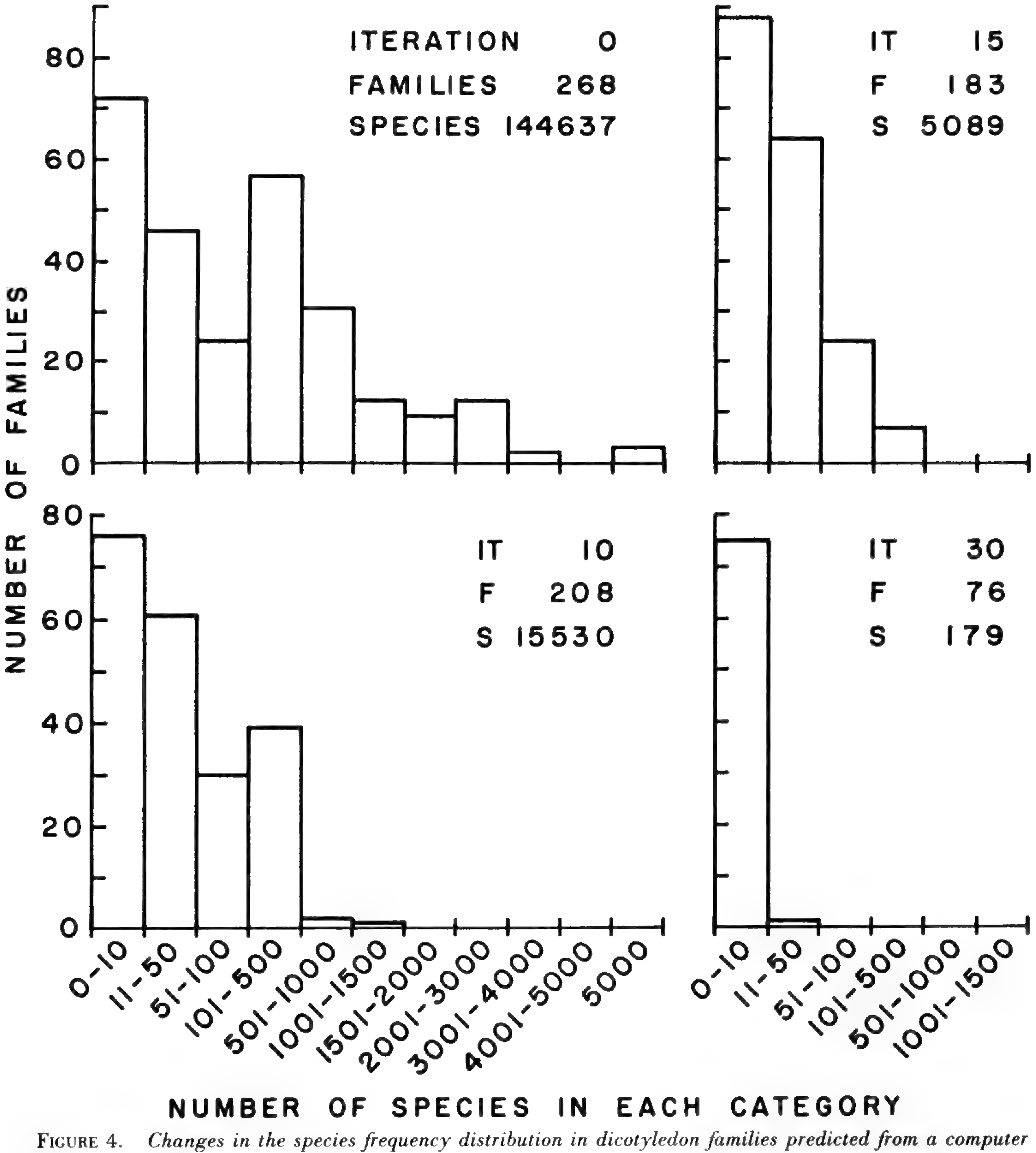

FIGURE 4. *Changes in the species frequency distribution in dicotyledon families predicted from a computer simulation of random species extinction. Data from Cronquist (1968) were used to construct the initial histogram (= iteration 0) representing 268 dicot families and 144,637 species (the Compositae are not included in this simulation). Random species extinction (20% reduction in number of species every iteration) results in a "mass species-extinction event" at iteration 1. Sequential extinction events result in the reduction of dicotyledon families (cf. Figs. 5, 6).*

logarithmic distribution. Consequently, the following arguments against the use of family compilations for determining mass extinction events can be extended to the use of genus tabulations.

A computer simulation technique was devised to track the family extinction rate as a constant percentage of species is reiteratively removed from each clade. The species undergoing extinction were selected randomly among all families by means of the standard linear congruent method, which does not bias

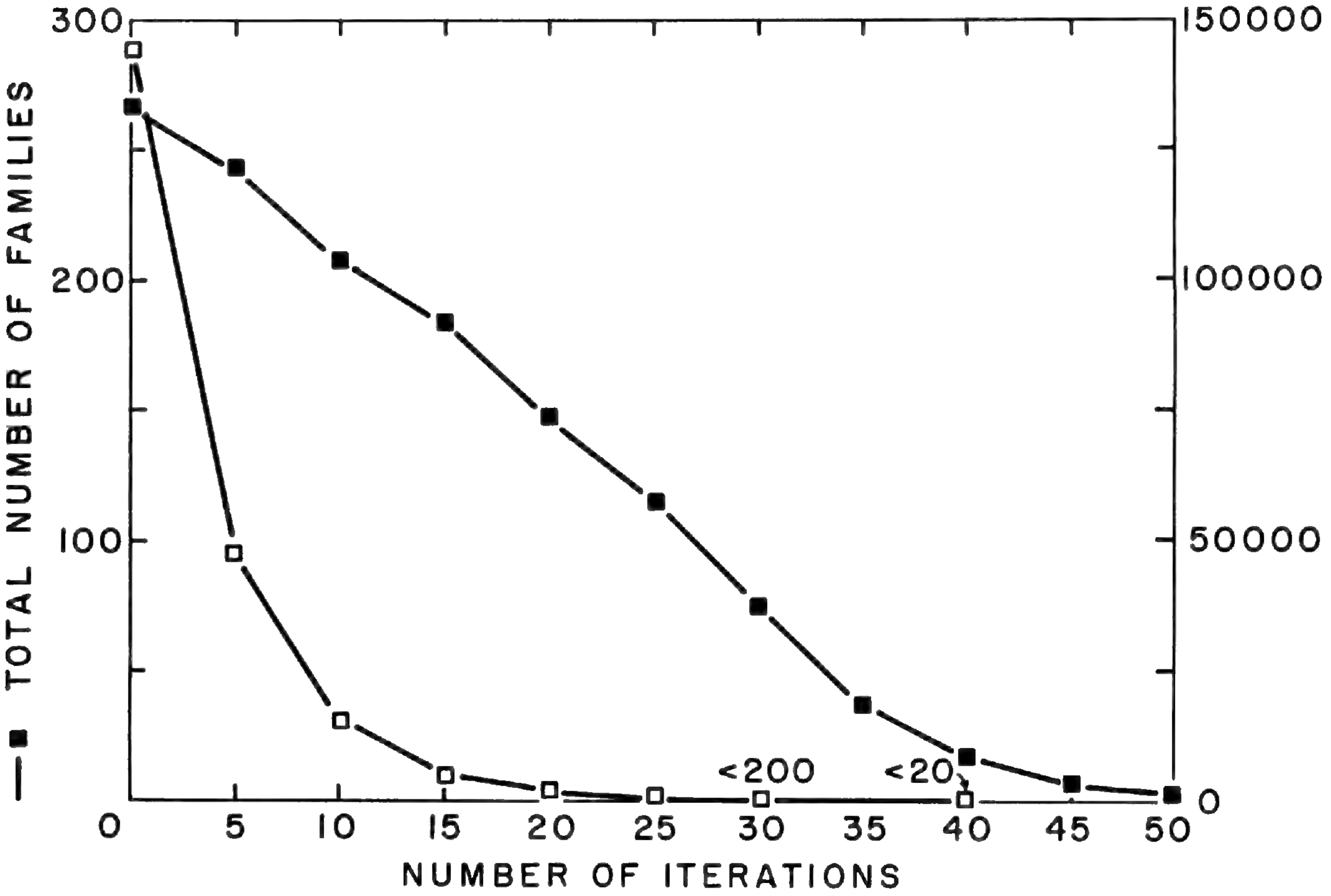

FIGURE 5. *Changes in the total number of dicotyledon species and families over 50 iterations of species extinction (20% reduction in number of species every iteration). Numbers of species decline exponentially; numbers of families decline in as near linear function until the 35th iteration.*

the probability of species extinction toward large or small families. Consequently, all species have an equal probability of going to extinction. If a constant percentage of species goes to extinction, then a "mass-species" extinction event occurs on the first iterative cycle of each simulation, i.e., each simulation starts out with the maximum number of species; therefore, the first cadre of species to go to extinction is the largest in absolute number. Successive extinction events result in a progressive decline in the absolute number of species undergoing extinction. The use of a constant percentage extinction rate provides an opportunity to look for possible correlations between mass-species and mass-family extinction events. Simulations in which a constant number of species go extinct ($ds/dt = k$) rather than a constant percentage of species yield similar patterns of family extinction but require extended reiterative cycles of species extinction. Each simulation based on a constant-percentage rate of species extinction was run for 50 reiterative cycles. At this point most families (99%) became extinct.

The consequences of successive iterative species extinctions on the frequency distributions of monocot and dicot families is shown in Figures 3–5. As expected, each histogram gradually shifts toward the left (= numerous species-poor families). Figure 5 shows that species numbers exponentially decrease and asymptotically approach the x-axis (which is a very crude analogue to time, since there is no a priori way to relate an iteration of species extinction to an interval of geologic time); decrease in the number of families with successive iterative species extinctions is nearly linear. Various species-extinction rates ranging from 10% to 50% yield comparable patterns. Significantly, however, total family-extinction rates (number of families going to extinction per iteration) are not constant. Comparisons between the dicot and monocot simulations are shown in Figure 6. The total family-extinction rate, E_F, for dicots increases

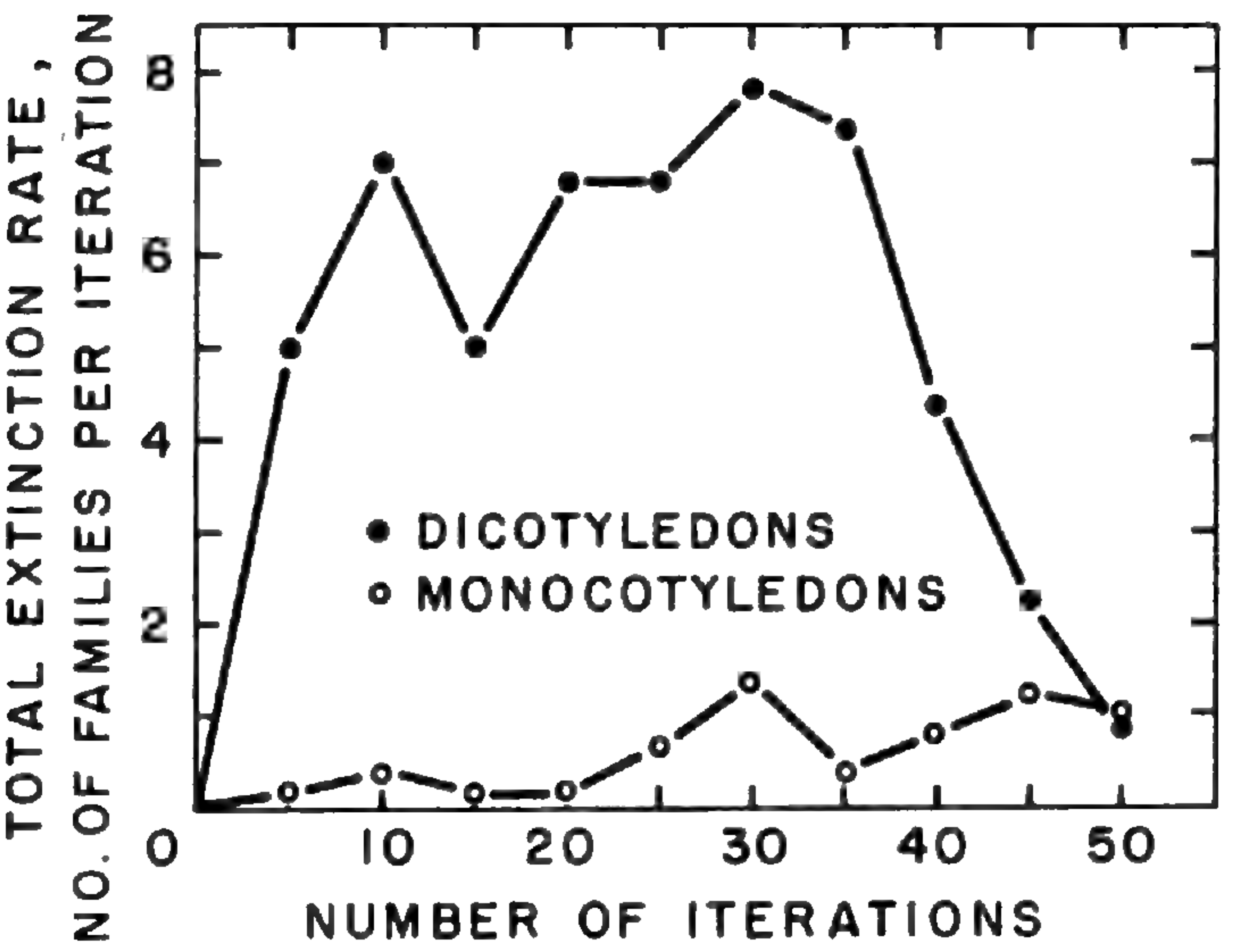

FIGURE 6. *Patterns of the total extinction rate of dicotyledon and monocotyledon families resulting from a 20% species-extinction rate. These values were computed on the basis of data shown in Figure 5.*

sharply to 7.0 (after 10 iterations), decreases to 5.0 (after 15 iterations), and then plateaus before it sharply declines after 35 iterations. A pattern that is qualitatively and quantitatively dissimilar to dicots is observed for the monocot simulation, e.g., E_F never exceeds 1.4 and increases only slightly over many iterations.

Differences between the patterns of family-extinction rates for monocots and dicots are due solely to differences in their respective initial species frequency distribution in families. To test the sensitivity of patterns of family-extinction rates to the frequency distribution of species among families, three artificial distributions were created: (1) one in which the majority of families contains many species (skewed to the right); (2) a distribution having an equal number of families in each category of species-richness (= horizontal distribution); and (3) one in which the majority of families contains few species (= the frequency distribution is skewed to the left). In each case, the total number of families was held constant (N = 111). Owing to the nature of the distributive functions, the total numbers of species and families in each distribution cannot be equal in each of the three cases. However, species-extinction rates are based on percentages, and family-extinction rates are the subject of concern. Therefore, the inequality of species numbers in the three frequency distributions does not appreciably influence comparisons among the three trends in family extinctions.

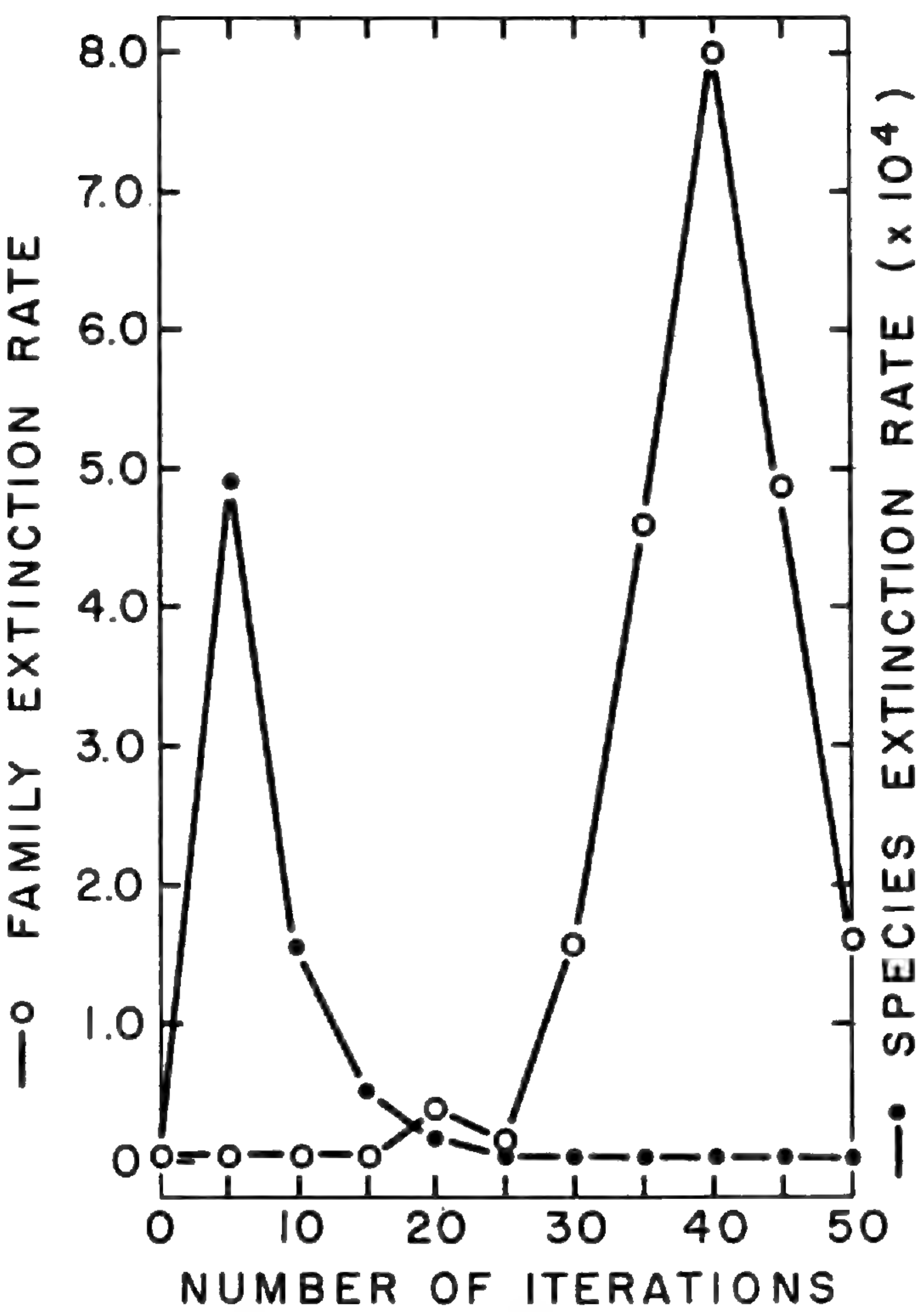

FIGURE 7. *Patterns of the total extinction rate computed for an artificially constructed species frequency distribution in which many families are species-rich and only a few families are species-poor. The total number of families in this simulation is 111; the total number of species is 360,871. A "mass species-extinction event" is apparent by the fifth iteration of 20% species extinction. The largest absolute number of species to go extinct occurs at the first iteration. However, data are graphed showing the summation of extinction events for intervals of five iterations. This is necessary because family extinction rates per iteration are very low. A "mass family-extinction event" is simulated at the 40th iteration.*

Figures 7–9 show the resulting patterns of total family-extinction rates for the three artificially created frequency distributions. A greater resolution of these peaks (in which family-extinction events are plotted every iteration) is possible. However, the number of families eliminated per iteration is very small (1–3 families); therefore, the magnitude of peaks in family-extinction rates would be small (1–3 families per iteration). By calculating family-extinction rates every five iterations,

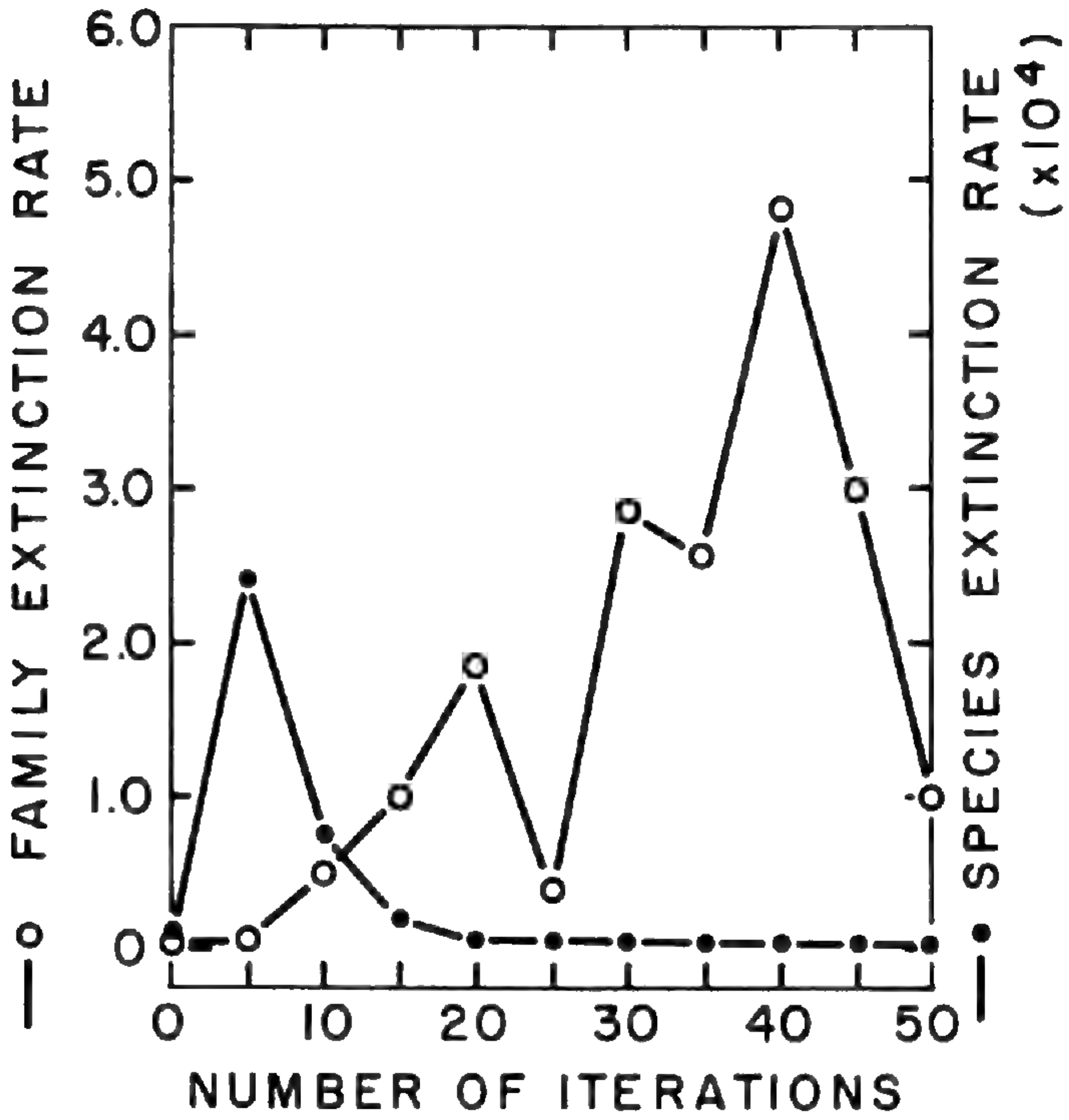

FIGURE 8. *Patterns of the total extinction rate computed for an artificially constructed species frequency distribution in which all categories of species richness are occupied by equivalent numbers of families (N = 111). The total number of species is 176,600. This species frequency distribution produces a "spiked" pattern of total family-extinction rate with a 20% species-extinction rate.*

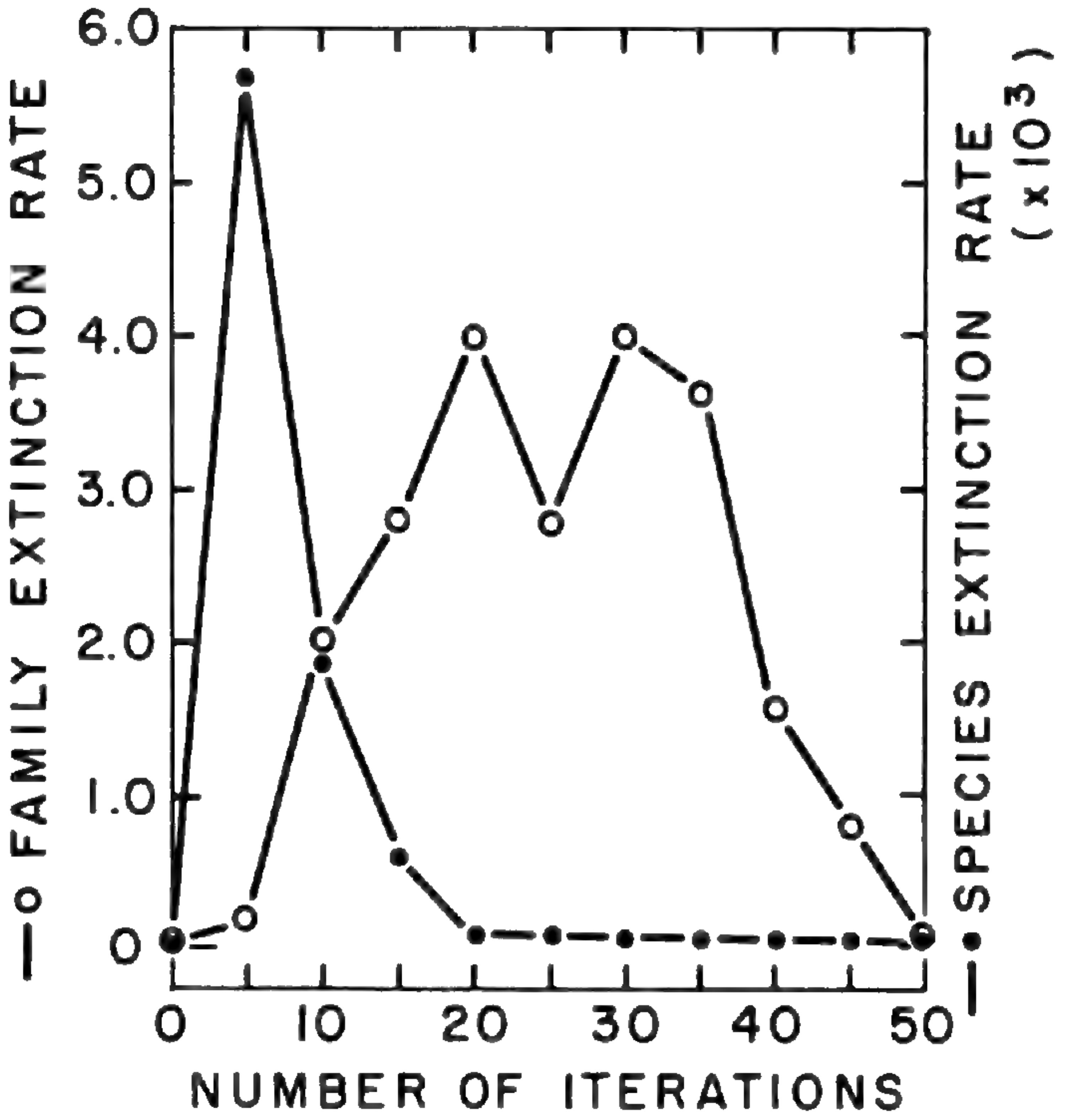

FIGURE 9. *Patterns of the total extinction rate computed for a species frequency distribution with many species-poor families and a few species-rich families (N = 111). A total of 43,070 species are represented in this artificially created distribution.*

the pattern of family extinctions is emphasized. The distribution skewed to the right (= most families with many species) shows a pattern vaguely reminiscent of a "mass extinction," in which the rate of family extinction varies little about a mean value of 0.12 through 25 iterations and then sharply increases to 8.0 after 40 iterations before declining to 1.6 at 50 iterations (Fig. 7). The pattern of extinction occurring up to 25 iterations results from the gradual and random extinction of a few species-depauperate families. With each successive iteration, however, species-rich families are reduced in numbers of species but, due to their large initial sizes, fail to go to extinction. After 25 iterations the "species buffering" experienced by these families is eroded and they become sufficiently depleted such that they collectively undergo a "mass family extinction." Only 2.7% of the total number of families are eliminated by the 25th iteration despite the extinction of over 99.5% of the original number of species. If this simulation reflected a real case from the fossil record, an abrupt increase in the rate of family extinction would not coincide with a mass species-extinction event: by the 15th iteration, over 96% of all species are eliminated, despite the survival of all families.

Similar incongruities between the extent to which family extinctions reflect or coincide with species extinctions are seen in the other two simulations. An even distribution in the number of families containing the various categories of species numbers produces an ascending but spiked pattern of family-extinction rates (Fig. 8). A distribution skewed toward many species-poor families yields a broad, irregularly plateaued pattern of family-extinction rates, which is somewhat similar to the pattern generated from the dicot data set (Fig. 9). These two frequency distributions are clearly artificial since neither is encountered in real species, genus, or family tabulations. Nonetheless, they are of interest because they indicate that no frequency distribution produces a correlation between species- and family-extinction patterns.

Computer simulations do not indicate that family-level compilations are necessarily inadequate to gauge "mass extinction" events. Clearly, there is no reason to assume that species extinctions are randomly distributed among all families. However, (1) "spikes" in the regression of family-extinction rates against geologic time can reflect the synchronous demise of many species-poor families belonging to a once robust taxonomic (or grade-level) cohort; (2) patterns in family-extinction rates are dependent upon the frequency distribution of species among the families considered; (3) mass species-extinction and mass family-extinction events may not coincide; indeed, the vast majority of species within a clade may disappear well before the event is noticeable at the family level (as in the case of *Ginkgo*); and (4) analyses of mass extinctions require information on the changing patterns of species distributions within suprageneric taxa. Similar arguments can be made for the use of generic tabulations to detect mass-extinction events (cf. Raup & Sepkoski, 1986; see also Hoffman, 1986). Similarly, diversity measured solely on the basis of species numbers ignores the relative abundance of individuals within taxa—an essential feature to understanding the ecological significance of an extinction event. The "mass extinction" of many species that contribute only a fraction of the biomass to a biota has a decidedly different effect than one involving species contributing many individuals to a biota.

NONTAXONOMIC MEASUREMENTS OF DIVERSITY

A treatment of diversity strictly from the perspective of changes in species numbers ignores many significant aspects of plant evolution. Qualitative changes in reproductive and vegetative morphology and quantitative changes in the numbers of individuals within a taxon are not reflected in patterns of changing species numbers. For example, the number of gymnosperm species during the Jurassic and Cretaceous remained relatively constant despite considerable taxonomic turnover within various lineages and significant alterations in morphology and anatomy of representative species. *Ginkgo biloba*, as a species, occurs from the Mesozoic to the present, yet the number of individuals significantly declined during the Cenozoic. Clearly, evaluations of diversity based on something other than species numbers are important in evaluating adaptive evolution and changes in community structure (Spicer & Hill, 1979; Phillips & DiMichele, 1981; DiMichele et al., 1985; Fisher, 1985).

Another reason for evaluating nontaxonomic measurements of diversity is that inferences on genomic (hence speciation) rates of evolution based on rates of morphological evolution may be faulty. Schopf et al. (1975) argued that differences in the number of species among lineages can be the consequence of dealing with taxa that differ in their degree of morphological complexity. If fossil species truly represent genomically distinct entities (sensu the biological species concept), then rates of morphological and genomic evolution would be highly correlated. These authors, however, assert that this direct correspondence can never be proven. Therefore, it is advisable to look at rates of morphological evolution and rates of paleospecies origination separately.

Fortunately, changes in species numbers and within-assemblage species composition, and morphological patterns of long-term evolution can be dealt with separately to visualize tracheophyte diversification. As in most cases with the use of paleontological data, however, quantitative analyses can only be used to construct qualitative comparisons or generalizations. Among these guarded generalizations are:

(1) The taxonomic composition of fossil plant assemblages is rarely, if ever, stable. It is altered most significantly by the substitution of taxa within related lineages during periods of relatively constant overall species numbers. These "intrataxonomic" alterations occur over extended geological time-scales and are generally discernable among lineages that share a common mode of sexual reproduction (Knoll, 1986).

TABLE 1. *Mean species numbers, x̄, of vascular plants in fossil assemblages for representative intervals.*

	Niklas et al., 1980 $\bar{x}$ (number of floras)	Knoll, 1986 $\bar{x}$ (number of floras)
Early Devonian	5 (7)	4.0 (8)
Late Devonian	8.2 (9)	10.7 (7)
Early Mississippian	10 (7)	11.9 (15)
Late Mississippian	22.5 (2)	23.3 (8)
Late Jurassic	27.5 (15)	30.8 (6)
Early Cretaceous	21.5 (15)	30.2 (22)
Late Cretaceous	43 (7)	54.4 (17)

(2) Global species numbers generally increase most significantly with the radiation of plants sharing a novel mode of sexual reproduction (Niklas et al., 1980, 1985).

(3) At least within the temporal resolution permitted by most paleontological studies, changes in taxonomic composition and large-scale species numbers are tightly linked to changes in vegetative morphology and the appearance of diverse growth habits (Niklas, 1987).

(4) The appearance of new reproductive modes and diverse morphologies within a clade or cohort of clades may not necessarily result in the ecological displacement of previously existing species. Throughout much of the Paleozoic and Mesozoic, taxonomic radiations are associated with the exploitation of environments not previously occupied (Tiffney, 1981; Knoll, 1986).

(5) The competitive advantages conferred upon a taxon by novel reproductive or vegetative capabilities are most pronounced early during its taxonomic radiation (Knoll et al., 1984; Knoll & Niklas, 1987).

Each of these generalities is not without exception or debatable inference, since each is based on a limited number of studies. It is more instructive to review the nature of the data upon which these statements are based and to examine their deficiencies.

To date, only two studies have examined changes in the mean species numbers of plants throughout the Phanerozoic (Niklas et al., 1980; Knoll, 1986). In both cases, fossil assemblages (= "floras") were selected from similar depositional environments so as to minimize the differential effects of sedimentological factors on preservation. The floras were selected from what were inferred to be warm climates. Comparison between the mean species numbers per flora for representative time periods is given in Table 1. Despite differences in the sources of data, both studies reported remarkably similar trends. Mean species numbers within floras have increased significantly at least twice during the last 420 million years—doubling between Late Devonian and Late Mississippian floras, and once again between Early and Late Cretaceous floras. (The lack of an objective baseline comparison for the Late Devonian floras precludes evaluation of the data from Early and Late Devonian floras.)

Each of the two increases in mean species number coincides with an increase in overall species diversity (Niklas et al., 1980, 1985). This is to be expected, since the latter incorporates data used to compile within-floras species numbers. However, each of the two increases in mean species numbers correlates with major transitions in the taxonomic composition of floras. This is shown elegantly in a study by Knoll (1986), who presented a unique analysis of the taxonomic composition of floras throughout the Phanerozoic. Figure 10 (redrawn from Knoll's study) shows two significant resortings of suprageneric groups within floras. One occurs with the advent of seed plants in the Late Devonian and Mississippian; another reflects the radiation of flowering plants in the Cretaceous. If the various plant lineages within Knoll's data set are grouped according to their principal modes of reproduction, then the changes in taxonomic composition are seen more clearly (Fig. 11). As in the plots of large-scale species numbers (Fig. 1), the early Paleozoic floras dominated by pteridophytes are replaced by gymnosperm-dominated Mesozoic floras, which in turn are replaced by floras dominated by angiosperms.

However, Figure 11 masks the taxonomic restructuring in floras that occurs within each category of reproductive mode. The expansion of gymnosperm species in Mesozoic floras occurs at the expense of pteridophytes made up of lineages that did not fall off at equal rates. In general, the numbers of fern species are much less affected than those of lycopods and sphenopsids. Similarly, gymnosperm lineages undergo a more or less continuous intrataxonomic restructuring.

The evolutionary appearance of novel modes of reproduction, for example, seeds and flowers, is often associated with alterations in growth habit (Tiffney, 1981; Tiffney & Niklas, 1985). The number of plant families characterized by cryptogamic (pteridophytes) and phanerogamic reproduction (gymnosperms and angiosperms), as well as the number of families with principally nonarborescent and arborescent growth forms, are plotted through time in Figure 12. In this figure a number of "cross-overs" are seen which can be related to changes in taxonomic composition. For example, during the Carboniferous and Permian, arborescence rises even though cryptogamic reproduction remains more common. Although seed plant species dominate Mesozoic floras, nonarborescence is more common than arborescence during the Jurassic. During the Cretaceous, the number of phanerogamic plant families gradually increases, until by the Late Cretaceous, arborescent/phanerogamic-dominated floras which persist through the Tertiary are established. The Permo-Triassic is a period of considerable restructuring in both the principal modes of reproduction and growth habits. Before the Triassic, arborescent cryptogamic families are dominant, while during the Triassic nonarborescent phanerogamic families are common.

From a much more comprehensive analysis, Tiffney & Niklas (1985) concluded that the history of clonality in land plants can be segregated into three stages: (1) *Silurian to lower Carboniferous* during which clonal lineages dominated, but in which arborescence appeared as a vegetative correlate with heterospory or the seed habit; (2) *Permo-Triassic to Cretaceous*, in which families of arborescent gymnosperms gradually increased and gained numerical dominance over families of arborescent and nonarborescent pteridophytes; and (3) *Cretaceous to present*, which marks the combination of rhizomatous growth and the seed habit (herbaceous angiosperms) which became increasingly more important in the later Tertiary and Quaternary.

Unfortunately these analyses are based on familial data (whole-plant reconstructions are too few to determine large-scale patterns in the evolution of tracheophyte growth habits). Accordingly they provide few insights into species patterns of growth habit or values of relative abundance. Although nonarborescent families dominate much of the early and middle Mesozoic, the abundance of arborescent gymnosperm species in these floras is much higher than that of pteridophytes (Fig. 10). Clearly the family-diversity plots shown in Figure 12 are not reflective of community structure.

As Schopf et al. (1975) pointed out, it is possible that paleontologists fail to recognize the true diversity of morphologically simple organisms and overestimate the diversity of morphologically complex organisms. Thus, periods of rapid taxonomic diversification may be inherently related to (and possibly the product of) episodes of rapid morphological diversification. New vegetative and reproductive features provide the potential to discriminate new phenetic taxa (= paleospecies). As the number of potential taxonomic characters increases, the number of possible permutations of characters increases exponentially. There is little agreement among specialists as to which feature(s) (anatomy, morphology, reproduction, or even geologic age) contribute(s) to identification of a new species. Certainly among disparate taxonomic groups of plants, species are recognized on often very divergent categories of features: more derived taxa, such as the angiosperms, have more numerous and potentially more complex fea-

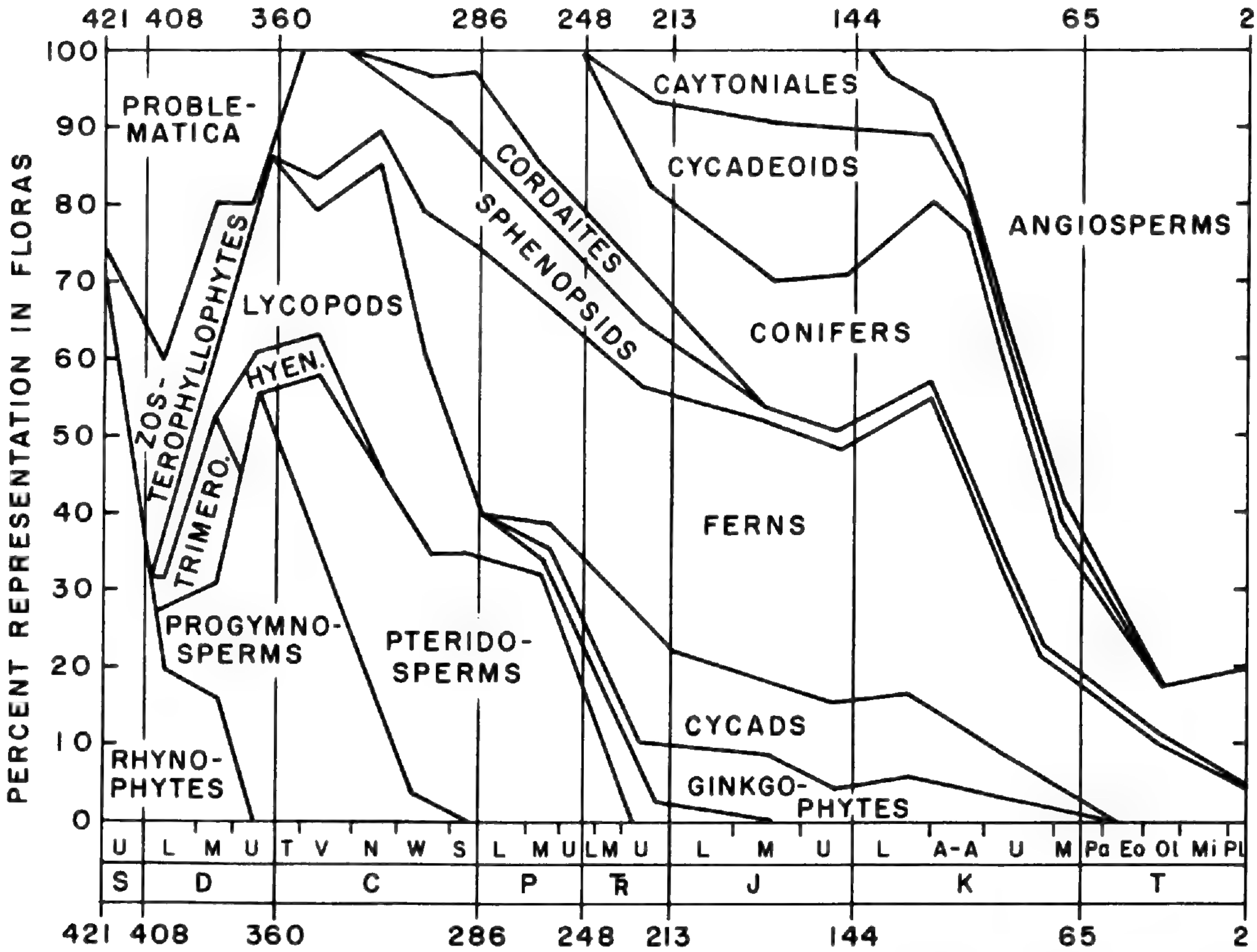

FIGURE 10. *Percent taxonomic composition of tracheophytes in fossil assemblages through the Phanerozoic (data redrawn from Knoll, 1986; courtesy of A. H. Knoll). These data show similarities with those presented by Niklas et al. (1985) for overall patterns in diversification within separate lineages of vascular land plants. Early Paleozoic floras were dominated by archaic pteridophytic groups (rhyniophytes, zosterophyllophytes, trimerophytes) which radiated into variously more derived groups during the Carboniferous. Mesozoic floras consist of diverse gymnosperm lineages supplemented by numerous ferns. With the radiation of angiosperms, the percent taxonomic representation of nonflowering groups declines abruptly during the Late Cretaceous and Tertiary.*

tures with which to identify species (e.g., floral structure) than more archaic taxa, such as pteridophytes (e.g., stelar anatomy, spore-wall characters).

The Devonian flora provides a convenient illustration of the potential relationship between taxonomic and morphological rates of evolution. There is considerable agreement among specialists as to the features that distinguish Devonian genera and higher taxa. Additionally, there are authoritative treatments of the stratigraphic occurrences of taxa and the first and last occurrences of various vegetative and reproductive features upon which they are based. For example, Chaloner & Sheerin (1979) provided a comprehensive stratigraphic treatment of Devonian genera as well as the first and last occurrences of various reproductive and vegetative features. Their data are plotted in Figures 13 and 14. (Nonvascular genera, such as *Sporogonites*, *Parka*, *Pachytheca*, or those having dubious status as tracheophytes, such as *Taeniocrada*, are excluded from these plots.) Anatomical (tracheid, stelar, and stomatal type; Chaloner & Sheerin, 1979, figs. 2, 3) features are plotted separately from reproductive features, such as the position, shape, and type of dehiscence of sporangia (Chaloner & Sheerin, 1979, fig. 4). The data indicate that the number of Devonian genera increases from the Pridolian to the Givetian and then undergoes a modest decline in the Frasnian and Famennian (Fig. 13). By contrast, the number of vegetative and reproductive features upon which Devonian taxa are based increases

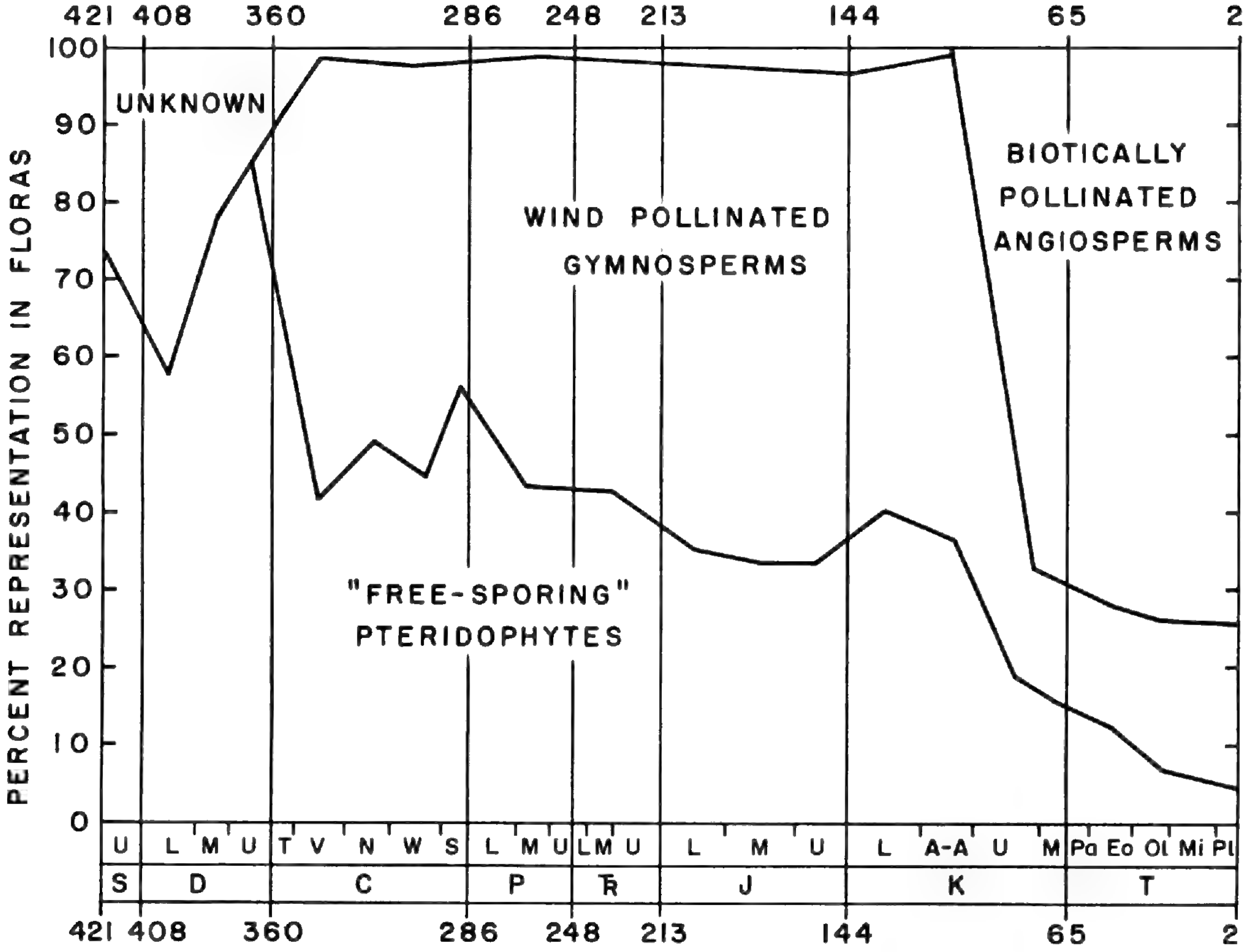

FIGURE 11. *Percent taxonomic composition of tracheophytes (shown in Fig. 10) converted to represent major categories of sexual reproduction. Free-sporing pteridophytes dominate most of the early Paleozoic floras; gymnosperms predominate through most of the Mesozoic; and angiosperms dominate the Late Cretaceous and Tertiary.*

throughout this interval. Linear regression analysis of the total number of taxonomic characters versus the number of genera yields $r = 0.96$ (N = 8), which is significant at the 1% level. This correlation, however, reveals very little with regard to the quantitative decrease in Late Devonian genera despite an increase in the potential number of taxonomic characters in the Frasnian-Famennian. Clearly, as the number of genera increases it is reasonable to expect an increase in the number of taxonomically distinguishable features. Analyses of the appearance of new genera and of new vegetative/reproductive features yield poor correlations (Fig. 14). For example, a regression of the number of new genera against that of the number of reproductive features yields $r = 0.283$. Regressions of either the number of vegetative or the total number of features against the number of Devonian genera yield lower coefficients of correlation. Consequently, the taxonomic recognition of new Devonian genera does not appear to be correlated necessarily with the evolutionary appearance of novel reproductive or vegetative features. In addition, a review of the generic descriptions for Devonian vascular plants compiled by Gensel & Andrews (1984) suggests that paleobotanical treatments of early Paleozoic floras are taxonomically conservative. Therefore, at least at the generic level, it does not appear that estimates of taxonomic diversification in the Devonian are artifacts of rapid morphological evolution. Since most Devonian genera have few species, this conclusion appears warranted at the species level as well (cf. Knoll et al., 1984).

Although the perceived taxonomic diversification of early vascular land plants appears not to be biased by rapid morphological evolution, other episodes of large-scale increases

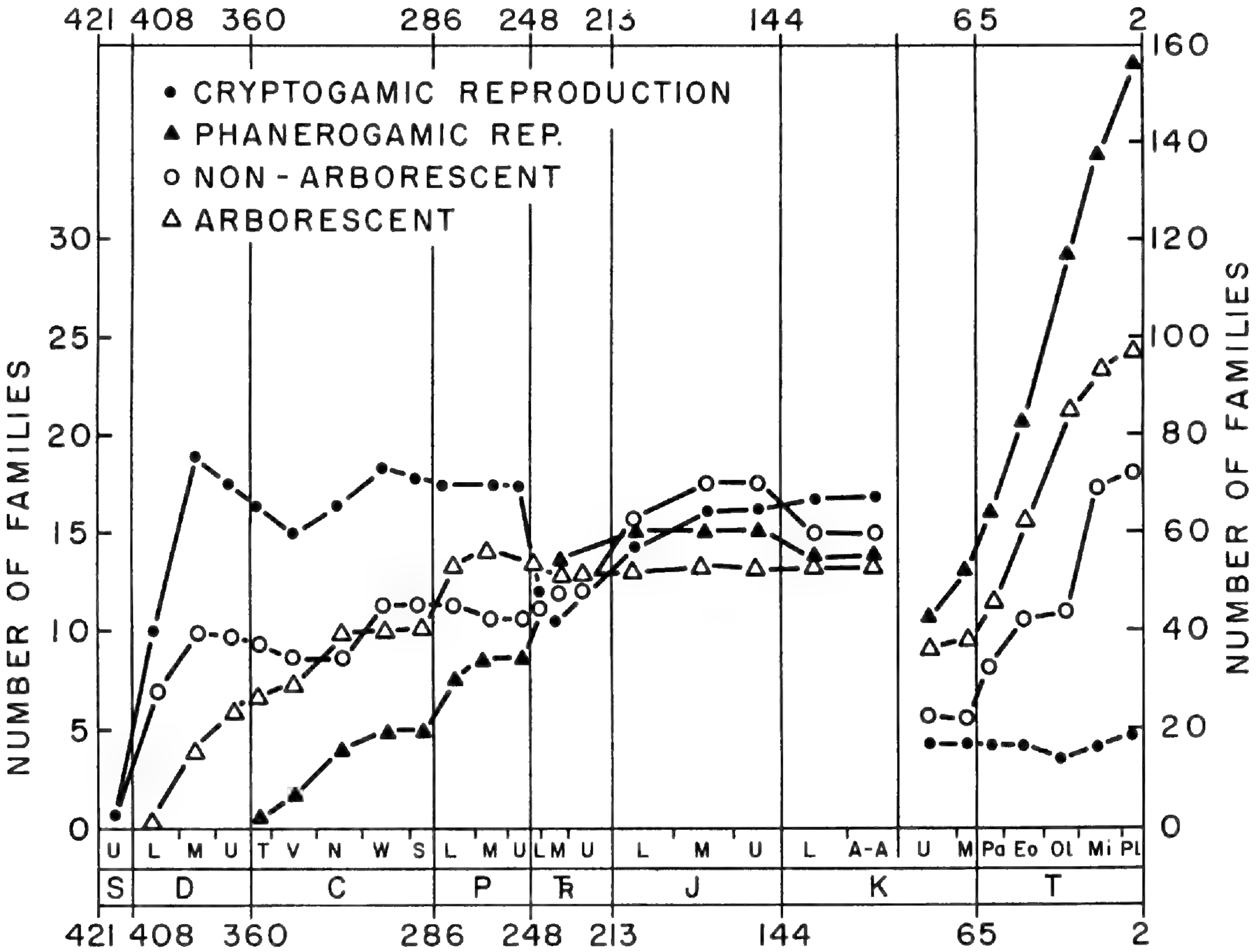

FIGURE 12. *Absolute numbers of spore- and seed-bearing, nonarborescent and arborescent tracheophyte families through the Phanerozoic (redrawn from Tiffney & Niklas, 1985). The scale of the vertical axis changes from increments of five families to increments of 20 between the Lower and Upper Cretaceous.*

in numbers of species have not been rigorously examined. For philosophical and practical reasons, therefore, it is reasonable to view conservatively the overall patterns of tracheophyte species diversification in terms of anatomical, morphological, and reproductive evolutionary trends, rather than strictly in the context of patterns of species origination.

NULL OR BIOLOGICAL HYPOTHESES?

Historically, evolutionary theory has come almost exclusively from observations made on living organisms. Charles Darwin was able to use the fossil record as evidence for evolution but derived his notion of natural selection from insights gained from animal and plant breeding, biogeography, and natural history. Indeed, he found the fossil record singularly intractable in supporting many features of his theory (Rudwick, 1976). The Modern Synthesis incorporated paleontology, but even the work of George Gaylord Simpson may be viewed as an ad hoc rationalization of patterns seen in the fossil record based on neontologically derived theory (cf. Gould, 1980). Recently, however, paleontology has generated evolutionary hypotheses based on patterns seen in the fossil record. This significant shift in the source of evolutionary speculation has had many effects, not the least of which is a re-evaluation of the biases, artifacts, and limitations that are inherent to paleontological data. Clearly, the fossil record can be used to generate evolutionary hypotheses, but only provided it reasonably reflects biological phenomena. For a long time paleontologists have recognized the numerous geological factors that contrive to filter and distort biological processes preserved in the record. Much of the recent literature focuses on attempts to

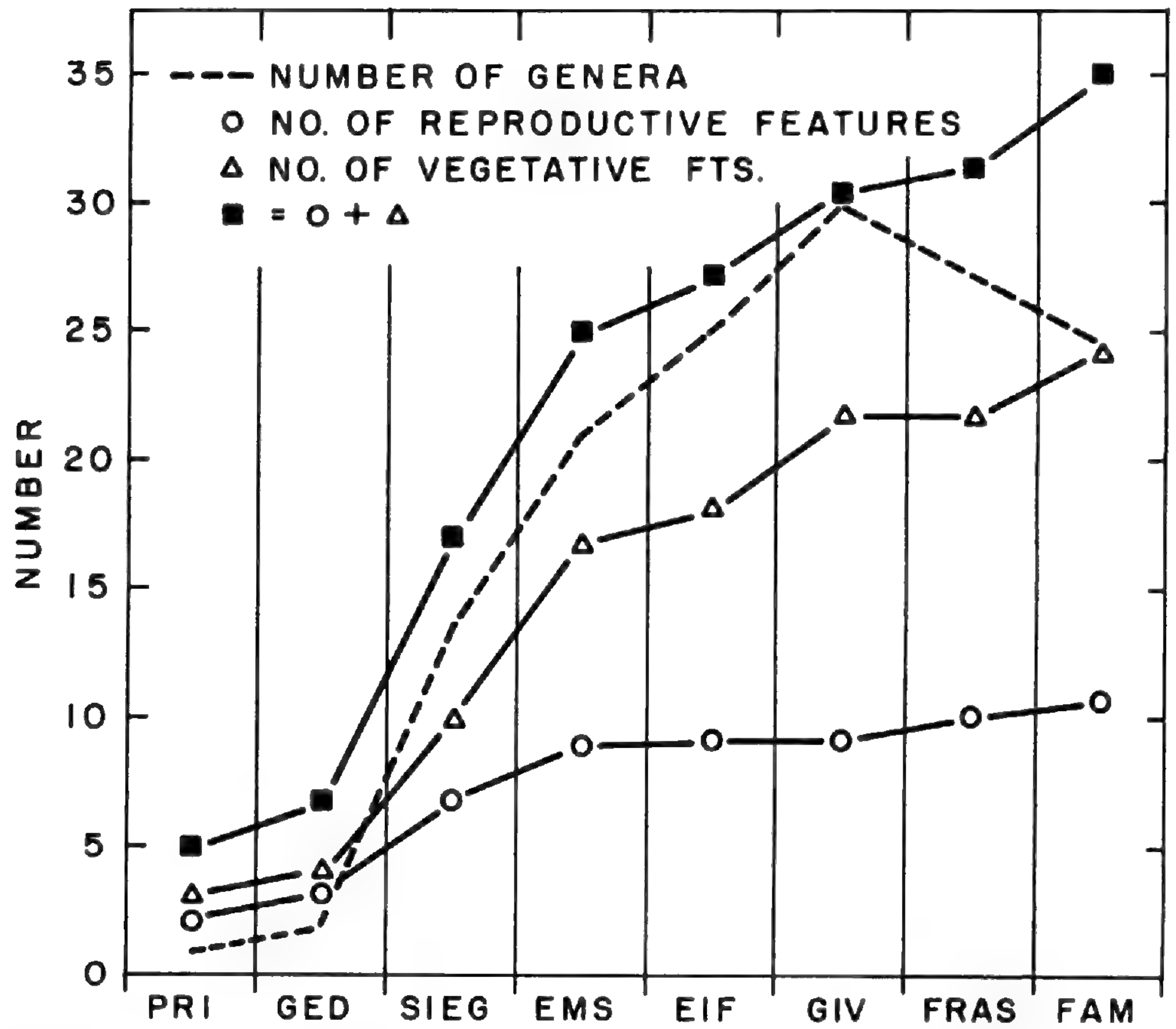

FIGURE 13. *Changes in the total number of Devonian vascular plant genera and the number of reproductive and vegetative characters used to identify taxa. Data taken from Chaloner & Sheerin (1979, figs. 1–4). Devonian genera are exclusive of nonvascular and dubiously vascular plants (e.g.,* Parka, Pachytheca, Taeniocrada, Prototaxites, Sporogonites, Spongiophyton, Protosalvinia*): Pri = Pridolian, Ged = Gedinnian, Sieg = Siegenian, Ems = Emsian, Eif = Eifelian, Giv = Givetian, Fras = Frasnian, Fam = Famennian.*

deal with these factors and to reconstruct information lost from the fossil record (Nichols & Pollock, 1983).

The fossil record is the principal source of information on long-term patterns of evolution. Retained within it are imperfect records of taxonomic diversification, major episodes of adaptive radiations, and major extinctions. This paper has focused on the quality of these patterns for vascular land plants. Quantitative analyses of the paleobotanical literature provide a basis for reconstructing the broad patterns of floristic and vegetational change occurring over the last 400 million years. In particular, large-scale patterns in numbers of species have been used to reconstruct and identify two major floristic changes, one at the end of the Paleozoic and another toward the end of the Mesozoic; within-assemblage taxonomic compositions have been used to treat broad patterns in vascular plant ecology; and morphological/anatomical data have been used to reconstruct trends in organography and adaptation. As has been seen, however, potentially serious limitations and distortions exist in the data. In almost all cases, quantitative analyses can be used comfortably only to draw qualitative conclusions.

The most serious difficulty with the fossil record comes from attempts to infer mechanisms from patterns. Ecologists are currently debating the use of patterns as data, as the recent furor over the use of null models attests (Harvey et al., 1983). Is there a null hypothesis for the pattern of species diversification seen in the fossil record? The answer is an equivocal yes. The fossil record of land plants exists because of processes of nonmarine clastic and pyroclastic deposition. The vast majority of fossil plants are preserved in lowland flood plain or lakeside environments or are entombed in volcanic ashfalls and mudflows. Consequently, it is conceivable and even probable that much of the patterns seen in tracheophyte species diversification can be explained in terms of factors that influence patterns of nonmarine sedimentation. Principal among these is tectonics, which controls

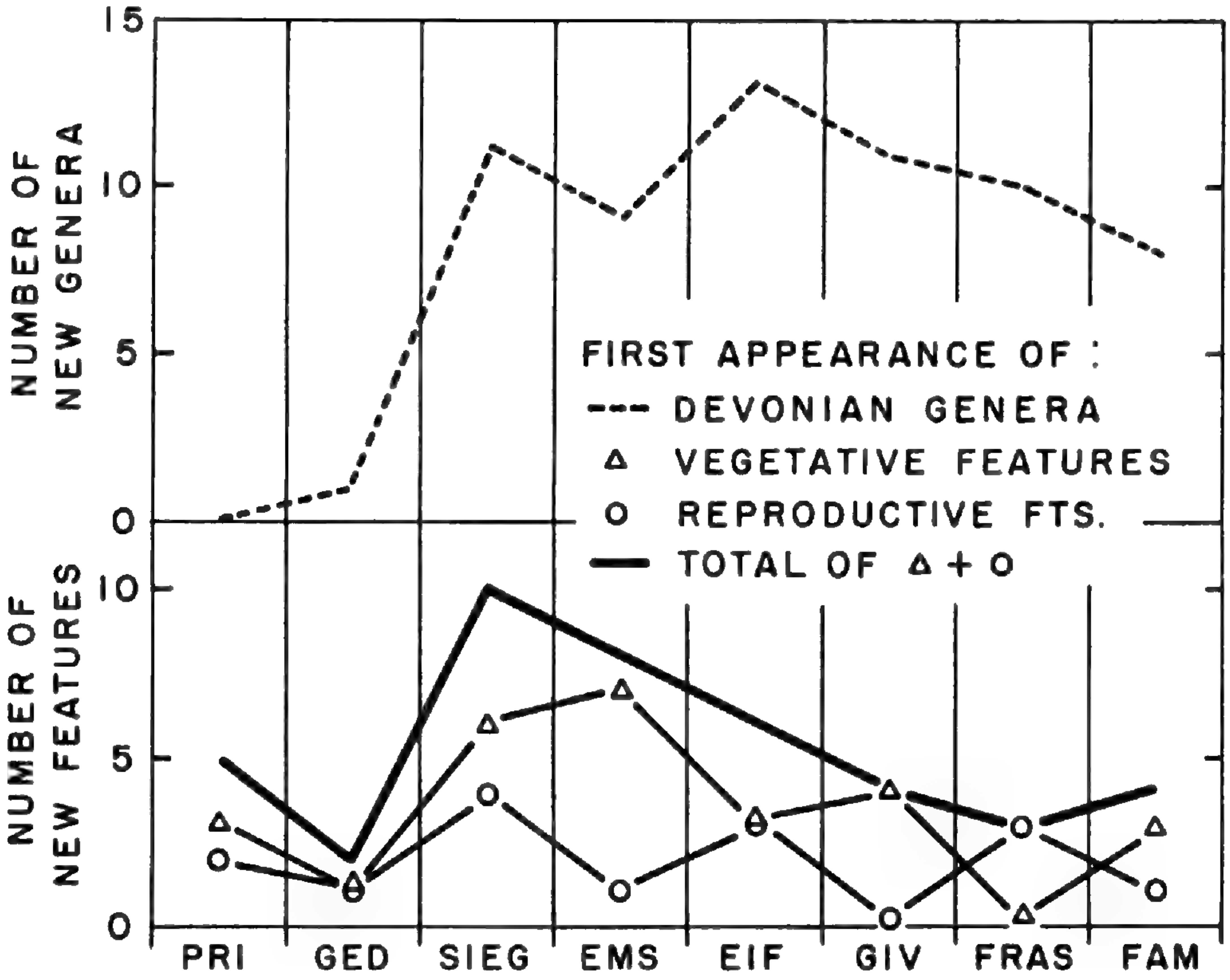

FIGURE 14. *Numbers of first appearances of Devonian genera, and vegetative and reproductive features. Data from Chaloner & Sheerin (1979, figs. 2–4).*

rates of uplift, erosion, subsidence of sediment-accumulating basins, and volcanism (Blatt et al., 1972).

For example, variation in the type of nonmarine sediments deposited during a geologic period could contribute to the apparent pattern of species diversification. Are periods of high numbers of species also those in which geological factors favored the deposition of sediments in which fossils are easily recovered? Fossil plants are preserved most often and with high morphological fidelity in fine-grained carbonaceous detrital sediments and volcanic ash deposits. Niklas et al. (1980) attempted a limited analysis of data on coal resources to estimate coarsely the variation in nonmarine carbonaceous sediments through the Phanerozoic. We concluded that the Carboniferous, Cretaceous, and Tertiary were qualitatively different from other geologic periods. These three "coal eras" have large coal tonnages *per unit of outcrop area.* High numbers of species for these three coal-rich eras could reflect a combination of extensive sedimentological "sampling" of terrestrial floras, excellent preservation (e.g., coal ball petrifactions), and the consequence of intensive economic exploration of coal resources. These factors probably account for the unusually high numbers of species reported for the Carboniferous and Cretaceous-Tertiary.

Therefore, it is safe to assume that tectonics and erosional patterns of deposition have contributed to the fluctuation in numbers of species in substantial ways. Nonetheless, these nonbiological or null hypotheses are inadequate to explain the patterns of taxonomic turnover within fossil assemblages or broad patterns in plant organographic/reproductive evolution. Regardless of the quantity of sediment deposited or the preservational status of plant parts recorded for a geologic period, there exists no necessary and sufficient correlation between the magnitude and direction of physical factors operating in the fossil record and patterns in taxonomic turnover and morphological evolution. Patterns in plant fossil record can be viewed either from the perspective of "objects" (taxa and their origination, persistence, and extinction) or "properties" (morphological and reproductive innovations and elaborations). A strictly exclusive treatment of either perspective is unlikely to lead to any insights into the relationship between evolutionary patterns and mechanisms (Sober, 1985). Null hypotheses are an essential component to this type of inquiry, but the assessment of alternative hypotheses and multiple-causation in paleontology requires both geological and biological insights.

The salient conclusions that emerge from a review of the plant fossil record can be briefly summarized under five points. (1) The concepts of a paleospecies and an extant species are significantly different (see Gingerich, 1985). (2) Consequently, the fossil record of species diversification is best viewed as a document of trends in morphological/reproductive diversification. Quantitative estimates of "diversity" can be used to draw primarily qualitative conclusions. (3) The taxonomic richness recorded for any geologic period does not provide information on species equitability, which is an essential component to considerations of paleoecology and the ramifications of phenomena such as extinction. (4) Although the properties of taxa above the level of species are potentially interesting, they do not necessarily reflect those of species, which are the primary focus of evolutionary mechanisms. Finally, (5) much of the pattern of taxonomic diversification could be explained by factors operating in a strictly geological context; however, identification of long-term patterns in biological phenomena requires the examination of trends in morphology, anatomy, and reproductive systems, in conjunction with patterns of species diversification (Raup, 1983).

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EFFECTS OF ARIDITY ON PLANT DIVERSITY IN THE NORTHERN CHILEAN ANDES: RESULTS OF A NATURAL EXPERIMENT[1]

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and Carolina Villagrán[2]

ABSTRACT

Hyperarid climates in western South America from 15°S to 29°S, extending up to 3,000 m in the northern Chilean Andes, result primarily from the Andes intercepting precipitation from the Intertropical Convergence and the drying effect of the equatorward-running Humboldt Current bathing much of the Pacific coast of South America. Paleobotanical, paleontological, and geological evidence suggests that such harsh climatic conditions developed very recently in Holocene times, following a turbulent Pleistocene history of alternating wet/cold and warm/dry periods. Seasonal climates probably first emerged in the Pliocene after a long, warm/wet Miocene during which precipitation is thought to have increased from east to west, as opposed to west to east, as occurs north of 25°S today. For the three remaining intact vegetation belts (desert scrub, Andean, and high Andean) in the northern Chilean Andes above the Atacama Desert, surveys on six transects, each approximately one-fourth of a degree latitude wide, located at 18°S, 19°S, 21°S, 24°S, 26°S, 28°S, revealed only 769 species of vascular plants in 290 genera. Altitudinally, species richness decreases with elevation in the winter rainfall zone, where precipitation is received from the southwest ("invierno chileno"; transects 26°S, 28°S), to peak at mid elevations in the summer rainfall zone where precipitation is received from the east ("invierno boliviano"; transects 18°S, 19°S, 21°S, 24°S). Species richness decreases by 80% and cover by 50% over the very severe rainfall gradient from 18–24°S. In spite of its greater reliance on water, the azonal bog flora has been less affected than the zonal flora by aridity, probably because of greater chances of reintroduction of species following their loss through long-distance dispersal. Species richness, when considered on a broad biogeographical scale, was significantly positively correlated with mean annual rainfall, as it was for most 500-m elevational levels when considered separately. The effect of cold temperatures at the higher elevations was completely obliterated by aridity on a biogeographical scale. Although diversity (measured as a synthetic characteristic combining richness and abundance) and species richness showed similar trends as aridity increases, loss of diversity tended to be more gradual in comparison with reductions in species richness. Aridity leads to community features analogous to those seen in the early stages of primary succession, maintained on a permanent basis. Losses in species richness with aridity along the western side of the Andes and from east to west across the Andes were overlain by highly characteristic life form tendencies. Perennial herbs are proportionately most abundant in areas of highest rainfall, annual herbs gain greatest prominence in areas of intermediate aridity, while woody species were proportionately most strongly represented under extreme dry/warm and extreme dry/cold conditions. The woody habit is generally more common in the northern Andes than in some similar North American plant communities. The maintenance of considerable diversity (in spite of severe loss in species richness) coupled with emphasis on long-lived woody species in the harshest environments in the northern Chilean Andes are tendencies also seen in many species-rich, climatically benign tropical plant communities. The hypothesis is developed that convergence in these features results from the similar selective effects of certain abiotic and biotic factors in the harsh arid environments of the northern Chilean Andes and in species-rich tropical communities, respectively. We predict that additional life-history trait similarities (e.g., in breeding systems) will emerge for the plant species of abiotically and biotically "harsh" environments, respectively.

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Areas of the earth's surface where local mountain ranges exert strong influence over precipitation and temperature patterns experience especially radical environmental alterations during major global climatic changes. How floras adjust to rapidly emerging harsh environmental conditions, and the patterns of species richness and community diversity resulting from such restructuring should be just as relevant for the development of comprehensive diversity theory as phenomena seen in highly productive, abiotically benign environments. Diversity trends in harsh habitats should also have direct bearing for conservation in that changes induced in ecosystems by human activities are frequently similar in nature and magnitude to those engendered by natural climatic change. Yet, as perusal of the literature on species diversity and community structure (e.g., Tilman, 1986) will show, harsh habitats have received relatively little attention.

Apriorily, reductions in species richness are expected in harsh habitats because productivity is limited by abiotic factors. Such losses, moreover, might be exponential due to the compound direct (physiological) and indirect (historical and, on other organisms such as pollinators, seed dispersal agents) effects of habitat harshness. Patterns of species loss in harsh habitats, nevertheless, are likely to be far more complex than this. Expected losses could be mitigated by a number of factors related to community dynamics. During their evolutionary histories, floras accumulate many life forms varying in ecophysiological and demographic properties. At the onset of harsh conditions, loss of richness could be suppressed by life-form shuffling. In many warm deserts, for example, the annual habit is selectively favored (Raven & Axelrod, 1978; Pavlik, 1985), and species richness levels may be relatively high. Much present knowledge of life form shifts derives from comparative studies of distinct plant communities with floras of heterogeneous phytogeographic origin. Because such comparisons could be confounded by phylogenetic constraints in certain taxa, a critical assessment as to whether life form shifts stall losses in diversity will be best obtained by comparing life forms in floristically homogeneous communities subject *internally* to different degrees of habitat harshness. To facilitate the interpretation of results, moreover, such gradients in habitat harshness must be well documented as to their abiotic characteristics.

Maintenance of diversity in harsh environments should also be affected by changes in the relative balance of biotic and abiotic selective factors. In early successional communities, because of low dominance levels, local diversity may be high despite total low numbers of species present (Houssard et al., 1980). In that resources are severely limited, and competition for light is reduced due to abiotically induced low productivity, harsh habitats may be likened to the early stages of primary succession maintained on a long-term basis. For harsh habitats with low species richness, then, diversity as reflected in the relative abundance of species might be relatively high. Another way of viewing this postulated analogy is that loss of diversity with greater harshness should be partially, and increasingly, counteracted as harshness increases. This hypothesis may be tested by comparing species numbers (species richness) with measurements of diversity as a synthetic characteristic combining richness and abundance, following Whittaker (1972).

The objectives of this paper are, first, to assess how plant species richness, life forms, and community diversity patterns are affected by severe aridity, and, second, to discuss some implications of diversity patterns in harsh habitats for community structure in general. The northern Chilean Andes located at 18°–28°S in western South America provide a unique setting for this. Close to 10 degrees latitude of absolute desert at low elevations gives way to a sequence of three high-elevation vegetation belts (desert scrub, Andean, and high Andean), these exhibiting varying degrees of aridity latitudinally and altitudinally. Because aridity gradients are overlain by temperature variation, the Andean system is also ideal for assessing the relative effects of temperature versus aridity on plant diversity.

As Diamond (1986) pointed out, to interpret the results of any "natural experiment," as the above would be classed, clear understanding of the timing of historical events that led to the "observed results" is essential. As we mentioned above, the identification of salient present-day abiotic parameters responsible for maintaining the "particular species mix in the test tube" is equally important if unequivocal answers to the kinds of theoretical questions outlined earlier are sought. Consequently, before examining plant diversity patterns in the northern Andes (Section III), we will devote considerable space to outlining the present climatic characteristics of the northern Andes (Section I), and the historical development of arid climates at subtropical latitudes in western South America in general will be reviewed in detail (Section II).

DATA BASE AND METHODS

For species richness patterns and estimates of diversity we compiled data over a number of years in six altitudinal transects (18°S, 19°S, 21°S, 24°S, 26°S, 28°S) running from the upper margin of the Atacama Desert (1,500–3,000 m elevation) to the upper limit for vascular plants (4,500–5,000 m, depending on latitude) (Fig. 1). Records of species present every 50 or 100 m of elevation were obtained by walking the transects and by climbing a number of high summits in each area. The transects followed the main Andean penetration routes and for this reason had no fixed courses. In each case routes taken traversed approximately one-fourth of a degree of latitude. For these transects plant cover was measured in altogether 1,620 minimum area quadrats. Replicate quadrats were sampled at 50–100 m elevational intervals along each transect. Cover of shrub and perennial herb species was estimated from the surface area projected by each individual of a species within a quadrat. The largest and smallest diameter of the individual's crown was measured for calculation of an elliptic to circular area. Annual herb cover was initially measured on a phytosociological scale (transects 18°S and 19°S). In later work annual herb cover was estimated from the percentage of points 10 cm apart on line transects intercepted. The data for all 50–100 m elevational sampling intervals was subsequently pooled for 500–1,000 m elevational intervals.

Species richness for equivalent 500 m elevational intervals at different latitudes was compared with mean annual precipitation using regression analysis, employing linear, semilogarithmic and log–log models, and with mean annual precipitation and mean annual temperature using multiple regression analysis. Precipitation and temperature for the series of 500 m elevational levels on each transect were estimated from curves constructed from weather station data available for the particular area under consideration. Weather data were obtained from di Castri & Hajek (1976) and from records supplied by the Ministerio de Obras Publicas (MOP) in Santiago.

For life form analyses, species were classed as annual herbs, perennial herbs, and woody plants (primarily shrubs). For the small number of Cactaceae present, columnar species and large cushion species were included in the woody category. The smaller cacti species were categorized as perennial herbs. To facilitate statistical analysis (*G*-tests) the life form data for pairs of adjacent transects were combined.

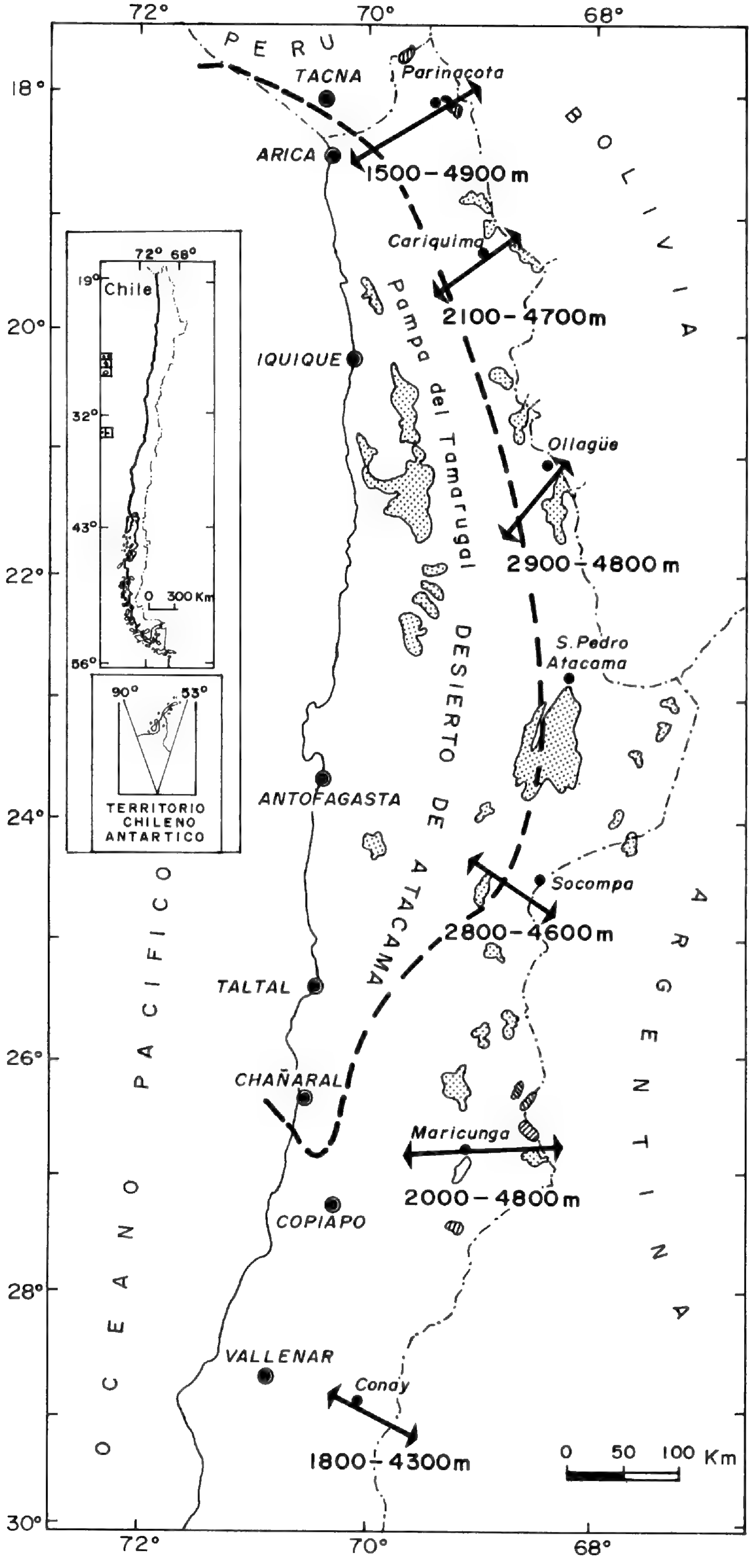
The indices exp H' where

$$H' = -\sum_i p_i \ln p_i,$$

and $1/\lambda$ where $\lambda = p_i^2$ (Peet, 1974), were employed to measure community diversity. In these indices p_i = the proportional abundance of the *i*th species. Relative cover was used as the proportional abundance of a species. Details on some of these transects appear in Arroyo et al. (1982, 1984) and in Villagrán et al. (1982, 1983).

I: PRESENT-DAY CLIMATES IN THE NORTHERN CHILEAN ANDES

Intensely arid climates in western South America extend from 15°S in southern Peru to around 29°S in Chile. True absolute desert (without vegetation except along main water courses as the Río Lluta, Río Azapa, and Río


72°
70°
68°
18°
20°
22°
24°
26°
28°
30°
PERU
BOLIVIA
ARGENTINA
OCEANO PACIFICO
TACNA
Parinacota
ARICA
1500–4900 m
Cariquima
2100–4700m
Pampa del Tamarugal
IQUIQUE
Ollagüe
2900–4800 m
DESIERTO DE ATACAMA
S. Pedro Atacama
ANTOFAGASTA
Socompa
2800–4600m
TALTAL
CHAÑARAL
Maricunga
2000–4800m
COPIAPO
VALLENAR
Conay
1800–4300m
0 50 100 Km
72° 68°
19°
Chile
32°
43°
56°
0 300 Km
90° 53°
TERRITORIO CHILENO ANTARTICO

Loa, or in coastal fog pockets such as Paposo and Taltal) occurs south of 17°S to 25°S (Fig. 1). The desert rises abruptly from a narrow coastal strip to 1,500 m at the Arica deflection (18°S) in northern Chile and reaches a maximum elevation of 3,000 m at 24°–25°S, in from the coastal cities of Antofagasta and Taltal. South of 25°S aridity decreases again.

The Chilean–Peruvian arid diagonal is a "rain shadow" and a "cold air" desert (Rauh, 1983). The present climate (Figs. 2, 3) is determined primarily by the annual behavior of the Intertropical Convergence situated over equatorial latitudes (Gomez & Little, 1981) which brings moisture from the northeast, and by a Polar front bringing precipitation from the southwest, together with the interplay of these precipitation sources and the major ocean currents. South of 24°–25°S, most precipitation is received during the winter months (May–August; "invierno chileno") from a northward extension of the Polar front. Consequently, the climate is essentially an arid version of the true Mediterranean climate further south at 30°–38°S. Here there is no east–west reduction in rainfall (Fig. 2). Most precipitation above 3,000 m in the Chilean Andes for these latitudes is in the form of snow.

North of 24°S, where a southward extension of the Intertropical Convergence during the summer months comes into play and the Polar front is negligible, precipitation is received during the summer months (November–March; "invierno boliviano") as rainfall below 4,000 m or as transient snow and hail above 4,000 m. The winters are cold and dry. At these latitudes the Andes generate a rain shadow by forcing moisture-laden air from the northeast to rise and cool on their eastern slopes. The greatly diminished saturated air masses ascending onto the western side of the Andes undergo adiabatic heating, further reducing potential precipitation. As the air masses reach lower elevations towards the Pacific, they are further dried by cold surface waters from the Circumantarctic Current carried northward by the equatorward-running Humboldt Current (Peru Current) (Zinsmeister, 1978) and by cold bottom water upwelled from the Pacific by the Humboldt Current as it is deflected away from the coast by the Coriolis effect in subequatorial latitudes. As a result of these features and southward weakening of the Intertropical Convergence, the Chilean Andes north of 24°–25°S are characterized by steep east–west and north–south reductions in precipitation (Fig. 2). Typical of the east–west gradient, recorded annual precipitation for Parinacota (18°S), situated at 4,395 m, is 372 mm. Murmuntane, situated at 3,280 m and less than 100 km to the west, receives only an average of 156 mm of rainfall annually, while mean annual rainfall for Arica on the coast (29 m) is less than 1 mm. Southwards at 21°S, recorded annual precipitation for Cebollar at 3,730 m is 53 mm, while at 24°S (at Imilac, 3,232 m) recorded annual rainfall is 2.4 mm.

In the northern Chilean Andes, as a result of reduced cloudiness due to higher than average adiabatic heating, the normal latitudinal decrease in temperature is essentially absent to at least around 24°S (Fig. 3) (from 25° to 28°S there are too few temperature records for the Andean highlands). This fortuitous situation avails easy temperature control of comparisons of diversity with increasing aridity. The average lapse rate above 1,000 m is about 6.5°C per 1,000 m increase in elevation. Below 1,000 m, where coastal fog results in abnormal cooling, the lapse rate is lower. Mean annual temperature at Murmuntane (3,280 m) is 9.7°C. Mean annual temperature at Parinacota (4,395 m) is 2.5°C.

←

FIGURE 1. *Location and altitudinal ranges of transects in the northern Chilean Andes. Heavy dashed line denotes upper limit of absolute desert in the Andean highlands. Stippled areas: major present-day salt lakes. Hatched areas: freshwater lakes.*

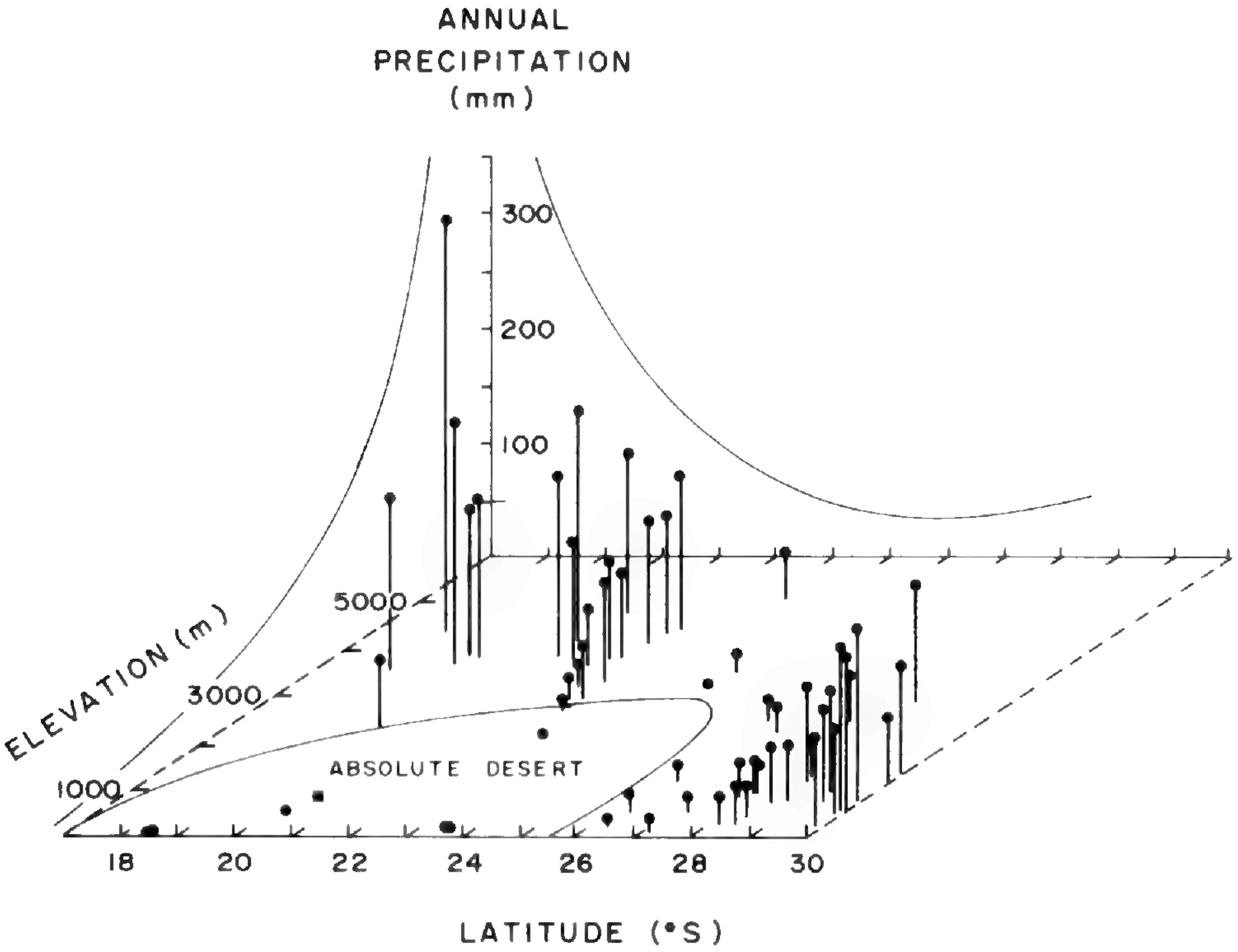


FIGURE 2. *Mean annual precipitation related to elevation and latitude in northern Chile. Data from Ministerio de Obras Publicas (MOP), Santiago, and di Castri & Hajek (1976). Precipitation data unavailable for the Andean highlands between 26° and 28°S.*

II: HISTORICAL DEVELOPMENT OF ARIDITY IN THE NORTHERN CHILEAN ANDES

Proposed timetables for development of arid climate in western South America span Miocene (e.g., Muizon & DeVries, 1985) to Quaternary initiation dates (e.g., Ochsenius, 1983a). Ochsenius & Santana (1974), Ochsenius (1983b), and Axelrod (1979b) agree that maximum aridity was reached very recently.

EMERGENCE OF THE ANDES

That many of the high Andean summits rose rapidly and only very recently is critical to understanding the development of harsh arid climates at subtropical latitudes in western South America.

From the late Cretaceous into early Paleocene times, volcanic rocks and associated sediments, deposited close to the present continental margin in Mesozoic times as a result of the closure of the Nazca and American plates (Rutland, 1971; Mortimer et al., 1974), were uplifted to form a proto-Andean divide west of the present Cordillera Occidental (Mortimer, 1980). This primitive axis, however, was almost entirely eroded away, leaving the Altos de Camilica Formation in southern Peru (Tosdal et al., 1984) and the Putani Formation east of Arica (Mortimer & Saric, 1972). The modern landscape differentiated

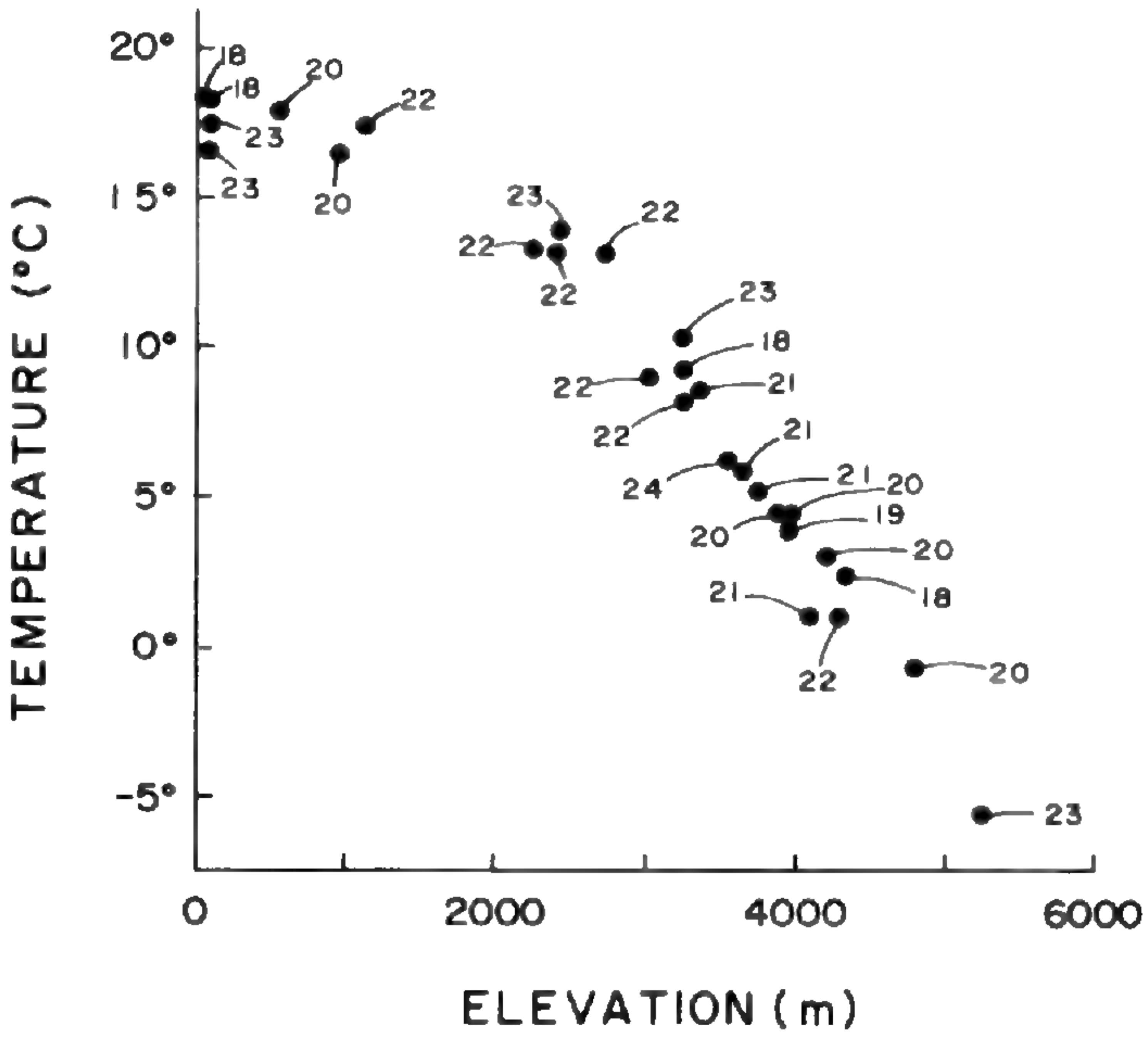


FIGURE 3. *Mean temperature plotted against elevation for areas between latitude 18° and 24°S in the northern Chilean Andes. Data sources as for Figure 2. Data point for 5,300 m at 23°S is from Corrida de Cori (Ruthsatz, 1977), Argentina, close to the Chilean border. The numbers associated with each datum point indicate the corresponding latitude.*

initially in the late Paleocene–early Miocene interval. It comprises (a) the nonvolcanic Cordillera de la Costa, (b) a low-lying depositional basin referred to as the Pampa de Tamarugal in northern Chile or Llanuras Costaneras in southern Peru, (c) the precordillera, a loosely defined transition zone at 2,000–4,000 m, and (d) the parallel cordilleras Occidental and Oriental with summits close to 7,000 m. These cordilleras are separated by (e) a broad intervening high-altitude plain, the Altiplano, of some 500,000 km^2 (Allmendinger, 1986) at 3,700–4,000 m (Fig. 4).

The Cordillera Occidental and the Cordillera Oriental emerged relatively late after two major focal points of rhyolitic volcanic activity developed in the late Oligocene and into the early Miocene (Tosdal et al., 1984; Naranjo & Paskoff, 1985) following extensive north–south block faulting and differential uplifting (Mortimer & Saric, 1972). Such activity persisted well into the late Miocene and early Pliocene (Megard et al., 1985), by which time deposition of sediments derived from the surrounding eroding volcanic axes produced the Altiplano (Fig. 4). During the same epoch, lava flows moving westward and sediments from the Cordillera Occidental backed up against the Cordillera de la Costa (Naranjo & Paskoff, 1985), elevating the northern part of the Pampa de Tamarugal in Chile and the Llanuras Costaneras in southern Peru.

The major increase in height in the Andes, nevertheless, occurred only as of the middle Miocene and onward (Mortimer et al., 1974) in north Chile and the Pliocene in southern Peru (Tosdal et al., 1984) as the result of andesitic volcanism (Fig. 4). Andesitic activity continued across the Cordillera Occidental and Cordillera Oriental throughout the Pliocene and Pleistocene into the Holocene, giving rise to the some 800 volcanoes present in northern Chile. Over 30 of these exceed 6,000 m elevation. Tosdal et al. (1984) estimated that the southern Peruvian Andes were uplifted 0.06–0.19 mm per year throughout the Neogene. The Cordillera Occidental at its southern edge is thought to have increased in height by 0.5 mm per year as of Holocene times (Rutland et al., 1965).

MIOCENE CLIMATES

Although significant uplifting had occurred by the Miocene, there is no evidence at this stage of the strong east Andean rain shadow seen in the Andes today. Axelrod (1979b) reviewed the limited paleobotanical evidence for the Miocene. Berry (1919) described leaf remains from the Tumbez area in northern Peru. Included is material identified as *Annona*, *Banisteriopsis*, *Ficus*, *Persea*, and *Styrax*. Although Berry's identifications require verification, the leaf types present are indicative of a fairly closed tropical viney forest and of productive environments.

A second flora studied by Berry (1917, 1939) from Potosí, Bolivia, now above 4,000 m and immediately to the east of the Cordillera Occidental, was considered by Ahlfeld (1956) to be of Miocene age and would have thus been deposited during the early phases of the uplifting of the Altiplano. It reportedly contains *Calliandra*, *Cassia*, *Copaifera*, *Dalbergia*, *Escallonia*, *Passiflora*, *Terminalia*, *Inga*, and *Weinmannia*. Today similar floras strongly dominated by woody leguminous taxa typically occur in neotropical formations under high rainfall regimes but usually with a distinct dry season in the Venezuelan llanos and adjacent Orinocan forests and areas transitional between Amazonia and the Brazilian Planalto. Elements reminiscent of *Weinmannia*, *Escallonia*, and *Inga* suggest that a semiseasonal forest gave way to a middle-altitude montane forest similar to that seen today further north in the Andes in Colombia where rainfall is very high.

A third flora, from Psillypampa, Bolivia, still further to the east of the main Andean axis, today at 2,600 m, was regarded as Pliocene age by Berry (1922) but suspected by Axelrod (1979a) as possibly of Miocene age. It contains material identified as *Heliconia*, *Myrica*, *Pisonia*, and *Pithecellobium* and many other genera with fairly small leaves. For the Miocene then, there appears to have been a transition from viney forest on the extreme Pacific border, into semiseasonal vegetation types at mid elevations on the Altiplano, and finally into more xeric, small-

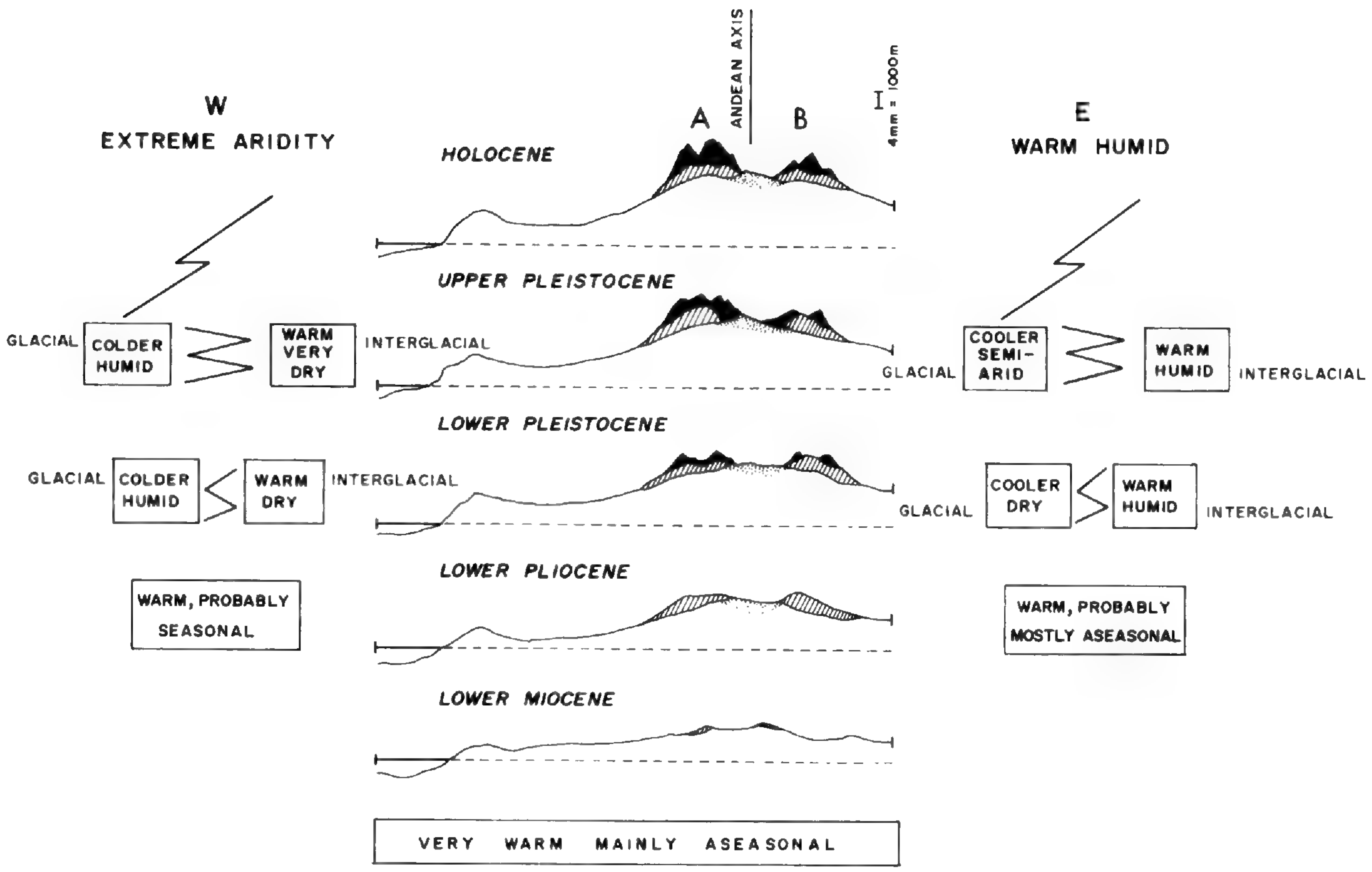


FIGURE 4. *Stages in the evolution of the Cordillera Occidental (A) and Cordillera Oriental (B) as of the Miocene and climatic tendencies west and east of the northern Andes during the Quaternary. Hatched areas: rhyolitic volcanic activity. Stippled areas: Atiplano. Black areas: andesitic volcanoes.*

leaved forms at lower elevations on the eastern side of the Altiplano. This suggests that, in contrast to today, the western side of the Miocene Andes may have been wetter than the eastern side.

The expected positions and water temperatures of currents in the Pacific Ocean support the above interpretation. Prior to the consolidation of the Antarctic Icesheet, the west wind drift is believed to have lain further south than today; moreover, as Zinsmeister (1978) suggested, cold surface waters would have been directed between East and West Antarctica rather than up the South American coast. With a less active and considerably warmer Humboldt Current in the Miocene, the counter-running warm current bathing the coasts of Ecuador and Peru today most likely extended south of its present position, very possibly engendering precipitation patterns similar to that in recent El Niño events (Cane, 1983), which brought torrential rains to coastal and lowland areas of southern Ecuador and northern Peru (Rasmusson & Wallace, 1983).

A warm, wet Miocene for the western flanks of the subtropical Andes finds good support from marine fossils deposited in high coastal cliffs in northern and central Chile during marine transgressions (Mortimer, 1972) and in the related Pisco Formation in the Llanuras Costaneras of southern Peru (Muizon & DeVries, 1985). At 30°S on the coast of Chile, dendrophyllid corals accompanied a warm-water ostracod fauna, of which some subtropical elements extended as far south as 47°S (Herm & Paskoff, 1967; Herm, 1969). The Pisco Formation contains turtles, sloths, terrestrial carnivores, and other large-bodied animals that could only have existed under fairly productive environments. Vertical incisions up to 1,000 m deep traverse the central depression in northern Chile (e.g., quebradas Vitor, Azapa, Lluta, Camarones). These, which geologists agree are indicative of high pluviosity, were initially cut down in the Miocene (see Mortimer, 1973; Paskoff & Naranjo, 1979; Naranjo & Paskoff, 1980a). Finally, the Miocene was the time of maximum copper enrichment in the Chilean Andes

(Clark et al., 1967). The high water table that this process requires and an active period of erosion seen in canyon development seem to be indisputable evidence against dry climates in the western deserts at this stage.

PLIOCENE CLIMATES

The Pliocene is poorly known for arid subtropical latitudes in western South America. Marine faunas on the Chilean coast at 30°S (Herm, 1969) and in the Pisco Formation in southern Peru (Muizon & DeVries, 1985) show declines in species richness and an influx of elements from cooler waters at the Miocene–Pliocene boundary. Zinsmeister (1978) related such changes to increased incorporation of cold water into the Humboldt Current due to northward displacement of the west wind drift and reduced flow through Drake Passage. Certain periods in the Pliocene in the Colombian Andes, situated away from the influence of the Humboldt Current, saw lower tree lines than at present and the first appearance of a high-elevation flora (Hooghiemstra, 1984). Thus changes in marine faunas along the Pacific coast must have been due at least partially to a general global trend toward climatic cooling. Climates were evidently drier than in the Miocene—canyon cutting in the Atacama ceased abruptly at this stage (Mortimer, 1973). *Vallea, Borreria, Niphogeton,* and *Eryngium,* genera considered indicative of open conditions, became abundant occasionally in high-elevation Colombian forests (Hooghiemstra, 1984). During this period large mammals (*Equus, Megatherium*) appeared in the present area of the Atacama desert. This scant information for the Pliocene suggests a gradual transition from the closed Miocene forests into more open, savannalike vegetation at low elevations, with small, evergreen treelets developing at mid elevations. The presently disjunct montane genus *Kageneckia* (Rosaceae), which occurs in central Chile and again in eastern Bolivia and southern Peru, could have been present in these Pliocene montane forests. *Prosopis,* the only surviving tree genus at low elevations in the Atacama today, probably dates to lowland Pliocene vegetation.

PLEISTOCENE–HOLOCENE CLIMATES

The fairly uneventful, drier and cooler, but far from hyperarid Pliocene of the western margin of subtropical South America gave way to a Pleistocene characterized by marked alternating wet and dry periods.

For tropical and subtropical lowland areas east of the Andes in South America the glacials were *cold-dry* times of forest contraction, while the interglacials were *wet-warm* times of forest expansion (Damuth & Fairbridge, 1970; Colinvaux, 1979; Ab'Saber, 1982; Prance, 1982). It has not been sufficiently appreciated that the wind systems proposed by Damuth & Fairbridge (1970) to account for dry glacial periods in the Amazon Basin predict precisely the opposite climatic trends for corresponding periods on the western side of the Andes, i.e., *warm-dry* periods alternating with *wet-cold* periods (Fig. 5).

During the glacials, the Damuth & Fairbridge model sees a low-pressure focus over Antarctica moving northward, bringing increased moisture from a southwestern source to mid- and subtropical latitudes in South America (Fig. 5). Because the cordilleras were now strongly elevated, the destination of much of this precipitation would have been the western side of the central Andes. Geological evidence suggests that the Atacaman area indeed experienced very wet climates in the Pleistocene. Many of the salt lakes (salares) presently occupying 2,800 km^2 bear extensive deposits of Pleistocene lacustrine and diatomaceous earth (Stoertz & Ericksen, 1974; Naranjo & Paskoff, 1980b). Analyses of old shoreline lines (Tricart, 1969) indicate that approximately one-half of the present salares in northern Chile (e.g., salares de San Martín, Ollague, Uyuni, Coipasa) formerly constituted extensive, deep, perennial lake systems (Stoertz & Ericksen, 1974). Wet glacial periods on the western side of the central Andes are also suggested by the fact that the Pleistocene snow line was depressed to a greater

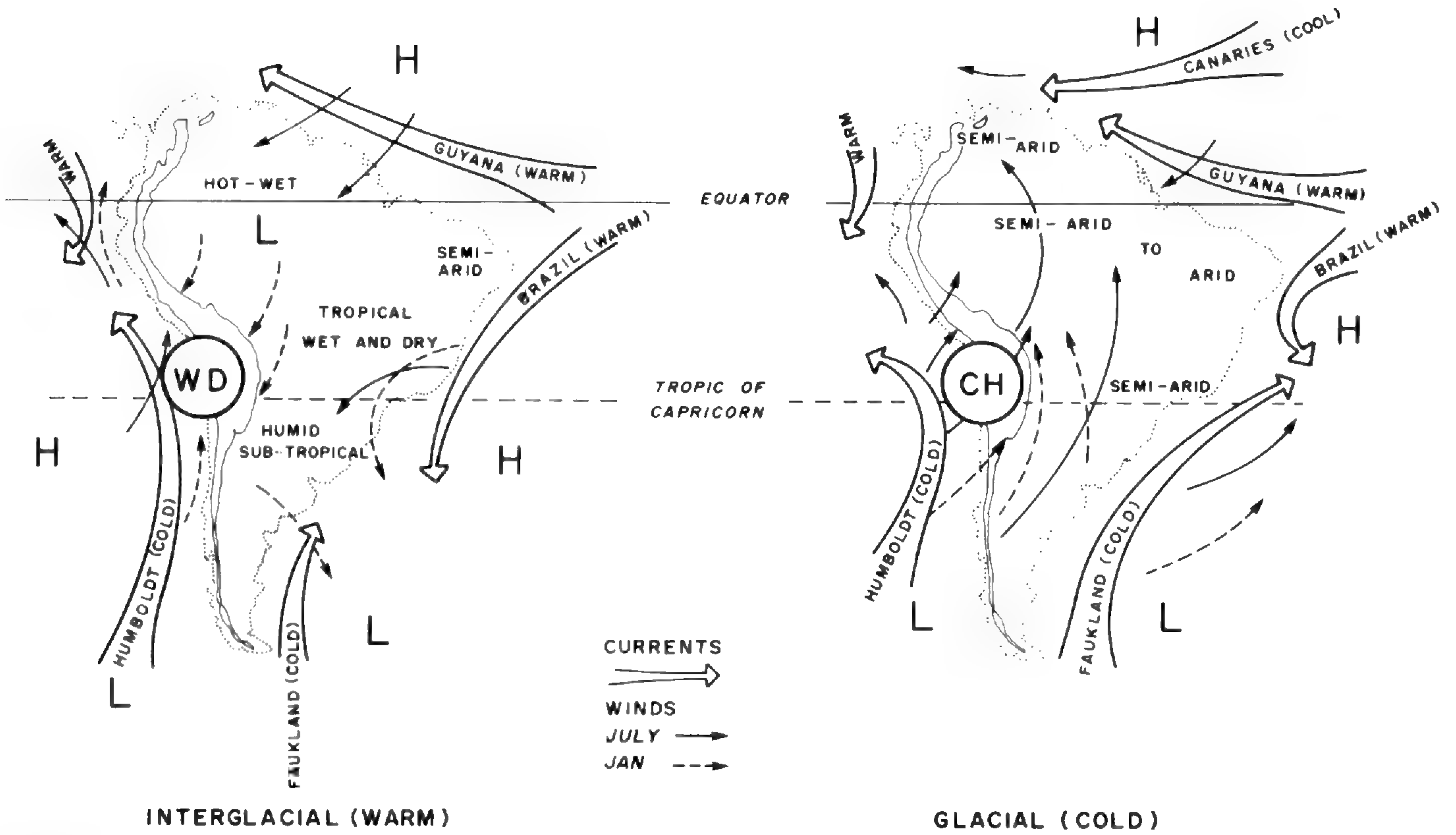


FIGURE 5. *Probable glacial and interglacial climates for the present Atacama desert region (area under large circles) in relation to the rest of South America. WD: warm-dry. CH: cold-humid. Modified from Damuth & Fairbridge (1970).*

extent on the western side of the Andes (Hastenrath, 1967).

The pollen record for the Andes, although still sparse, is also consistent with strong east–west climatic differentiation in the northern Andes during the Pleistocene. Heusser (1983) provided evidence of northward migrations of *Nothofagus* and *Podocarpus* in central Chile during glacial phases. This evidence indicates wet-cold climates for the western side of the Andes. On the eastern side of the subtropical Andes, in contrast, drought-tolerant taxa appeared on the border of the puna in the Junín area in Peru (Hansen et al., 1984) and close to the Bolivian–Peruvian border (Graf, 1981) during cold periods of the Pleistocene and of the Holocene, respectively. Late glacial assemblages from eastern Patagonia at 41°S are also consistent with colder and drier conditions than today (Markgraf, 1983). Eastern high elevations at Mediterranean latitudes, however, and the extreme edge of the puna in Jujuy (unlike the puna further north in Bolivia and Peru, and the Patagonia further south) were wetter than today during cold periods (Markgraf, in press). Such simultaneously wetter climates on the western (cf. Heusser, 1983) *and* eastern sides of the Andes at Mediterranean latitudes (out of the range of the Intertropical Convergence and hence very dry during the interglacials) are not unexpected; the greatly increased westerlies there relative to interglacial periods would have increased precipitation on the Pacific side of the Andes and augmented that making its way across the Andes.

As each interglacial ensued and climates warmed, the southwesterlies would have resumed their present position (Fig. 5) with the Intertropical Convergence coming back into play in the northern Andes as seen today. Because the Andes rose significantly during the several wet-cold and warm-dry cycles of the Pleistocene, east–west climatic differentiation must have increased as the Pleistocene progressed. As a result, aridity should have intensified at each new interglacial.

Throughout the climatically turbulent Pleistocene, nevertheless, the Atacaman region continued to support large mammals, including *Mastodon* and *Macrauchenia* (Mares, 1985). That such animals did not

TABLE 1. *Comparison of the number of species present (species richness) for the total vascular flora and for zonal and azonal (bog) components of each flora considered separately at different latitudes in the northern Chilean Andes. Number of species per genus and number of genera per family are also given for the total flora at each latitude.*[1] *See Figure 1 for exact locations. Latitude 18°S receives the most precipitation; latitude 24°S receives the least precipitation.*

	Summer Precipitation				Winter Precipitation	
	18°S	19°S	21°S	24°S	26°S	28°S
Total flora						
Number of species	391	219	164	77	144	270
Number of genera	195	138	110	55	90	162
Species/genus	2	1.6	1.5	1.4	1.6	1.7
Number of families	64	53	37	30	42	58
Genera/family	3	26	3	1.8	2.1	2.8
Zonal flora						
Number of species	333	190	141	59	110	200
% of total flora	85.2	86.7	86	76.6	76.4	74.1
Azonal flora (bogs)						
Number of species	58	29	23	18	34	70
% of total flora	14.8	13.2	14	23.4	23.6	25.9

[1] Species/genus and genus/family ratios exclude some Cactaceae of doubtful generic affinity.

become extinct until the end of the Pleistocene (Ochsenius, 1983a) agrees entirely with Axelrod's (1979b) suggestion that the climate on the western slopes of the northern Chilean Andes reached its present intensely arid state only very recently in Holocene times.

III: PATTERN OF DIVERSITY IN THE NORTHERN CHILEAN ANDES

SPECIES RICHNESS

Excluding a small number of systematic problems that still require attention, the succession of vegetation belts (desert scrub, Andean, high Andean) up from the desert edge to the upper vegetation limit on the six transects (Fig. 1) yielded 769 species in 290 genera of vascular plants. Five hundred twenty-one species have been collected on the four northernmost summer-rainfall gradients (Table 1). Here species richness peaks at mid elevation, where conditions are intermediately arid and cold (Fig. 6). The resultant curves tend to be steeper towards the north where the east–west precipitation gradient is most severe.

Three hundred twenty-seven species occur on the winter-rainfall transects at 26°S and 28°S; here maximum species richness, in contrast with the northern transects, occurs at lower elevations. These winter-rainfall transects nevertheless tend to show a mid-elevation bulge of their own which reflects the lowermost elevation of permanent winter snow in these areas.

Latitudinally, species richness drops off by 80% from 18°S (maximum rainfall from the

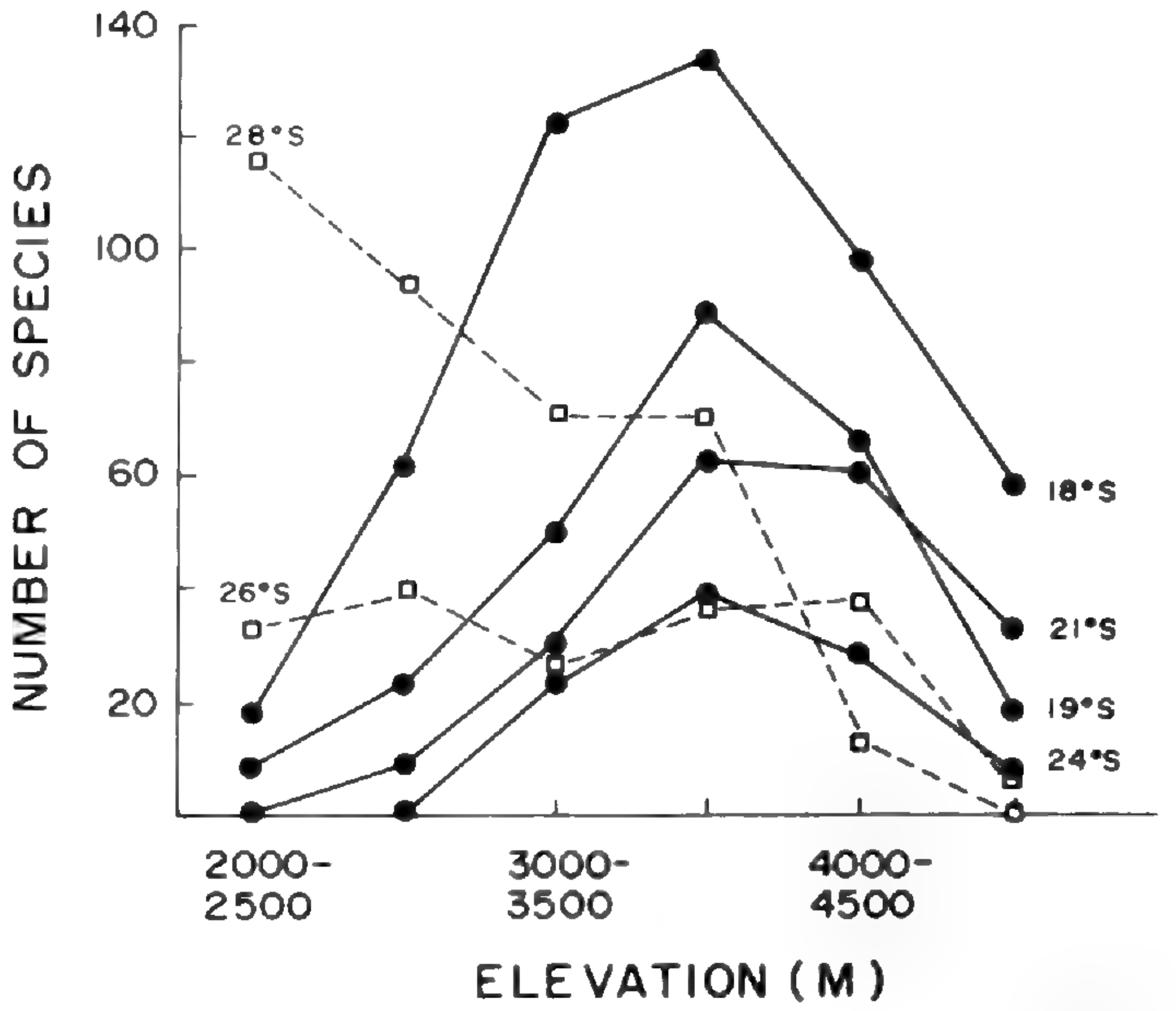


FIGURE 6. *Variation in number of species (species richness) with elevation at different latitudes in the northern Chilean Andes.* ● = *summer-rainfall zone (solid line)*; □ = *winter-rainfall zone (broken line).*

TABLE 2. *Life forms on the western (Chilean) and eastern (Argentine) side of the northern Andes. Data for the Chilean region correspond to the floras present on the six transects in Figure 1. Data for the Argentine region are from Ruthsatz (1977). The G-tests compare the percentage of a given life form for the pair of floras indicated. Estimates of precipitation for the western floras are averages of amounts used in the regressions in Table 3.*[1] *Estimates for the eastern floras are averages of weather station data reported in Ruthsatz (1977).*

	Western Andes			Eastern Andes	G-test (Western Comparisons)			G-test (East–West Comparisons)	
	18–19°S (A)	21–24°S (B)	26–28°S (C)	22–24°S (D)	A vs. B	A vs. C	B vs. C	D vs. A	D vs. B
2,000 3,000 m									
Estimated precipitation	68 mm	6 mm	—	200 mm					
Shrubs & trees	28 40.6%	7 70.0%	62 42.5%	53 40.8%	NA[2]	0.08; NS[3]	NA	No Significant Differences	NA
Perennial herbs	24 34.8%	2 20.0%	41 28.1%	58 44.6%	NA	1.00; NS	NA		NA
Annual herbs	17 24.6%	1 10.0%	43 29.4%	19 14.6%	NA	0.50; NS	NA		NA
	(69 spp.)	(10 spp.)	(146 spp.)	(130 spp.)					
3,000–4,000 m									
Estimated precipitation	153 mm	30 mm	—	249 mm					
Shrubs & trees	70 32.4%	32 36.0%	54 35.8%	84 34.1%	0.30; NS	0.48; NS	0.00; NS		0.06; NS
Perennial herbs	107 49.5%	32 36.0%	61 40.4%	131 53.3%	4.73*	3.00; NS	0.22; NS		5.92*
Annual herbs	39 18.1%	25 28.1%	36 23.8%	31 12.6%	3.67; NS	1.84; NS	0.52; NS		10.21***
	(216 spp.)	(89 spp.)	(151 spp.)	(246 spp.)					
4,000–5,000 m									
Estimated precipitation	266 mm	97 mm	—	330 mm					
Shrubs & trees	25 17.4%	32 37.6%	25 26.0%	42 17.9%	11.48***	2.6; NS	2.83; NS		12.68***
Perennial herbs	107 74.3%	43 50.6%	48 50.0%	175 74.8%	13.11***	14.80***	0.02; NS		16.16***
Annual herbs	12 8.3%	10 11.8%	23 24.0%	17 7.3%	1.84; NS	11.80***	4.60*		1.52; NS
	(144 spp.)	(85 spp.)	(96 spp.)	(234 spp.)					

[1] Precipitation data unavailable for 26–28°S; hydrological considerations (Ministerio de Obras Publicas, Santiago) suggest that this area is intermediate between 18 and 19°S for precipitation.

[2] G-test not applicable.

[3] Significance levels for G-test: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$; NS = not significant.

Intertropical Convergence) to 24°S (minimum rainfall from the Intertropical Convergence) (Table 1); however, recuperation is rapid around 26°S and 28°S in the influence of the winter-rainfall pattern. Species/genus ratios are low in all cases (1.4–2; Table 1), although *Senecio* (18°S: 26 species), *Adesmia* (28°S: 13 species), *Nototriche* and *Werneria* (18°S: 12 species each), *Stipa* (18°S: 11 species), *Deyeuxia* and *Baccharis* (18°S: 7 species each), *Calandrinia*, *Festuca*, and *Solanum* (18°S; 7 species each), and *Chaetanthera* (28°S: 7 species) are speciose. Under both precipitation regimes, as aridity increases, trends for fewer species per genus and fewer genera per family are seen (Table 1). Thus fewer genera and fewer species have survived in the most arid regions, and/or these appear to have undergone less local speciation. Precise records of precipitation for the highlands at 28°S are unavailable. Hydrological estimates (Ministerio de Obras Publicas, Santiago) suggest levels roughly similar to those midway between 18° and 19°S. Species richness is lower at 28°S than midway between 18° and 19°S, indicating that the decline in species richness from 18° to 24°S is probably slightly inflated by a small latitudinal effect independent of precipitation.

By comparing floras on the east side and west side of the Andes for areas with equivalent precipitation, the degree to which historical and biogeographical factors contribute to present richness patterns may be assessed. Similar amounts of precipitation are received at 18°–19°S on the Chilean side of the Andes and at 21°–24°S on the Argentinian side at 4,000–5,000 m (Table 2). Nevertheless, around a third more species occur on the eastern side, which experienced less severe fluctuations during the Pleistocene. Such lower richness levels on the western side of the Andes undoubtedly also reflect reduced north–south migration possibilities there on account of the desert extending above 3,000 m at 24°S (Arroyo et al., 1982; Villagrán et al., 1983). Thus, in addition to the direct effect of lowered precipitation on species richness, there seems to be a substantial indirect effect of the evolution of aridity.

TABLE 3. *Best fit regressions of number of species (species richness) on mean annual precipitation in the northern Chilean Andes. Each regression is based on species numbers at 18°S, 19°S, 21°S, and 24°S. Mean annual temperature for these latitudes is relatively constant with elevation (see Fig. 3)*. y = *number of species;* x = *mm precipitation. Degrees of freedom for all regressions = 2.*

Elevation	Regression	*F*-ratio[1]
2,000–2,500 m	$y = -0.17e^{0.05x}$	23.95***
2,500–3,000 m	$y = -0.60x^{0.98}$	3.78 NS
3,000–3,500 m	$y = 3.09e^{0.01x}$	4.61*
3,500–4,000 m	$y = 0.42x + 32.67$	18.09***
4,000–4,500 m	$y = 2.29x^{0.38}$	11.27**
4,500–5,000 m	$y = 0.12x + 5.03$	6.03*

[1] Significance levels for regressions: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$; NS = not significant.

A more precise appreciation of the combined indirect and direct effects of aridity on species richness in the northern Chilean Andes may be obtained by relating species richness to precipitation for areas with similar mean annual temperatures. Most regressions (best fits varied from a linear, through semilog to log–log model) (Table 3) were significant. The degree of curvature where fits were curvilinear, however, was always very shallow. The overall regression of species richness on precipitation, combining all elevations, was also highly significant ($F = 14.087$; d.f. = 22; $P = 0.002$), emphasizing very high penetrance of precipitation on species richness on a biogeographical scale. Aridity, moreover, completely obliterates the effects of temperature regionally. In the multiple regression of species richness on mean annual precipitation and mean annual temperature as independent variables ($y = 0.216x_1 + 0.017x_2$; d.f. = 21; $P = 0.005$, where x_1 is mean annual precipitation and x_2 is mean annual temperature), the partial regression coefficient for precipitation was highly significant ($P = 0.007$), whereas that for temperature (normally a strong determinant of species-richness patterns along elevational gradients) was nonsignificant ($P = 0.991$).

There are also clear reductions in total plant cover with aridity (Fig. 7). In the most benign of the wettest areas in the northern Andes, total cover does not exceed 50%.

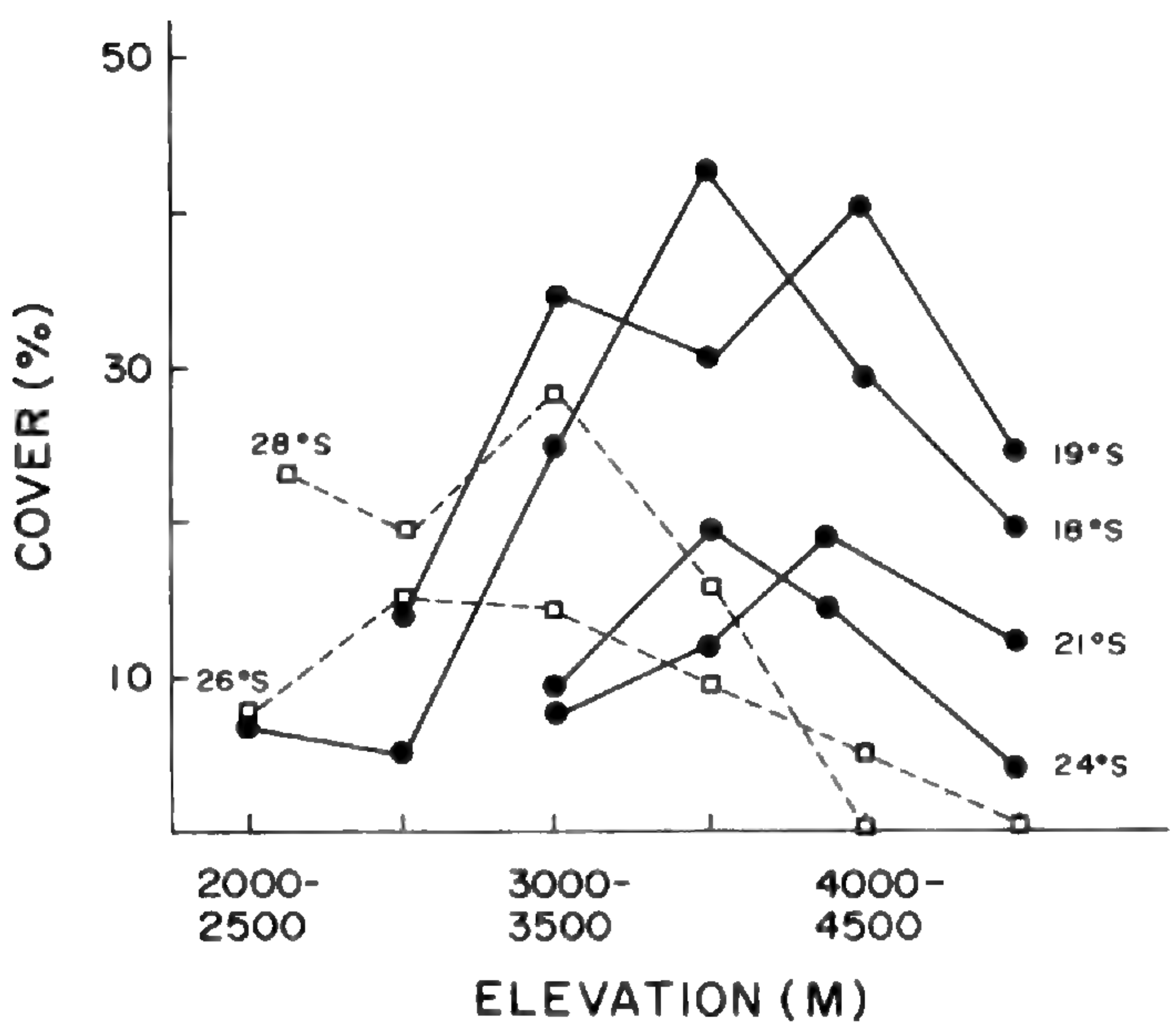


FIGURE 7. *Variation in plant cover (% of ground vegetated) with elevation at different latitudes in the northern Chilean Andes.* ● = *summer-rainfall zone (solid line);* □ = *winter-rainfall zone (broken line).*

However, at 24°S, less than 25% of total surface is covered. The regression of plant cover on plant species richness ($y = 0.22x + 8.21$; $F = 12.31$; d.f. = 17; $P = 0.003$) was highly significant. However, as indicated by the regression coefficient (also compare Figs. 6, 7), reduction in plant cover and species richness reduction are not strictly parallel. This suggests that although relatively few species survive on the most arid sectors of the northern Andes, some (e.g., *Adesmia polyphylla, Stipa frigida, Philippiamra fastigiata*) thrive. Species that are rare at latitudes 18°S and 19°S (e.g., *Portulaca philippii, Solanum phyllanthum, Dunalia spinosa,* many species of *Senecio*), on the other hand, are conspicuously absent on the drier 21°S and 24°S transects. Stochastic effects bearing on the smaller populations of such species perhaps have prevented survival in the most arid habitats. This last factor probably contributes to the lower species/genus ratios seen with severe aridity.

HIGH ANDEAN BOGS VERSUS ZONAL VEGETATION

In the wettest area of the northern Chilean Andes (18°S) above 4,000 m, previous freshwater lakes dating to the pluvial cycles of the Pleistocene support azonal cushion bogs (bofedales). In the driest areas (24°–26°S) such lakes have been reduced to salares with small marginal patches of bog vegetation. These important grazing resources for the Altiplano economy (Castro et al., 1982) contain such typical species as *Gentiana sedifolia, Azorella trifoliolata, Lachemilla* spp., *Werneria* spp., and *Colobanthus quitensis.* They are unique to the central and drier sectors of the southern Andes and are unknown in the far northern Andes, where azonal and zonal vegetation types tend to intergrade imperceptibly (Cleef, 1980).

Despite reduction in area suitable for development of bog vegetation towards 24°S in the northern Andes and the greater dependence of bog elements on fresh water, bog habitats have lost proportionately fewer species than zonal habitats (Table 1). For example, bog species constitute only 14.83% of the total flora at 18°S in comparison with 23.38% at 24°S.

Relatively lighter losses in species richness in the bog floras possibly result from new introductions repeatedly offsetting losses due to reduced habitat size. Figure 8 plots floristic divergence for zonal and azonal (bog) elements for all possible pairs of the six transects against the geographical distance separating each pair of transects. For both vegetation types, floristic divergence increases with distance; however, the bog floras are notably less disparate than the zonal floras for equivalent separation distances. Floristic affinity of the bog floras is higher because of lack of local endemic speciation and because the latitudinal ranges of bog species along the Andes are wider in comparison with zonal elements (Arroyo et al., 1982). The broader latitudinal ranges of bog species, in turn, may be related to aspects of reproductive biology. Many bog elements are strongly autogamous (e.g., *Colobanthus quitensis, Gentiana prostrata, Cardamine glacialis*), greater reliance on wind-pollination is also evident (Arroyo et al., 1983), and some dominant bog species (e.g., *Distichia muscoides, Oxychloe andina*) are clearly adapted for bird dispersal. These three features should facilitate long-distance dispersal between the islandlike high-Andean bogs, thereby maintaining their floras relatively homogeneous. They should also promote reintroductions of species lost due to reduced habitat size.

LIFE FORMS—INTERANDEAN TRENDS

Table 2 compares life-form spectra for the wettest (18°–19°S) and driest (21°–24°S) extremes of the summer-rainfall area (comparison A vs. B) and for the summer-rainfall areas vs. the winter-rainfall area (26°–28°S) (comparisons A vs. C & B vs. C) at three elevational levels. Comparing the wet and arid extremes of the summer-rainfall area, perennial herbs are statistically underrepresented at the arid extreme for 3,000–4,000 m and 4,000–5,000 m. Because of small numbers of species, the data for 2,000–3,000 m could not be tested statistically; however, a similar trend is evident with relatively fewer perennial herbs occurring at 21°–24°S. The difference is most pronounced in the upper Andean belt (4,000–5,000 m) and along the desert edge (2,000–3,000 m).

Woody species, in contrast, tend to be more strongly represented as aridity increases; the trend is clear in the driest (2,000–3,000 m) of the three vegetation belts and where aridity is overlain with cold stress (4,000–5,000 m). Contrary to expectations, annual herbs did not increase proportionately with greater aridity. For the mid-elevation belt (3,000–4,000 m) there is a weak, nonsignificant trend for more annual species at 21°–24°S; however, there were proportionately fewer annuals on the desert edge at 21°–24°S and no significant increase again in the upper Andean belt. The difference was exceedingly dramatic along the desert edge at 21°–24°S, where the flora is comprised of seven species of shrubs, two perennial herbs, and one annual (*Philippiamra fastigiata*). In the most stressful climate (aridity confounded by cold stress; 4,000–5,000 m; 21°–24°S) the relative loss of perennial herbs and annuals has been to the extent that the shrub life form becomes dominant for species number. Clearly therefore, in the summer-rainfall area in the northern Andes, the perennial herb life form has been most affected by aridity, followed by the annual herb life form; woody elements have been least affected.

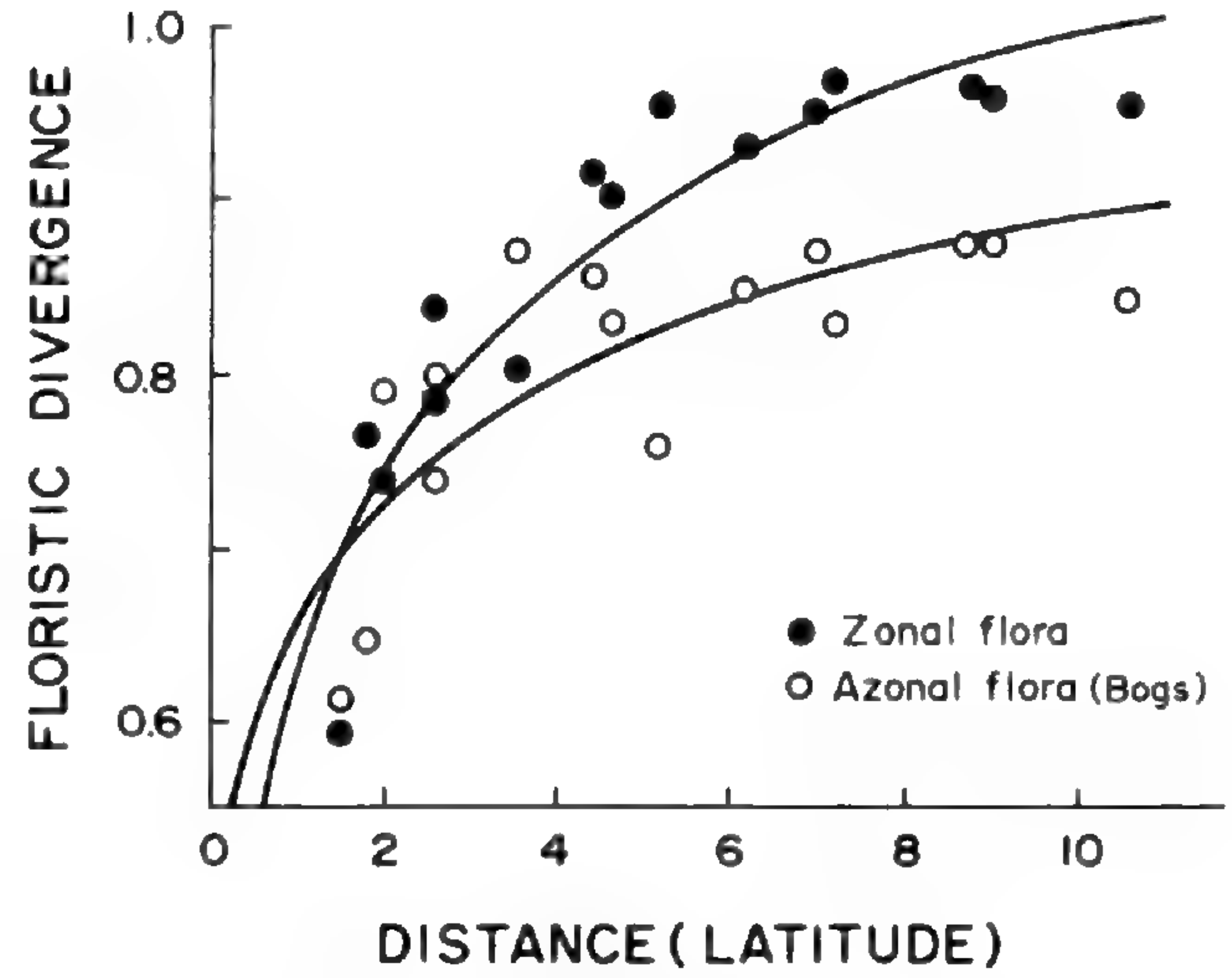


FIGURE 8. *Floristic divergence for all pairs of zonal and azonal (bog) floras between 18° and 28°S in the northern Chilean Andes plotted against the latitudinal distance in degrees separating the pairs of floras compared. Floristic divergence for pairs of floras* (A, B) = $(N_A + N_B) / (N_A + N_B + N_C)$, *where* N_A = *number of species confined to area* A; N_B = *number of species confined to area* B; N_C = *number of species common to areas* A *and* B.

For 26°–28°S (winter rainfall), intermediate proportions of annuals relative to 18°–19° and 21°–24°S were predicted. For the lowermost desert belt (2,000–3,000 m) and mid-elevation belt (3,000–4,000 m), there were no significant differences for any life form when 26°–28°S was compared with 18°–19°S (highest rainfall). For these latitudinal comparisons, however, annuals are more common and perennial herbs less common in the high-elevation (4,000–5,000 m) belt in the summer-rainfall area. When 26°–28°S is compared with 21°–24°S (lowest rainfall), contrary to expectation, annuals did not prove to be in excess in the 21°–24°S area. For the mid-elevation belt (3,000–4,000 m), as is indicated by the nonsignificant difference, the winter-rainfall area has proportionately just as many annual species as the much drier 21°–24°S summer-rainfall region. For the low- and high-elevation belts there are more annuals at 26°–28°S than in the very low rainfall area at 21°–24°S. The higher proportion of annuals at 26°–28°S, where there is winter snow (and hence much local moisture) in place of rainfall received gradually over the summer months, as at 21°–24°S, again suggests that the annual life form is only adaptive in arid climates up to a certain limit.

To test the robustness of these trends (decrease in perennial life form, increase in annual life form up to a certain level of aridity, dominance of shrub habit in areas of extreme aridity) over a wider sector of the Andes, we compared our data with higher rainfall Andean communities on the eastern side of the Andes (Ruthsatz, 1977) situated immediately opposite the most arid area of the Chilean Andes considered by us (Table 2). Ruthsatz (1977) gave the life forms of over 90% of the species she considered. For 22°–24°S (east) and 18°–19°S (west), most similar in precipitation amounts, there were no significant differences in life forms for any of the three altitudinal levels (comparison D vs. A; Table 2). From east (22°–24°S) to west (21°–24°S) over a very severe rainfall gradient (comparison D vs. B) the life form trends were in very good agreement with those seen previously in north–south comparisons along the western side of the Andes: i.e., perennial herbs are more strongly represented on the wetter eastern side of the Andes and shrubs more strongly represented on the drier western side in the most extreme environments, with annuals increasing only in the more benign mid-elevation belt on the western side. Thus the life-form tendencies revealed on the western side of the northern Andes are also valid on a regional scale.

LIFE FORMS—INTERCONTINENTAL COMPARISONS

Collins et al. (1983) provided life-form data for an altitudinal sequence of floras in the Great Basin in Utah, North America, sharing several floristic elements with the Andes (e.g., *Atriplex, Ephedra*) but where rainfall is generally higher. Comparisons for the Andes and Great Basin vegetation belts with similar mean annual temperature (Table 4) reveal the same life-form trends seen across aridity gradients within the Andes, now on an intercontinental scale. For the Andes, with lower precipitation, the woody life form is twice as common and the perennial herb life form only one-half to one-third as common as in the Great Basin. Annual herbs are in excess in the mid-elevation belt on the western side of the Andes compared with Mt. Nebo. However, despite the much lower rainfall along the desert margin and in the high-elevation belt compared with Arches and Bald Mountain, respectively, there is no proportional increase for annuals in these harshest climates in the Andes. This once again emphasizes that annuals increase with aridity but that there is a critical point at which the woody habit becomes relatively more appropriate for arid climates.

Most surprisingly, as the Arches vs. 2,000–3,000 m (22°–24°S, eastern Andes) shows, woody species continue to be in excess and perennials in deficit in the Andes when annual precipitation is relatively similar. This indicates that the northern Andes exhibit a generalized excess in woody species over the Great Basin beyond local trends in the latter for increased frequency of woody species with habitat harshness.

COMMUNITY DIVERSITY PATTERNS

In harsh arid habitats, as was argued earlier, relatively higher community diversity levels, as seen at the early stages of primary succession, are to be expected as a permanent community feature in spite of overall low species richness.

In the Andes, regressions of exp H' and $1/\lambda$ on species richness and cover show (Figs. 9, 10) that harsh environmental conditions, on a biogeographical scale, lead to an overall trend for loss of diversity. Thus the primary succession analogy proposed is not entirely supported. Over each gradient (Fig. 11) diversity peaks at mid elevations, where conditions are neither the coldest nor the most arid, as was seen for species richness and cover; however, decreases in diversity are not commensurate with reductions in species richness. This phenomenon is more easily appre-

TABLE 4. *Statistical comparisons (G-tests) for life forms in the flora of the northern Andes (west and east sides) and the Great Basin, Utah. Comparisons are made for elevational levels with the closest mean annual temperatures. Data for the Andean areas are those in Table 2. Data for the Great Basin taken from Collins et al. (1983).*

		G-test (Utah vs. Western Side of Andes)		G-test (Utah vs. Eastern Side of Andes)
Great Basin, Utah		18–19°S (2,000–3,000 m)	21–24°S (2,000–3,000 m)	22–24°S (2,000–3,000 m)
Arches (1,200 m)				
(13.5°C; 217 mm)[1]		68 mm	6 mm	200 mm
Shrubs & trees	18.32%	12.59*** (Andes[2])	NA[4]	17.66*** (Andes)
Perennial herbs	62.73%	11.80*** (Utah)	NA	12.34*** (Utah)
Annual herbs	18.94%	3.09; NS[3]	NA	1.20; NS
(322 spp.)				
Mt. Nebo (2,500 m)				
(9.4°C; 641 mm)		153 mm	30 mm	249 mm
Shrubs & trees	12.98%	37.88*** (Andes)	25.48*** (Andes)	48.12*** (Andes)
Perennial herbs	76.51%	53.04*** (Utah)	56.58*** (Utah)	44.08*** (Utah)
Annual herbs	10.51%	5.90* (Andes)	17.82*** (Andes)	0.76; NS
(647 spp.)				
Bald Mt. (3,200 m)				
(−2.4°C; 1,028 mm)		266 mm	97 mm	330 mm
Shrubs & trees	8.96%	6.38* (Andes)	26.48*** (Andes)	5.85* (Andes)
Perennial herbs	85.82%	5.86* (Utah)	32.81*** (Utah)	6.50* (Utah)
Annual herbs	5.22%	1.10; NS	3.19; NS	0.29; NS
(134 spp.)				

[1] Mean annual temperature and mean annual precipitation.
[2] Area for which life form is proportionately better represented.
[3] Significance levels for G-test: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$; NS = not significant.
[4] G-test not applicable.

ciated in Figure 12, in which diversity and species richness are compared for equivalent elevations from the wetter 18°S to the drier 24°S. At 3,000–3,500 m and 3,500–4,000 m, where conditions are more favorable on each transect, there are significant reductions in diversity as aridity increases; however, they are shallower than for species richness. As higher elevations doubly stressed by aridity and cold temperature are reached, there is no significant difference in diversity from 18° to 24°S in spite of considerable reduction in species richness. Thus, in the sense that community diversity is maintained relatively high in the face of large losses in species richness, the diversity trends seen in the most arid areas of the northern Andes are indeed analogous to a primary succession situation.

The more gradual loss of diversity relative to species richness may be related to the relative contribution of each life form and the presence of far more rare species in the relatively benign areas. In the most productive environments (18°S), one life form typically stands out as strongly dominant. Moreover, within that life form a few fairly abundant species tend to be accompanied by large numbers of relatively rare species. At mid elevations at 18°S, for example, in spite of the fact that *perennial herbs* are well represented in numbers of species (see section on life forms), the woody life form is more abundant than the herbaceous life forms (which can persist in low densities because of the relatively benign conditions). Within the shrub guild, close coexistence, moreover, seems to have precipitated fairly strong dominance hierarchies as seen in great abundance of such

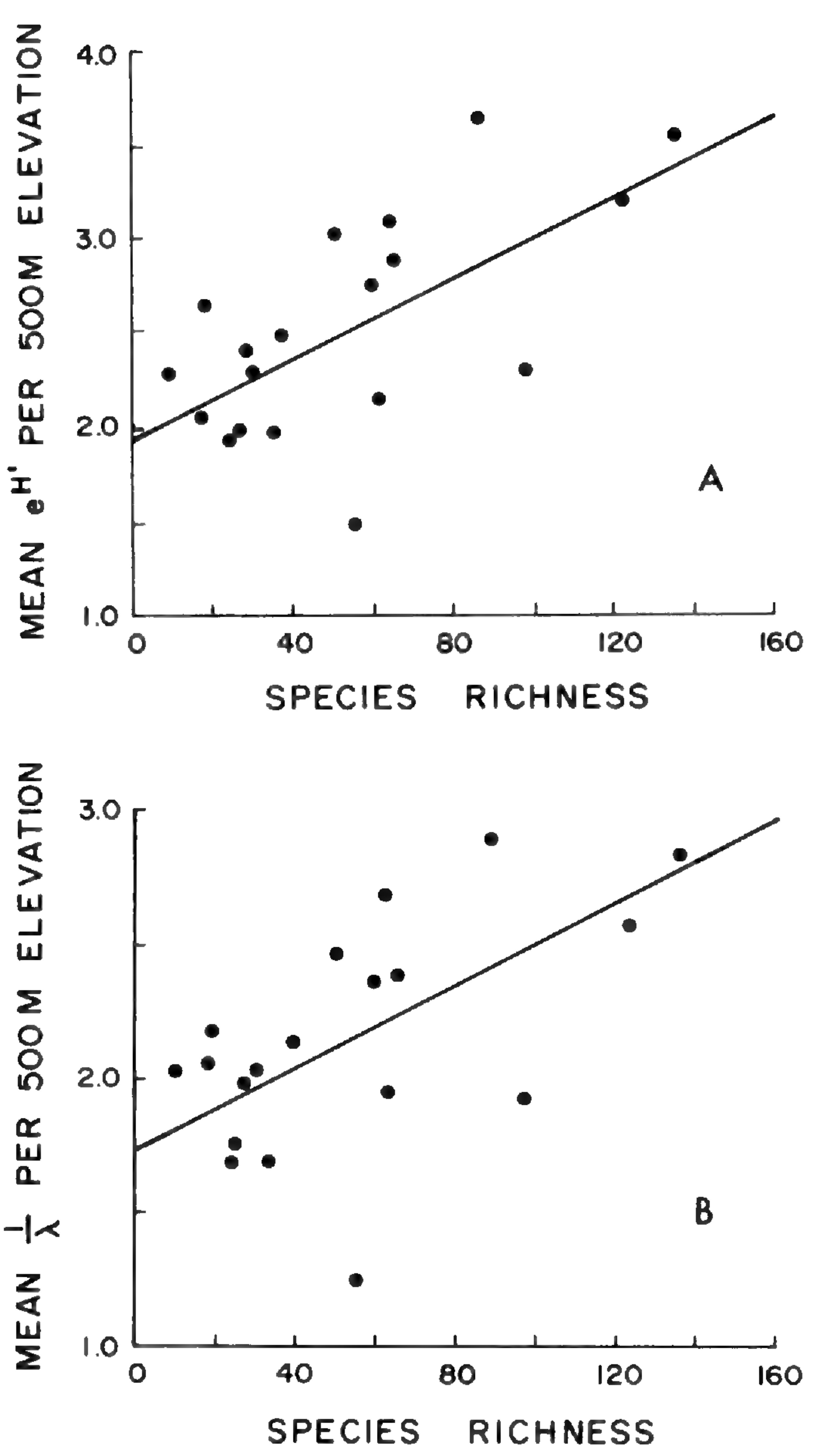


FIGURE 9. *Linear regressions of diversity on number of species (species richness).—A. exp H' vs. species richness* ($y = 0.010x + 1.96$; $F = 11.511$; *d.f.* $= 17$; $P = 0.003$, *where* $y = \exp H'$ *and* x = *species richness).—B.* $1/\lambda$ *vs. species richness* ($y = 0.019 + 0.007x + 1.78$; $F = 2.811$; *d.f.* $= 17$; $P = 0.01$, *where* $y = 1/\lambda$ *and* x = *species richness). Points on graphs correspond to 500-m elevational intervals on the four summer-rainfall transects.*

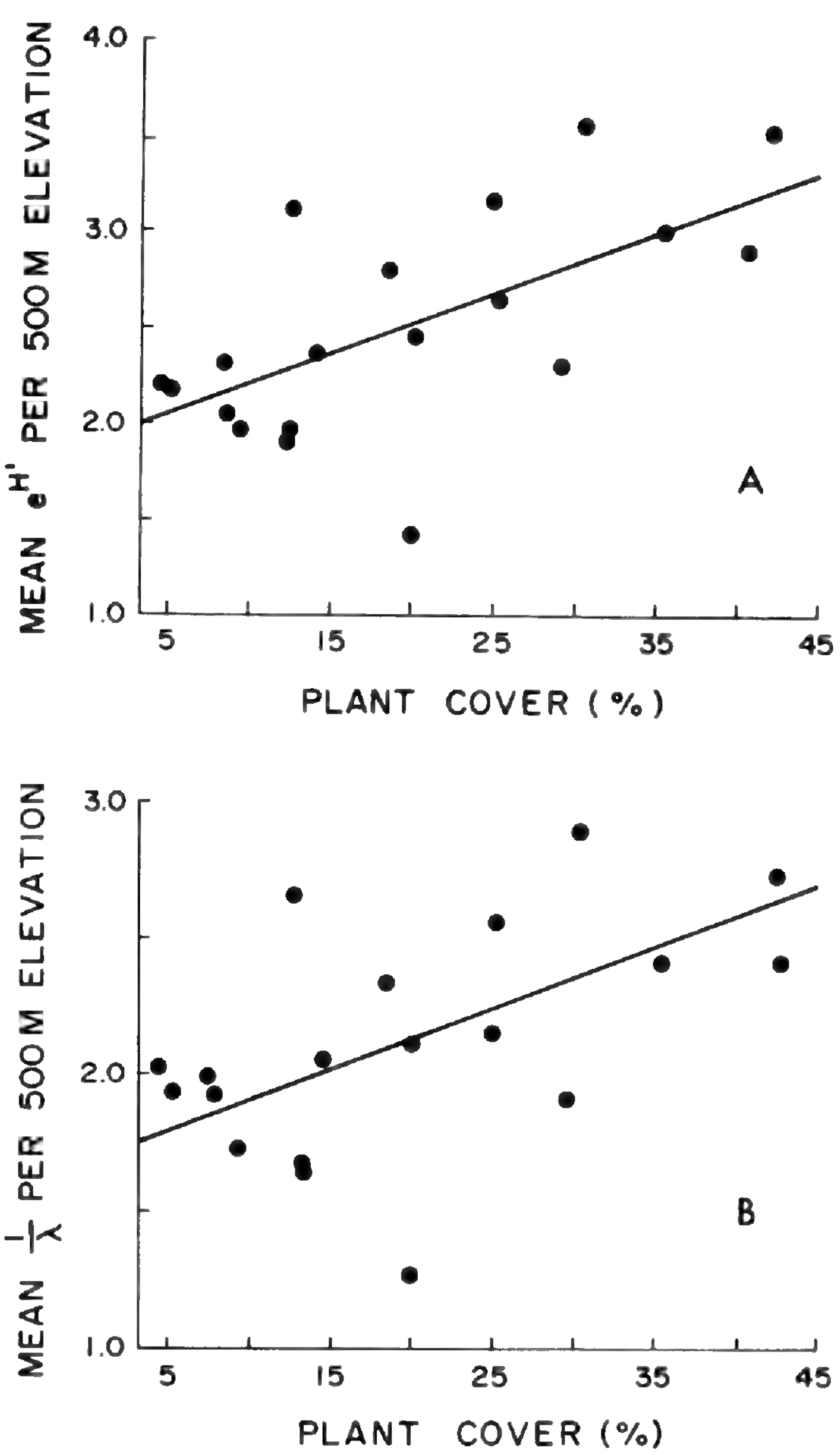


FIGURE 10. *Linear regressions of diversity on plant cover (% ground vegetated).—A. exp* H' *vs. plant cover* ($y = 0.032x + 1.904$; $F = 12.06$; *d.f.* $= 17$; $P = 0.005$, *where* $y = \exp H'$ *and* x = *plant cover).—B.* $1/\lambda$ *vs. plant cover* ($y = 0.019x + 1.762$; $F = 7.06$; *d.f.* $= 17$; $P = 0.05$, *where* $y = 1/\lambda$ *and* x = *plant cover). Points on graphs correspond to 500-m elevational intervals on the four summer-rainfall transects.*

species as *Fabiana densa, Baccharis boliviensis, Ephedra breana,* and *Diphlostephium meyenii.* From 4,500 to 5,000 m at 18°S, bunch grasses become strongly dominant over shrubs, and again there are few strongly dominant species (*Festuca orthophylla, Poa* sp.). In the less productive environments at 21°–24°S, in contrast, for the high elevations in particular, abundance levels for shrubs and herbaceous species are probably more equitable, in spite of the fact that there are relatively fewer species of perennial herbs. These last considerations are based on direct observation; much analytical work is still required to characterize dominance relations in the Andean flora.

DISCUSSION

Patterns of plant diversity have been described for an area that underwent dramatic environmental upheavals in the Pleistocene and which acquired its present extreme arid character over a relatively short period.

The effects of aridity on species richness in the northern Andes clearly have been severe. The 769 species for all transects are believed to include about 75% of all species

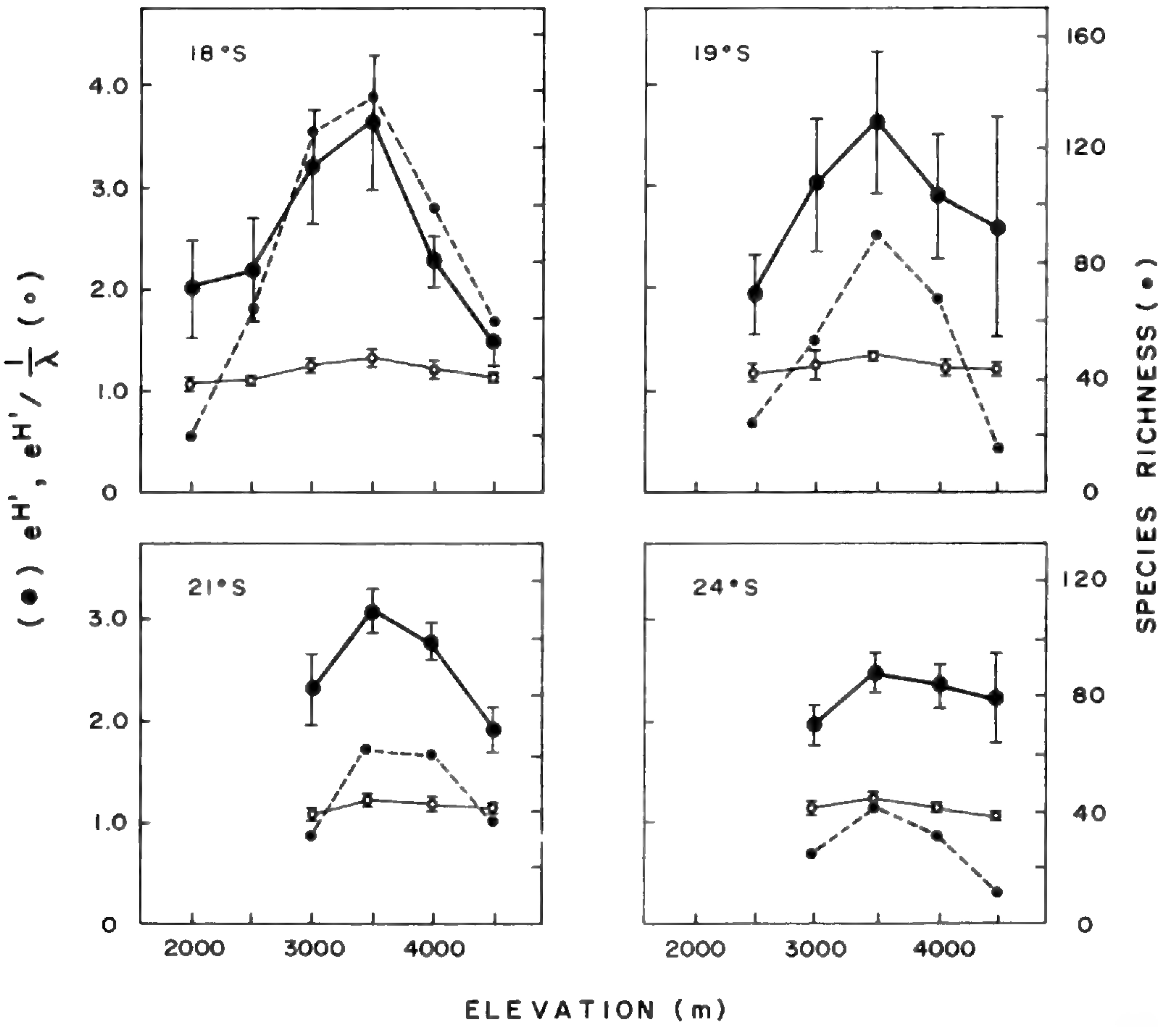


FIGURE 11. *Mean exp* H', *exp* H'/ (1/λ), *and species richness vs. elevation at different latitudes in the northern Chilean Andes. Lack of variation in exp* H'/ (1/λ) *indicates that diversity trends resulting from application of 1/λ as a diversity index are similar to those obtained using exp* H'. *Vertical bars are 95% confidence intervals for the means.*

from 1,500 m to the upper vegetation limit from 17°S to 28°S. This leads to an estimate of under 1,000 species per 10° latitude or the equivalent of less than one-fifth of the total Chilean flora (Marticorena & Quezada, 1985). This is only one-sixth more species present over 1° of latitude from 3,500 to 5,000 m in Parque Nacional Huascaran (8°S) in the northern Peruvian Andes (estimated by David Smith, pers. comm., to have 660 species). It is only just over three times the number above tree line (309 species) at 33°S (Arroyo et al., 1983) for an area similar to that sampled in the individual northern transects and in the paramos of Colombia (4°N; Rangel et al., 1983), where 321 species occur above tree line on an area covering much less than 1° of latitude. The Andes of Jujuy in northwestern Argentina (22°–24°S) immediately across the main divide, where it was seen that rainfall is much higher, support 622 species (Ruthsatz, 1977), in contrast to only 199 at 21° and 24°S on the Chilean side.

Areas least affected by aridity and cold temperature proved to be richest in species. Such areas also exhibit high community diversity. Highly stressed areas with low species richness, nevertheless, are relatively robust for community diversity. Any seasonal variation in annual growth, as along the desert edge, could greatly affect community diversity estimates. Revisits to the Andean highlands in from Arica (18°S) in a very wet year subsequent to vegetation sampling leave little doubt that annual cover at lower elevations there fluctuates widely. However, the trends above 4,000 m, where there are very few species of annuals, are unambiguous.

Maintenance of relatively high local levels of community diversity in the most arid areas will probably turn out to be the result of lowered dominance levels in the drier areas. Thus aridity, the very feature driving lowered species richness in the Andes from the outset, probably eventually reduces the rate at which local diversity declines. In this sense the not

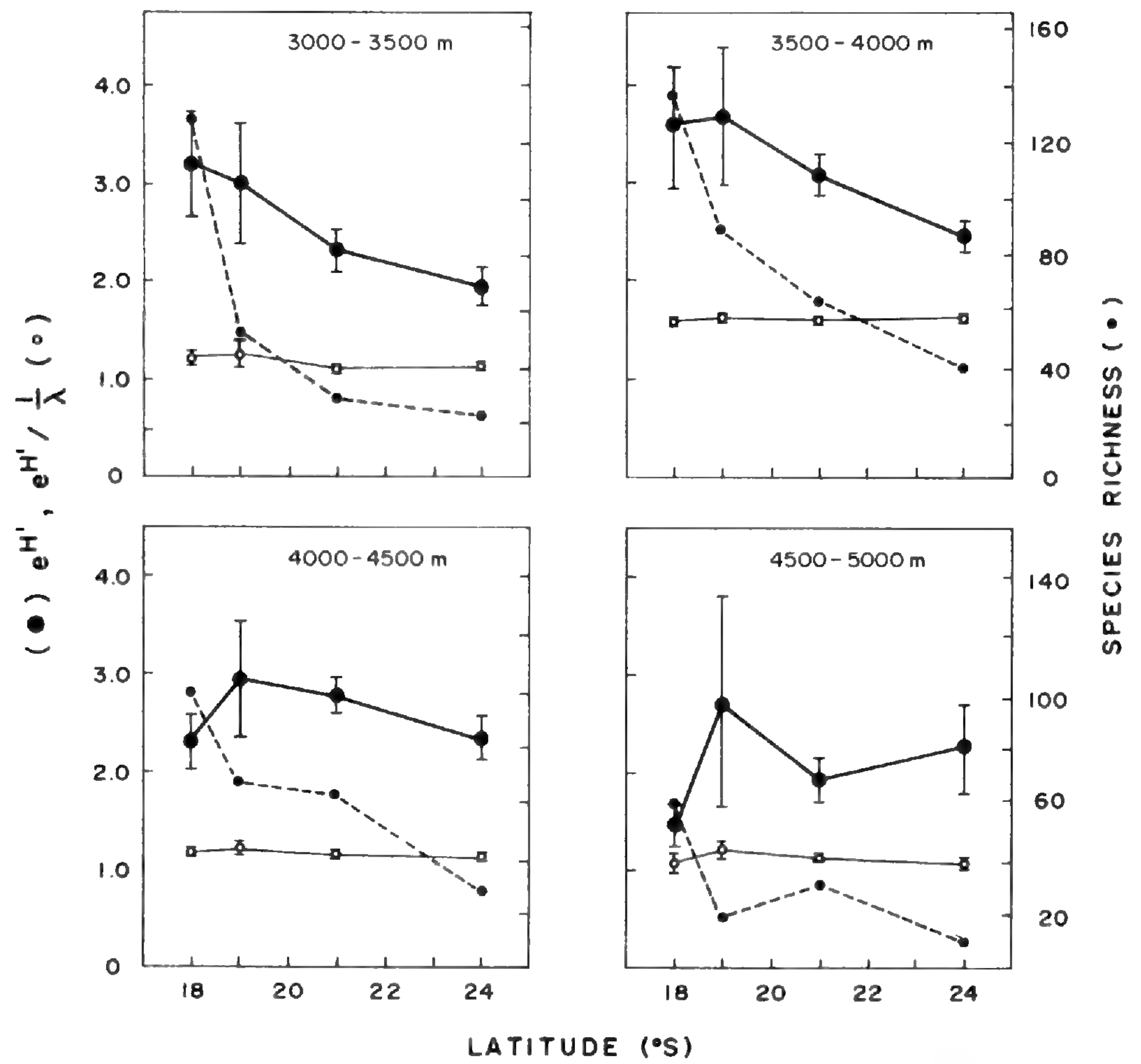


FIGURE 12. *Mean exp* H', *exp* H'/ $(1/\lambda)$, *and species richness vs. latitude from 18°S (maximum precipitation) to 24°S (minimum precipitation). Lack of variation in exp* H'/ $(1/\lambda)$ *indicates that diversity trends resulting from application of* $1/\lambda$ *as a diversity index are similar to those obtained using exp* H'. *Vertical bars are 95% confidence intervals for the means.*

strongly exponential drops in species richness with aridity should be recalled. They seem to indicate that loss of species richness has been counteracted to some extent. The life-form changes we have demonstrated must also be important here; however, it is far too early to sort out the relative contributions of different factors against species richness loss.

Stress-tolerant (e.g., annual life form) and stress-resistant (e.g., shrub life form) strategies are often considered as hierachically equivalent alternatives for harsh environments. Our results suggest that woody species gain prominence over annuals on the harshest of the Andean habitats. Significantly, moreover, some of the most successful "perennial herbs" from the driest areas of the Andes (e.g., *Sisymbrium philippianum, S. lanatum, Tarasa operculata*) have semiwoody stems. Thus the trend towards woodiness goes beyond simple reshuffling of the taxa present and is probably being actively selected for in some individual taxa.

Woody species are probably best adapted to extreme aridity through a combination of ecophysiological and demographic features. Root/shoot ratios for warm-desert species are usually around one, and there is relatively little vertical root growth (Barbour, 1981). In contrast, root/shoot ratios in excess of four have been reported for shrubs in cold North American and Eurasian deserts (Caldwell, 1985). This suggests that for cold arid areas, where growth is relatively slow, large long-lived species might be favored by being able to produce larger root systems that would reach deep into the soil over a prolonged growth season. Soils in the northern Chilean Andes are largely volcanic, hence surface water is probably always limited. Further, in the driest areas of the summer-precipitation zone, rain comes in light morning showers and is never abundant at any one time. We suspect that this factor favors shrubs in the driest areas and, as was mentioned earlier, explains why annuals are generally less frequent in the summer-rainfall zone.

Because they tend to be long-lived, woody species require less frequent establishment events (Schaffer & Gadgil, 1975). This should be highly advantageous in habitats where seed germination and seedling establishment are precarious, as is the case with strongly arid climates. Seed production is not only a function of pollination success and of resources allocated to reproduction, but also of the probability of an adult reaching reproductive maturity and its physiological state at that stage. Woody-stemmed shrubs are more likely to reach reproductive maturity than soft-stemmed herbs because of their greater resistance to drought. In spite of the fundamental nature of the question, as far as we know, to date there have been no attempts to appraise the relative importance of the physiological and demographic features of woody species in harsh environments.

The greater representation of woody species in the northern Andes might reflect the Andes being located some ten degrees of latitude closer to the equator than is the Great Basin. The floristic matrix out of which the Andean flora evolved, as a result, probably possessed a higher percentage of woody elements initially. Fossil floras for the Great Basin (Axelrod, 1979a, 1983) and as far south as the Chihuahuan desert (Wells & Woodcock, 1985) show North American desert floras emerging out of open woodland with many herbaceous elements. The radical climatic changes at each glacial/interglacial interface in the Andes should have further impoverished the herbaceous flora. These historical factors, apart from effects of present climatic characteristics, should have produced a gradual accumulation of woody elements in the northern Andes.

Heavy grazing in the Andes (alpaca, llama) has possibly influenced the broad intercontinental differences in life form. Interestingly, areas of the northern Andes in which woody species are most strongly represented today are least affected by grazing (e.g., 21°–24°S), while those with well-developed herbaceous floras can be heavily grazed (north of 19°S). Very plausibly, climatic and biotic factors have acted in concert to produce the intercontinental differences in life form.

Emphasis on the long-lived, woody life form, as seen in harsh environments in the northern Chilean Andes, is also a feature of tropical and other forests developed in abiotically benign conditions. For the tropics in particular, longevity is usually seen as a correlate of large body size resulting from selection for competition for light (Grime, 1979). Much woodiness in the tropics could equally bear relation to the demographic advantages of being long-lived, as was suggested for abiotically harsh habitats. In the tropics, seed predation (Ramirez & Arroyo, 1987) and fungal infections (Ramirez & Arroyo, 1984) can significantly lower successful seed germination. Additionally, juvenile mortality can be high due to strong intra- and interspecific competition for light and nutrients (Connell et al., 1984) and leaf predation (Clark & Clark, 1985). These features have direct parallels in the extremely arid Andean ecosystem, the difference being that in the tropics they are mediated through the biotic environment rather than the abiotic environment. Grime (1979) recognized that "stress" in productive environments arises mainly through competitive depletion of resources (the biotic environment). Yet he perhaps placed undue emphasis on longevity in tropical ecosystems as being a result of selection for direct competitive ability without paying much attention to the demographic advantages. As in arid environments, the role of longevity for tropical forests needs more critical assessment.

Diversity patterns in the kinds of "abiotically" harsh environments we studied and in "biotically harsh" tropical forest communities might also show convergent trends. Many tropical forests lack clear dominants—dominance is probably less well developed in the most arid environments we studied. Lack of dominance in tropical forests has been seen as an effect of reduced opportunities for coevolution resulting from low interspecific connectance sensu Pimm (1984) (Connell, 1980), or in Buckley's (1983) words, "in diverse, well-mixed communities individuals cannot predict their neighbours." Hubbell & Foster (1986) proposed a similar but not identical hypothesis: individual species are seen to reflect the temporal and spatial average of biotic selective conditions created by ever changing and diffuse competitors, leading to guilds of functionally equivalent generalists. Sustained biotic interactions are also seen to be limited in very arid environments. Wetter deserts like the Mohave and Sonoran provide some evidence of root competition between widely spaced individuals (Yeaton & Cody, 1976; Phillips & MacMahon, 1981). Gulmon et al. (1979), by contrast, concluded that limited opportunities for establishment lead to little competition between individuals of the long-lived *Copiapoa* (Cactaceae) in the Chilean coastal desert at 25°S, where ca. 25 mm of rain falls annually. This is tantamount to low connectance, the abiotic environment assuming the role of the biotic environment in a tropical forest.

We suspect that a suite of common features will be revealed for these two kinds of "harsh" environments for the organisms that inhabit them. Convergence could be expected in breeding system (e.g., levels of sexual dimorphism), seed size, and sexual selection. Some of these possibilities are presently being studied by us in cold alpine habitats in the Chilean Patagonia (e.g., Arroyo & Squeo, 1987).

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PATTERNS OF SPECIES DIVERSITY IN ANURAN AMPHIBIANS IN THE AMERICAN TROPICS[1]

William E. Duellman[2]

ABSTRACT

The Neotropical Region has a greater species richness of anuran amphibians than any other region in the world. Approximately 44% of the total number of species of anurans of the world (3,533) occur in the American tropics, and many new species are discovered every year. Patterns of species diversity were determined by analyzing data from 48 sites—32 in the lowland tropics (11 Middle American, 21 South American), nine in montane cloud forests (four Middle American, five South American), and seven in supra-treeline regions of the Andes. Taxa also were noted as to their reproductive mode (site of egg deposition, site of larval development, and associated parental care, if any). As expected, for the entire anuran fauna, there are gradients from lower diversity in dry regions to higher diversity in wet regions, and from lower diversity at high elevations to higher diversity at low elevations. The greatest species diversity is in the equatorial region of the upper Amazon Basin. However, different patterns emerge when taxonomic groups (families, subfamilies, and large genera) are examined independently. Two factors contribute significantly to the different patterns observed: (1) the historical biogeography of different taxa, especially in relation to the separation of Central America from South America during most of the Cenozoic, and (2) reproductive modes of the taxa. Seventeen reproductive modes can be identified among anurans at the 48 sites. The generalized reproductive mode (eggs and tadpoles in lentic water) is characteristic of all lowland sites but is rare or nonexistent in montane regions where there are few ponds. Some reproductive modes involve terrestrial eggs and/or larvae that are dependent for their survival on high moisture content of the air; anurans having these modes are most diverse in regions having high humidity. Other modes necessitate the presence of high-gradient streams or aerial aquatic habitats (bromeliads) for the development of eggs and tadpoles. Sites having the highest species diversity also have the greatest diversity of reproductive modes; these sites are in lowland rainforest near the base of the Andes and in the Atlantic forest of southeastern Brazil at the edge of the Brazilian Highlands. Thus, although total species diversity in anurans is dependent on rainfall, patterns of diversity of component groups results partly from their geographic histories and partly from the consequences of the nature of their reproductive modes.

Despite the fact that most amphibians have rather narrow physiological tolerances and ecological distributions, in their successful attainment of independence from water and the colonization of the land they have undergone a remarkable adaptive radiation. The living amphibians exhibit a greater diversity of life histories than any other vertebrates. The nearly 4,000 living species of amphibians are grouped into three distinct orders—Caudata (salamanders), Gymnophiona (caecilians), and Anura (frogs and toads). The last is by far the largest, with 3,533 currently recognized species.

Anyone who has spent a rainy night in a neotropical rainforest is aware of the nocturnal cacophony raised by calling males of many species of frogs. The American tropics are especially rich in species of anurans; at one site in the upper Amazon Basin in Ecuador

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[1] *The compilation of data from so many sites has been possible through the generosity of several colleagues who provided unpublished data on their own fieldwork; for their kind help I am grateful to Patricia A. Burrowes, Ronald I. Crombie, W. Ronald Heyer, John D. Lynch, Roy W. McDiarmid, Norman J. Scott, and Barbara L. Zimmerman. My own studies on neotropical anurans have been supported by the Museum of Natural History at The University of Kansas and by grants from the National Science Foundation and the National Geographic Society. Many persons have assisted me in the fieldwork, but I am especially indebted to John E. Simmons and Linda Trueb.*

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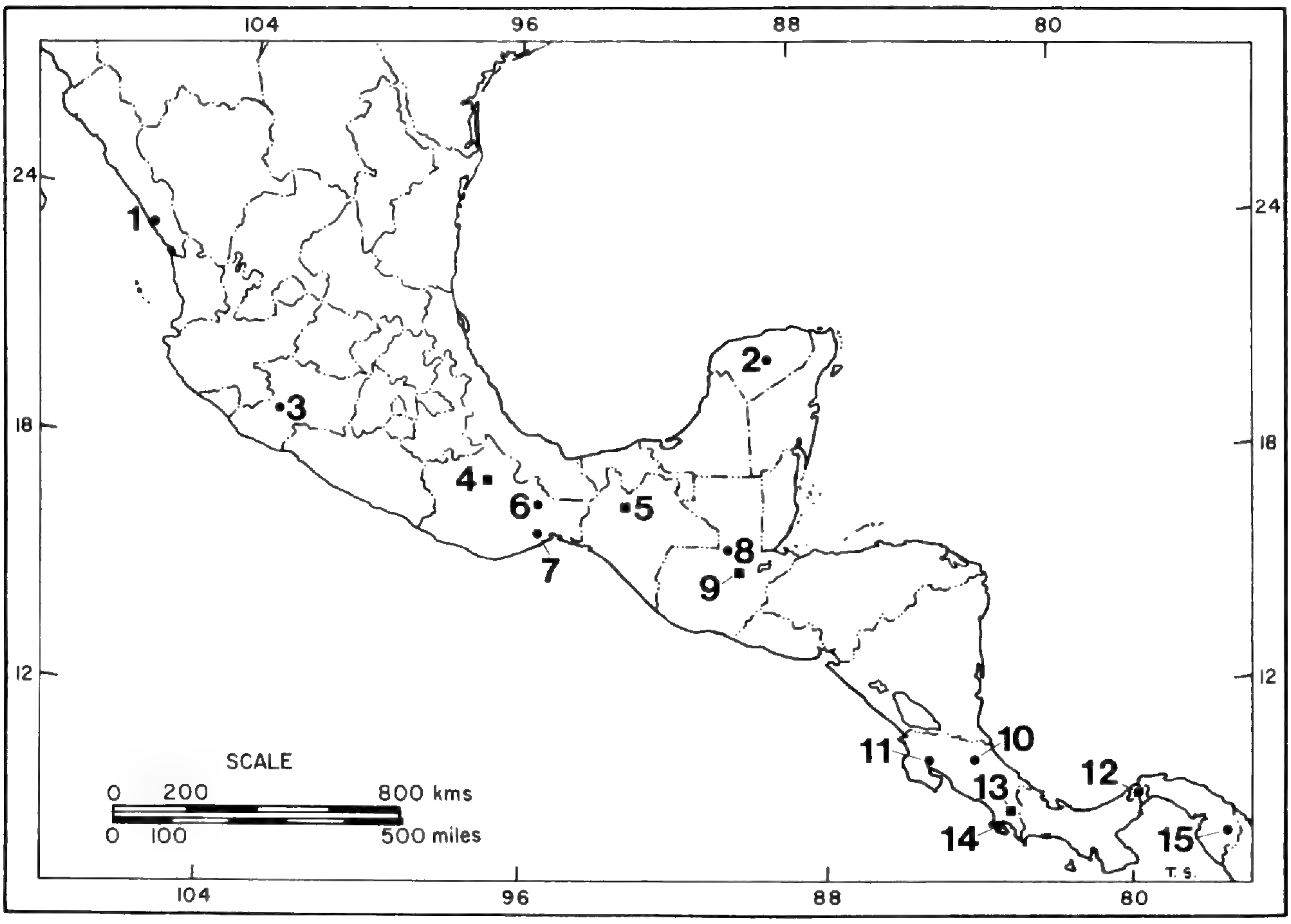

FIGURE 1. *Study sites in Mexico and Central America. Dots are lowland sites; squares are montane cloud forest sites. Numbers refer to the list of sites in the text: 1 = MAZA, 2 = PIST, 3 = APAT, 4 = VHER, 5 = RMES, 6 = SARA, 7 = TEHU, 8 = CHIN, 9 = PURU, 10 = LSEL, 11 = TABO, 12 = BCIS, 13 = CRUC, 14 = RINC, 15 = TUIR.*

there are more species of anurans than occur in all of the United States and Canada (Duellman, 1978). The diversity is much higher than on other Gondwanan continents—56.0 species/million km^2 in South America, as compared with 11.7 in Africa and 20.1 in Australia (Duellman, 1979a). Therefore, the American tropics represent an ideal region for investigation of patterns of species diversity in anuran amphibians. Salamanders and caecilians have been omitted because the former are poorly represented in South America and because the latter are too poorly known to be analyzed.

The purposes of this paper are to (1) summarize data on species diversity from many sites in the American tropics, (2) examine the patterns of species diversity, and (3) interpret these patterns in relation to present climatic patterns, historical biogeography, and reproductive modes. I consider the term species diversity to be synonymous with species density and species richness.

MATERIALS AND METHODS

For purposes of defining the anuran fauna of tropical America, I did not include any species confined to Argentina, Chile, or Uruguay, and I included no North American species that do not range into the tropical regions of Mexico. Lists of species of anurans were obtained for 48 sites in tropical South America, including the Andes (Figs. 1, 2); no sites were incorporated from the West Indies. Each site is a relatively small area, usually encompassing fewer than 10,000 hectares. I have worked at 30 of the sites.

In the following list of sites, each is identified by an abbreviation (used in tables), name, geographical coordinates, elevation, vegetation formation (Holdridge, 1964), and ref-

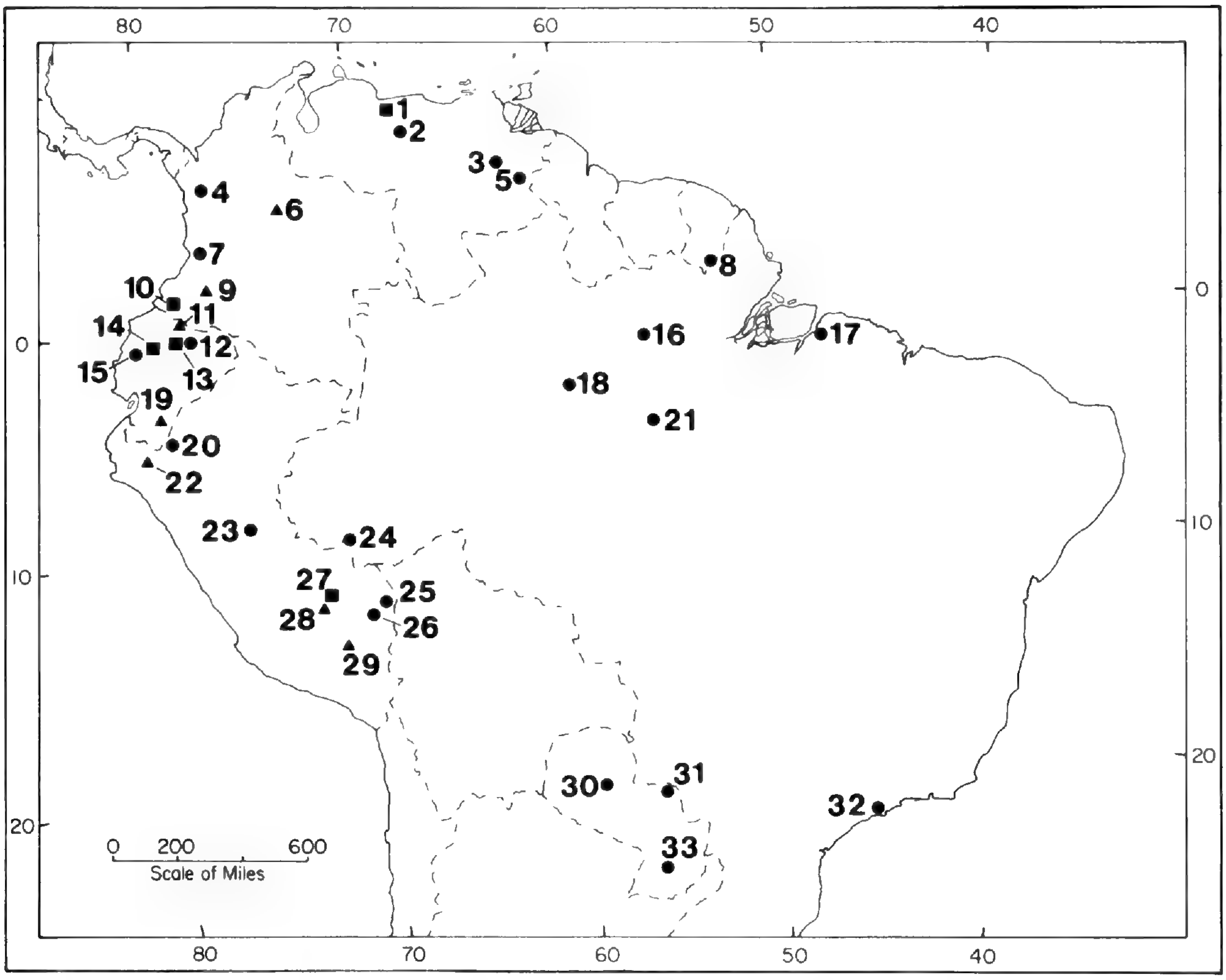

FIGURE 2. *Study sites in South America. Dots are lowland sites; squares are cloud forest sites, and triangles are high-Andean sites. Numbers refer to the list of sites in the text: 1 = RGRA, 2 = MASA, 3 = MANT, 4 = AMPA, 5 = CUYU, 6 = RUSI, 7 = CALI, 8 = OYAP, 9 = PURA, 10 = PLAN, 11 = ANGE, 12 = SCEL, 13 = SALA, 14 = QZAP, 15 = PALE, 16 = TROM, 17 = BELE, 18 = MANA, 19 = AZAM, 20 = CENE, 21 = TAPA, 22 = AHUA, 23 = PANG, 24 = BALT, 25 = CAMA, 26 = TAMB, 27 = COSN, 28 = ACAN, 29 = SROS, 30 = FILA, 31 = CCOR, 32 = BORA, 33 = YBYC.*

erences to the source(s) of data. Sites are referenced by numbers in brackets to the maps in Figures 1 and 2.

LOWLAND SITES

AMPA.—Río Amparradó, Antioquia, Colombia [4] 06°50′N, 76°25′W, 800 m. Very wet tropical forest. J. D. Lynch (pers. comm.).

APAT.—Apatzingán, Michoacán, Mexico [3] 19°06′N, 102°22′W, 335 m. Very dry tropical forest. Duellman (1961, 1965b).

BALT.—Balta, Loreto, Peru [24] 10°08′S, 71°13′W, 300 m. Wet tropical forest. Duellman (unpubl. data).

BCIS.—Barro Colorado Island, Panamá, Panama [12] 09°10′N, 79°50′W, 150 m. Wet tropical forest. Myers & Rand (1969).

BELE.—Belém, Pará, Brazil [17] 01°21′S, 48°30′W, 12 m. Wet tropical forest. Crump (1971).

BORA.—Boracéia, São Paulo, Brazil [32] 23°38′S, 45°50′W, 900 m. Wet subtropical forest. R. W. Heyer (pers. comm.).

CALI.—Río Calima, Valle, Colombia [7] 03°57′N, 76°44′W, 200–460 m. Wet premontane forest. J. D. Lynch (pers. comm.).

CAMA.—Cuzco Amazónico, Madre de Dios, Peru [25] 12°33′S, 69°03′W, 200 m. Wet tropical forest. Duellman (unpubl. data).

CCOR.—Cerro Cora (Parque Nacional), Amambay, Paraguay [31] 22°30′S, 56°05′W, 200–300 m. Dry tropical forest (and savanna). N. J. Scott (pers. comm.).

TABLE 1. *Distribution of species of anuran amphibians by family groups.*

	Total		Trop. Amer.		% Trop. Amer.	
Family Group	Genera	Species	Genera	Species	Genera	Species
Allophrynidae	1	1	1	1	100	100
Arthroleptidae						
Arthroleptinae	3	47	—	—	0	0
Astylosterninae	5	25	—	—	0	0
Brachycephalidae	2	3	2	3	100	100
Bufonidae	27	340	7	138	26	41
Centrolenidae	2	71	2	71	100	100
Dendrobatidae	3	117	3	117	100	100
Discoglossidae	5	16	—	—	0	0
Heleophrynidae	1	3	—	—	0	0
Hemisotinae	1	8	—	—	0	0
Hylidae						
Hemiphractinae	6	62	6	59	100	95
Hylinae	23	394	19	356	83	90
Pelodryadinae	3	147	—	—	0	0
Phyllomedusinae	3	42	3	42	100	100
Hyperoliidae						
Hyperoliinae	7	133	—	—	0	0
Kassininae	5	41	—	—	0	0
Leptopelinae	2	42	—	—	0	0
Leiopelmatidae	2	4	—	—	0	0
Leptodactylidae						
Ceratophryinae	2	9	2	7	100	78
Hylodinae	3	22	3	21	100	95
Leptodactylinae	11	117	10	104	91	89
Telmatobiinae	35	592	25	554	74	94
Microhylidae						
Asterophryinae	7	40	—	—	0	0
Brevicipitinae	4	17	—	—	0	0
Cophylinae	9	35	—	—	0	0
Dyscophinae	2	8	—	—	0	0
Genyophryninae	6	76	—	—	0	0
Melanobatrachinae	3	4	—	—	0	0
Microhylinae	27	95	17	38	63	40
Phrynomerinae	1	4	—	—	0	0
Scaphiophryninae	2	7	—	—	0	0
Myobatrachidae						
Limnodynastinae	10	42	—	—	0	0
Myobatrachinae	10	57	—	—	0	0
Pelobatidae						
Megophryinae	7	73	—	—	0	0
Pelobatinae	2	10	1	2	50	20
Pelodytidae	1	2	—	—	0	0
Pipidae						
Pipinae	1	7	1	7	100	100
Xenopodinae	3	19	—	—	0	0
Pseudidae	2	4	2	3	100	75
Ranidae						
Mantellinae	3	60	—	—	0	0
Petropedetinae	11	86	—	—	0	0
Raninae	24	459	1	21	4	3
Rhacophoridae						
Philautinae	1	63	—	—	0	0
Rhacophorinae	9	123	—	—	0	0

TABLE 1. *Continued.*

Family Group	Total		Trop. Amer.		% Trop. Amer.	
	Genera	Species	Genera	Species	Genera	Species
Rhinodermatidae	1	2	—	—	0	0
Rhinophrynidae	1	1	1	1	100	100
Sooglossidae	2	3	—	—	0	0
Totals	301	3,533	107	1,545	36	44

CENE.—Río Cenepa, Amazonas, Peru [20] 04°28'S, 78°10'W, 210 m. Wet tropical forest. R. W. McDiarmid (pers. comm.).

CHIN.—Chinajá, Alta Verapaz, Guatemala [8] 16°02'N, 90°13'W, 140 m. Wet tropical forest. Duellman (1963).

CUYU.—Río Cuyuni (13 km S of El Dorado–Santa Elena de Uairén road), Bolívar, Venezuela [5] 06°37'N, 61°32'W, 140 m. Wet tropical forest. Duellman (unpubl. data).

FILA.—Filadelfia, Boquerón, Paraguay [30] 22°15'S, 60°05'W, 200–300 m. Very dry tropical forest. N. J. Scott (pers. comm.).

LSEL.—La Selva, Heredia, Costa Rica [10] 10°25'N, 83°57'W, 90 m. Wet tropical forest. Scott et al. (1983).

MANA.—Manaus (INPA-WWF reserve), Amazonas, Brazil [18] 03°13'S, 60°02'W, 50 m. Wet tropical forest. Hödl (1977) and B. L. Zimmerman (pers. comm.).

MANT.—El Manteco, Bolívar, Venezuela [3] 07°25'N, 62°21'W, 305 m. Dry tropical forest (savanna). Hoogmoed & Gorzula (1979).

MASA.—Hato Masaguaral, Guárico, Venezuela [2] 08°33'N, 67°35'W, 75 m. Dry tropical forest (savanna). Staton & Dixon (1977).

MAZA.—Mazatlán, Sinaloa, Mexico [1] 23°13'N, 106°25'W, 10 m. Dry tropical forest. Hardy & McDiarmid (1969).

OYAP.—Upper Rivière Oyapock (Pina, Zidok, Trois-Sauts), French Guiana [8] 02°16'N, 52°52'W. Wet tropical forest. Lescure (1976).

PALE.—Río Palenque, Pichincha, Ecuador [15] 00°18'S, 79°11'W, 200 m. Wet tropical forest. R. W. McDiarmid (pers. comm.) and Duellman (unpubl. data).

PANG.—Panguana, Río Lullapichis, Huánuco, Peru [23] 09°35'S, 74°48'W, 200 m. Wet tropical forest. Toft & Duellman (1979) and Schlüter (1984).

PIST.—Pisté, Yucatán, Mexico [2] 20°42'N, 88°28'W, 10 m. Very dry tropical forest. Duellman (1965a).

RINC.—Rincón de Osa, Puntarenas, Costa Rica [14] 08°42'N, 83°29'W, 10 m. Wet tropical forest. Scott et al. (1983).

SARA.—Río Sarabia, Oaxaca, Mexico [6] 17°05'N, 95°02'W, 80 m. Wet tropical forest. Duellman (1960).

SCEL.—Santa Cecilia, Napo, Ecuador [12] 00°03'N, 76°59'W, 340 m. Very wet tropical forest. Duellman (1978).

TABO.—Finca Taboga, Guanacaste, Costa Rica [11] 10°20'N, 85°12'W, 40 m. Dry tropical forest. Scott et al. (1983).

TAMB.—Tambopata, Madre de Dios, Peru [26] 12°50'S, 69°17'W, 290 m. Wet tropical forest. R. W. McDiarmid (pers. comm.).

TAPA.—Rio Tapajós, Pará, Brazil [21] 04°36'S, 56°14'W, 85 m. Wet tropical forest. R. I. Crombie (pers. comm.).

TEHU.—Tehuantepec, Oaxaca, Mexico [7] 16°20'N, 95°14'W, 35 m. Dry tropical forest. Duellman (1960).

TROM.—Rio Trombetas, Lago Jacaré, Pará, Brazil [16] 01°17'S, 56°46'W, 110 m. Wet tropical forest. R. I. Crombie (pers. comm.).

TUIR.—Río Tuira at Río Mono, Darién, Panama [15] 07°42'N, 77°35'W, 130 m. Wet tropical forest. Duellman (unpubl. data).

YBYC.—Ybycuí (Parque Nacional), Paraguari, Paraguay [33] 25°50'S, 56°50'W, 300 m. Dry subtropical forest. N. J. Scott (pers. comm.).

TABLE 2. *Tropical American genera of anurans and numbers of species inhabiting different regions—South America (SAMER), Middle America (MAMER), West Indies (W IND) in lowlands (LOW) and highlands (HIGH).*[1]

Genus	SAMER LOW	SAMER HIGH	MAMER LOW	MAMER HIGH	MAMER & SAMER	W IND	Total
Allophrynidae							
Allophryne	1	—	—	—	—	—	1
Brachycephalidae							
Brachycephalus	2	—	—	—	—	—	2
Psyllophryne	1	—	—	—	—	—	1
Bufonidae							
Andinophryne	—	4	—	—	—	—	4
Atelopus	8	31	—	4	1	—	44
Bufo	23	16	10	10	2	—	61
Crepidophryne	—	—	—	1	—	—	1
Dendrophryniscus	3	—	—	—	—	—	3
Frostius	1	—	—	—	—	—	1
Melanophryniscus	3	1	—	—	—	—	4
Oreophrynella	—	2	—	—	—	—	2
Osornophryne	—	3	—	—	—	—	3
Peltophryne	—	—	—	—	—	9	9
Rhamphophryne	1	5	—	—	—	—	6
Centrolenidae							
Centrolene	—	1	—	—	—	—	1
Centrolenella	7	50	2	3	8	—	70
Dendrobatidae							
Colostethus	15	43	—	—	5	2	65
Dendrobates	32	8	2	3	2	—	47
Phyllobates	3	—	2	—	—	—	5
Hylidae							
Hemiphractinae							
Cryptobatrachus	—	3	—	—	—	—	3
Flectonotus	—	1	—	—	—	1	2
Fritziana	—	3	—	—	—	—	3
Gastrotheca	5	32	—	—	2	—	39
Hemiphractus	4	—	—	—	1	—	5
Stefania	—	7	—	—	—	—	7
Hylinae							
Anotheca	—	—	—	1	—	—	1
Aparasphenodon	2	—	—	—	—	—	2
Aplastodiscus	—	1	—	—	—	—	1
Calyptahyla	—	—	—	—	—	1	1
Corythomantis	1	—	—	—	—	—	1
Hyla	99	51	8	63	9	5	235
Nyctimantis	1	—	—	—	—	—	1
Ololygon	49	—	3	—	2	—	54
Osteocephalus	5	1	—	—	—	—	6
Osteopilus	—	—	—	—	—	3	3
Phrynohyas	4	—	—	—	1	—	5
Phyllodytes	3	—	—	—	—	1	4
Plectrohyla	—	—	—	13	—	—	13
Pternohyla	—	—	1	1	—	—	2
Ptychohyla	—	—	—	6	—	—	6
Smilisca	—	—	4	—	2	—	6
Sphaenorhynchus	10	—	—	—	—	—	10
Trachycephalus	3	—	—	—	—	—	3
Triprion	—	—	2	—	—	—	2

TABLE 2. *Continued.*[1]

Genus	SAMER LOW	SAMER HIGH	MAMER LOW	MAMER HIGH	MAMER & SAMER	W IND	Total
Phyllomedusinae							
Agalychnis	1	—	2	2	3	—	8
Pachymedusa	—	—	1	—	—	—	1
Phyllomedusa	21	10	—	1	1	—	33
Leptodactylidae							
Ceratophryinae							
Ceratophrys	5	—	—	—	—	—	5
Lepidobatrachus	2	—	—	—	—	—	2
Hylodinae							
Crossodactylus	4	—	—	—	—	—	4
Hylodes	—	16	—	—	—	—	16
Megaelosia	—	1	—	—	—	—	1
Leptodactylinae							
Adenomera	6	—	—	—	—	—	6
Edalorhina	2	—	—	—	—	—	2
Hydrolaetare	1	—	—	—	—	—	1
Leptodactylus	35	4	—	—	5	2	46
Lithodytes	1	—	—		—	—	1
Paratelmatobius	—	2	—	—	—	—	2
Physalaemus	34	—	—		1	—	35
Pleurodema	1	2	—	—	1	—	4
Pseudopaludicola	6	—	—	—	—	—	6
Vanzolinius	1	—	—	—	—	—	1
Telmatobiinae							
Adelophryne	1	1	—	—	—	—	2
Atopophrynus	—	1	—	—	—	—	1
Barycholos	2	—	—	—	—	—	2
Batrachophrynus	—	1	—	—	—	—	1
Crossodactylodes	3	—	—	—	—	—	3
Cycloramphus	—	23	—	—	—	—	23
Dischidodactylus	—	1	—	—	—	—	1
Eleutherodactylus	65	168	21	41	13	122	430
Euparkerella	—	1	—	—	—	—	1
Geobatrachus	—	1	—	—	—	—	1
Holoaden	1	1	—	—	—	—	2
Hylactophryne	—	—	—	3	—	—	3
Ischnocnema	2	1	—	—	—	—	3
Lynchophrys	—	1	—	—	—	—	1
Macrogenioglottus	1	—	—	—	—	—	1
Odontophrynus	3	1	—	—	—	—	4
Phrynopus	—	17	—	—	—	—	17
Phyllonastes	1	1	—	—	—	—	2
Phyzelaphryne	1	—	—	—	—	—	1
Proceratophrys	9	1	—	—	—	—	10
Scythrophrys	—	1	—	—	—	—	1
Syrrhophus	—	—	9	4	—	—	13
Telmatobius	—	17	—	—	—	—	17
Thorapa	3	—	—	—	—	—	3
Tomodactylus	—	—	—	9	—	—	9
Zachaenus	2	—	—	—	—	—	2
Microhylidae							
Arcovomer	1	—	—	—	—	—	1
Chiasmocelis	11	—	—	—	1	—	12

TABLE 2. *Continued.*[1]

Genus	SAMER LOW	SAMER HIGH	MAMER LOW	MAMER HIGH	MAMER & SAMER	W IND	Total
Ctenophryne	1	—	—	—	—	—	1
Dasypops	1	—	—	—	—	—	1
Dermatonotus	1	—	—	—	—	—	1
Elachistocleis	3	—	—	—	1	—	4
Gastrophryne	—		3	—	—	—	3
Glossostoma	—	1	—	—	1	—	2
Hamptophryne	1	—		—	—	—	1
Hyophryne	1	—	—		—	—	1
Hypopachus	—	—	1	1	—	—	2
Myersiella	1	—	—	—	—	—	1
Otophryne	1	—	—	—	—	—	1
Relictovomer	—			—	1	—	1
Stereocyclops	1	—	—	—	—	—	1
Synapturanus	3	—	—	—	—	—	3
Syncope	2	—	—	—	—	—	2
Pelobatidae							
Scaphiopus	—	—	1	1	—	—	2
Pipidae							
Pipa	6	—	1	—	—	—	7
Pseudidae							
Lysapsus	2	—		—	—	—	2
Pseudis	1	—	—	—		—	1
Ranidae							
Rana	—	—	4	16	1	—	21
Rhinophrynidae							
Rhinophrynus	—	—	1	—	—	—	1
Totals	537	537	78	183	64	146	1,545

[1] Lowland species are those distributed primarily below 1,000 m, whereas highland species are distributed primarily above 1,000 m.

CLOUD FOREST SITES

COSN.—Río Cosñipata, Cuzco, Peru [27] 13°05′S, 71°18′W, 1,700 m. Wet subtropical forest. Duellman (unpubl. data).

CRUC.—Las Cruces, Puntarenas, Costa Rica [13] 08°48′N, 83°00′W, 1,500 m. Premontane rainforest. Scott et al. (1983).

PLAN.—La Planada, Nariño, Colombia [10] 01°03′N, 77°55′W, 1,700 m. Very wet premontane forest. P. A. Burrowes (pers. comm.).

PURU.—Purulhá, Baja Verapaz, Guatemala [9] 15°26′N, 90°20′W, 1,600 m. Very wet subtropical forest. Campbell (1982).

QZAP.—Quebrada Zapadores, Pichincha, Ecuador [14] 00°17′S, 78°47′W, 2,010 m. Wet subtropical forest. Duellman (unpubl. data).

RGRA.—Rancho Grande, Aragua, Venezuela [1] 10°22′N, 67°42′W, 1,100 m. Very wet montane forest. Duellman (unpubl. data).

RMES.—Rayón Mescalapa, Chiapas, Mexico [5] 17°12′N, 93°02′W, 1,700 m. Very wet subtropical forest. Campbell (1982).

SALA.—Río Salado, Napo, Ecuador [13] 00°13′S, 77°44′W, 1,410 m. Subtropical wet forest. Duellman (unpubl. data).

VHER.—Vista Hermosa, Oaxaca, Mexico [4] 17°51′N, 96°20′W, 1,500 m. Very wet subtropical forest. Campbell (unpubl. data).

HIGH ANDEAN SITES

ACAN.—Abra Acanacu, Cuzco, Peru [28] 13°12′S, 71°42′W, 3,250 m. Subalpine pluvial páramo. Péfaur & Duellman (1980).

AHUA.—Abra Huancabamba, Piura, Peru [22] 05°22′S, 79°32′W, 2,800–3,100 m.

Very humid montane forest. Duellman (unpubl. data).

ANGE.—Páramo El Angel, Carchi, Ecuador [11] 00°43′N, 77°49′W, 3,350 m. Very wet montane forest. Duellman (unpubl. data).

AZAM.—Abra de Zamora, Loja, Ecuador [19] 03°59′S, 79°07′W, 2,700 m. Very wet montane forest. Duellman (unpubl. data).

PURA.—Páramo de Puracé, Cauca, Colombia [9] 02°19′N, 76°15′W, 3,400 m. Pluvial montane forest. Duellman (unpubl. data) and J. D. Lynch (pers. comm.).

RUSI.—Páramo de la Rusia, Boyacá, Colombia [6] 05°54′N, 73°12′W, 3,340 m. Very wet montane forest. Duellman (unpubl. data).

SROS.—Santa Rosa (4 km W), Puno, Peru [29] 14°36′S, 70°50′W, 4,010 m. Humid montane forest. Péfaur & Duellman (1980).

THE TROPICAL AMERICAN ANURAN FAUNA

Seventeen of the 46 family groups (families and subfamilies) of anurans occur in the American tropics; nine of these are endemic to the region and three others are extratropical only in southern South America. Of the 301 genera and 3,533 species of anurans known worldwide (figures updated from Frost, 1985), 107 genera (35.5%) and 1,545 species (43.7%) occur in the American tropics (Table 1). Ninety-six of the 107 genera are endemic to the American tropics.

Of the 1,545 species known from the American tropics, the majority (1,138) occur in South America; 64 of these also occur with an additional 261 species in Middle America (Mexico and Central America), and 146 species are known from the West Indies (Table 2). Thus, of the number of anurans known worldwide, 32.2% occur in tropical South America, 9.2% occur in tropical Middle America, and 4.1% occur in the West Indies.

Two families make the largest contribution to the anuran fauna of the American tropics. The Leptodactylidae (41 genera, 562 species) and the Hylidae (28 genera, 443 species) account for 72% of the 1,399 species of anurans on the mainland. Six endemic families (Allophrynidae, Brachycephalidae, Centrolenidae, Dendrobatidae, Pseudidae, and Rhinophrynidae) account for 14% of the mainland species. Four widespread families (Bufonidae, Microhylidae, Pelobatidae, and Ranidae) make up the remaining 14% of the fauna, with the Bufonidae (10 genera, 129 species) making the largest contribution. Two large genera—*Hyla* (Hylidae, 230 species) and *Eleutherodactylus* (Leptodactylidae, 308 species)—make up 38% of the anuran fauna of the mainland tropics.

PATTERNS OF SPECIES DIVERSITY

Patterns of anuran species diversity were determined from compilations of species from each of 48 sites in tropical America (Tables 3–7). For purposes of discussion these are divided into three categories: (1) lowland sites (N = 32) at elevations of less than 1,000 m, (2) montane cloud forest sites (N = 9) at elevations of 1,100–2,010 m, and (3) high Andean sites (N = 7) at elevations of 2,700–4,010 m. The patterns of species diversity are examined with respect to (1) climate and habitat, (2) taxonomic composition, (3) historical components, and (4) reproductive modes.

The comparisons reflect existing knowledge of the fauna at each of the sites. Disparity exists in the sampling effort at the sites. Thus, for sites that have been subjected to intensive study (e.g., Barro Colorado Island, Santa Cecilia), the species lists can be viewed as nearly complete. However, at other sites (e.g., Río Cuyuni, Rio Tapajós) sampling has been limited to short periods of time, and therefore additional species are expected.

CLIMATE AND HABITAT

In the lowlands of the American tropics, the greatest number of species of anurans is found in the equatorial part of the upper Amazon Basin. The greatest number of species known from one locality is 84 at Santa Cecilia in Amazonian Ecuador. Throughout the upper Amazon Basin in areas receiving more than 3,000 mm of rain per year and having only a limited dry season species diversity is high (55–84, $\bar{X}$ = 62.8, N = 6). Eastward

TABLE 3. *Anuran species diversity at 11 lowland sites in Middle America.*

	Wet Forest					
Genus	SARA	CHIN	LSEL	RINC	BCIS	TUIR
Bufo	2	2	3	4	2	3
Centrolenella	—	—	4	7	3	—
Colostethus	—	—	—	2	1	3
Dendrobates	—	—	1	2	1	1
Phyllobates	—	—	1	1	—	—
Hyla	4	1	4	3	2	2
Ololygon	1	1	2	2	1	2
Phrynohyas	—	—	—	1	—	—
Pternohyla	—	—	—	—	—	—
Smilisca	1	2	3	3	2	1
Triprion	—	—	—	—	—	—
Agalychnis	1	1	3	2	3	2
Pachymedusa	—	—	—	—	—	—
Phyllomedusa	-	—	—	—	—	1
Leptodactylus	1	1	2	4	2	3
Physalaemus	—	—	—	1	1	1
Eleutherodactylus	1	2	14	9	9	7
Syrrhophus	—	1	—	—	—	—
Tomodactylus	—	—	—	—	—	—
Gastrophryne	—	—	1	—	-	—
Glossostoma	—	—	—	1	—	—
Hypopachus	—	1	—	—	—	—
Scaphiopus	—	—	-	—	—	—
Rana	2	2	3	—	1	1
Rhinophrynus	—	—	—	—	—	—
Totals	13	14	41	42	28	27

in the middle and lower parts of the Amazon Basin, species diversity is lower (32–59, $\bar{X}$ = 46.3, N = 4). In those parts of the basin rainfall is less than 3,000 mm annually, and there is a prolonged dry season of four to six months. The same climatic pattern exists in the Guianan Region, where anuran species diversity is even lower (29–35, $\bar{X}$ = 32.0, N = 2). The correlation of decreased anuran species diversity with lower rainfall and more prolonged dry seasons is reflected in the number of species of anurans in the Venezuelan llanos and the Chacoan scrub forests of Paraguay, where rainfall is less than 2,000 mm annually and the dry season is more than six months long. In the Chaco, species diversity is 22–29 ($\bar{X}$ = 25.3, N = 3), and in the llanos, 16–26 ($\bar{X}$ = 21.0, N = 2).

This pattern seems to hold for the Atlantic coastal forests of southeastern Brazil where at one site with rainfall exceeding 3,600 mm annually there are 65 species of anurans. Although rainfall is high (over 4,000 mm) and aseasonal in the Trans-Andean rainforest, however, species diversity (35–49, $\bar{X}$ = 42.6, N = 3) is slightly lower than that in the middle and lower Amazon Basin characterized by less rainfall and a distinct dry season.

The same general pattern holds in the lowlands of Middle America. In the wet forests, species diversity is higher (13–42, $\bar{X}$ = 27.5, N = 6) than in the dry forests (6–22, $\bar{X}$ = 14.4, N = 5). However, both figures are much lower than for comparable habitats in South America.

Although montane rainforests may not receive as much precipitation as many lowland rainforests, the montane forests are shrouded in fog almost daily. Moreover, because of lower temperatures and insolation, evaporation is lower. Thus, cloud forests provide a moist environment for anurans. Average anuran species diversity is higher in some South American cloud forests (20–39, $\bar{X}$ = 25.4,

TABLE 3. *Continued.*

		Dry Forest		
MAZA	APAT	PIST	TEHU	TABO
5	3	2	4	3
—	—	—	—	—
—	—	—	—	—
—	—	—	—	—
—	—	—	—	—
1	1	—	—	1
—	—	—	1	2
1	—	—	1	1
1	—	—	—	—
1	1	1	1	2
1	—	1	1	—
—	—	—	—	—
1	1	—	1	—
—	—	—	—	—
1	2	—	2	5
—	—	—	1	1
—	—	—	1	3
—	—	—	1	—
—	1	—	—	—
2	—	—	1	—
—	—	—	—	—
1	—	—	—	1
1	—	—	—	—
1	1	1	1	2
—	—	1	1	1
17	10	6	17	22

N = 5) than in Middle American cloud forests (16–30, $\bar{X} = 20.5$, N = 4). Near the northern extent of both lowland rainforest and cloud forest in Mexico, the numbers of species of anurans are higher in the cloud forests than in the lowland rainforests. On the other hand, species diversity in South American cloud forests is considerably less than in lowland rainforests.

The high Andes provide a distinctive environment of supra-treeline habitats (páramo and puno). In these high-elevation sites anuran species diversity is low (5–15, $\bar{X} = 8.1$, N = 7). One of the sites (Abra Zamora, 2,700 m) is subpáramo; it has 15 species, whereas the other higher sites have 5–9 ($\bar{X} = 7.0$). Generally in the supra-treeline habitats in the Andes, the number of species of anurans diminishes from north to south (Duellman, 1979b; Péfaur & Duellman, 1980). This seems to be correlated at least in part with a decrease in the amount of moisture and an increase in the seasonality of precipitation.

The elevational gradient in anuran species diversity in the Andes has been discussed by Duellman (1979b, 1983) and by Lynch & Duellman (1980). This gradient is demonstrated well by an equatorial transect spanning the Andes and the lowlands on either side of the mountains (Fig. 3). Many species in cloud forests have rather narrow altitudinal ranges. Thus, although the number of species (17) at 2,600 m on the Amazonian slopes is not much fewer than that at 1,100 m (22 species), no species occur at both locations.

It is obvious that diversity generally decreases from wetter to drier regions and from lower to higher elevations. However, this explanation is simplistic and does not take into account some important aspects of the biology of anurans, such as reproductive mode.

TAXONOMIC COMPOSITION

Analysis of species diversity by taxonomic groups reveals a variety of patterns. Within the tropical lowlands, three family groups account for most of the taxa at any one site. Of these, the Hylinae and Leptodactylinae are present at all sites. Within the Amazon Basin, hylines are most numerous in the upper part of the basin, but they constitute a higher percentage of the anuran fauna in the middle and lower parts of the basin (Fig. 4). They are numerous in the Atlantic coastal forest of southeastern Brazil, but the hyline fauna is depauperate in the Chocoan and Central American rainforests. Likewise, the number of species of hylines diminishes in the dry forests of Middle America, the Chaco, and the Venezuelan llanos.

The leptodactylines present a different picture (Fig. 5). They are well represented throughout the cis-Andean lowlands and form a large part of the anuran fauna in the Venezuelan llanos (38–50%) and in the Chaco (36–44%). Leptodactylines constitute a much smaller part (3–15%) of the anuran fauna in the trans-Andean and Central American lowlands.

Telmatobiines contrast strongly with lep-

TABLE 4. *Anuran species diversity at 16 sites in lowland wet forest in South America.*

	Amazonian						
Genus	SCEL	CENE	PANG	TAMB	CAMA	BALT	MANA
Allophryne	—	—	—	—	—		—
Brachycephalus	—	—	—	—	—	—	—
Atelopus	—	1	—	—	—	—	1
Bufo	3	3	3	3	3	2	2
Dendrophryniscus	1	—	1	1	—	—	1
Rhamphophryne			—	—	—	—	—
Centrolenella	3	1	2	—	—	—	1
Colostethus	2	5	2	1	1	1	2
Dendrobates	4	2	5	2	3	4	1
Fritziana	—	—	—	—	-	—	—
Gastrotheca	—	1	—	—	—	—	—
Hemiphractus	1	2	—	—	–	—	—
Hyla	20	10	14	19	12	13	13
Nyctimantis	1	—	—	—	—	—	—
Ololygon	4	2	4	6	5	4	4
Osteocephalus	3	4	2	2	1	3	4
Phrynohyas	2	1	2	2	2	2	2
Smilisca	—	—	—	—	—	—	—
Sphaenorhynchus	2		—	1	1	1	—
Trachycephalus	—	—	—	—	—	—	—
Agalychnis	—	—	—	—	—	—	—
Phyllomedusa	4	3	3	5	5	4	3
Ceratophrys	1	—	1	1	1	1	1
Crossodactylus	—	—	—	—	—	–	—
Hylodes	—	—	—	—	—	—	—
Megaelosia	—	—	—	—	—	—	—
Adenomera	1	2	2	2	2	1	1
Edalorhina	1		1	—	1	1	—
Leptodactylus	5	5	3	7	7	6	8
Lithodytes	1	1	1	1	1	1	1
Paratelmatobius	—		—	—	—	—	—
Physalaemus	1	1	1	1	1	—	—
Vanzolinus	1	—	—		—	—	—
Barycholos	—	—	—	—	—	—	—
Cycloramphus	-	—	—	—	—	—	—
Eleutherodactylus	14	9	14	4	5	5	3
Holoaden	—	—	—	—	—	—	—
Ischnocnema	1	1	1	—	—	1	—
Phyzelaphryne	—	—	—	—		—	—
Proceratophrys	—		-	—	—	—	—
Thoropa	—	—		—	—	—	—
Chiasmocleis	3	—	1	1	1	2	2
Ctenophryne	1	—	1	—	1	1	1
Elachistocleis	—	—	—	1	1	1	—
Glossostoma	—			—	—	—	—
Hamptophryne	1	—	1	1	1	1	—
Myersiella	—	—	—	-	—	—	—
Otophryne	—		—	—		—	—
Synapturanus	—	—	—	—	—		2
Syncope	1	—	—	—	—	—	—
"microhylid"	—		—	—	—	—	—
Pipa	1	—	—	1	1	—	2
Lysapsus	—	—	—		—	—	1
Rana	1	1	—	—	—	—	—
Totals	84	55	65	62	56	55	56

TABLE 4. *Continued.*

Amazonian			Guianan		Trans-Andean			Atlantic Coastal Forest
TROM	TAPA	BELE	CUYU	OYAP	AMPA	CALI	PALE	BORA
—	—	—	1	1	—	—	—	—
—	—	—	—	—	—	—	—	1
1	1	—	—	1	—	—	1	—
3	5	2	2	3	2	4	3	2
1	1	—	—	1	—	—	—	1
—	—	—	—	—	1	—	—	—
—	1	—	—	2	8	5	5	2
—	3	—	—	—	3	3	2	—
1	3	2	1	2	2	1	3	—
—	—	—	—	—	—	—	—	2
—	—	—	—	—	—	1	1	—
—	—	—	—	—	1	1	—	—
9	14	11	6	7	7	2	4	15
—	—	—	—	—	—	—	—	—
5	6	6	3	1	1	—	3	7
1	2	1	2	2	—	—	—	1
1	2	2	1	1	—	—	—	—
—	—	—	—	—	1	1	1	—
—	—	1	1	—	—	—	—	1
—	—	—	—	—	—	—	1	—
—	—	—	—	—	1	1	1	—
1	3	3	4	2	—	1	—	2
1	1	—	—	1	—	—	—	1
—	—	—	—	—	—	—	—	1
—	—	—	—	—	—	—	—	2
—	—	—	—	—	—	—	—	1
1	2	1	1	1	—	—	—	1
—	—	—	—	—	—	—	—	—
4	5	5	3	4	2	1	4	3
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	1
—	2	2	1	—	—	—	1	4
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	1	—
—	—	—	—	—	—	—	—	3
2	5	1	—	1	13	13	16	9
—	—	—	—	—	—	—	—	1
—	—	—	—	—	—	—	—	—
—	1	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	2
—	—	—	—	—	—	—	—	1
—	—	—	—	1	—	—	—	—
—	—	—	1	—	—	—	—	—
—	—	—	1	—	—	—	—	—
—	—	—	—	—	1	1	1	—
—			—	—	—	—	—	—
—	—	—	—	—	—	—	—	1
—	—	—	—	1	—	—	—	—
1	1	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	2	—	—	—	—	—	—	—
—	—	1	—	1	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	1	1	—	1	
32	59	38	29	35	44	35	49	65

TABLE 5. *Anuran species diversity at five non-rainforest lowland sites in South America.*

	Llanos		Chacoan		
Genus	MANT	MASA	CCOR	FILA	YBYC
Bufo	3	2	1	2	1
Melanophryniscus	—	—	—	—	1
Hyla	5	2	7	1	4
Ololygon	3	1	4	2	4
Phrynohyas	—	1	1	1	1
Sphaenorhynchus	1	—	—	—	—
Phyllomedusa	1	—	1	2	1
Ceratoprhys	—	—	—	1	—
Chacophrys	—	—	—	1	—
Lepidobatrachus	—	—	—	1	—
Adenomera	1	—	1	—	1
Leptodactylus	5	5	5	6	6
Physalaemus	2	2	5	2	3
Pleurodema	1	1	—	—	—
Pseudopaludicola	1	—	1	—	1
Odontophrynus	—	—	1	—	1
Chiasmocleis	—	—	1	—	—
Dermatonotus	—	—	—	1	—
Elachistocleis	1	1	1	1	1
Pseudis	1	1	—	1	—
Rana	1	—	—	—	—
Totals	26	16	29	22	25

TABLE 6. *Anuran species diversity at nine montane cloud forest sites in Middle and South America.*

	Middle America				South America				
Genus	VHER	RMES	PURU	CRUC	RGRA	PLAN	QZAP	SALA	COSN
Atelopus	—	—	—	1	1	2	2	2	1
Bufo	2	2	1	3	—	—	1	1	3
Centrolene	—	—	—	—	—	—	1	—	—
Centrolenella	1	1	1	3	2	9	4	5	4
Colostethus	—	—	—	1	3	1	1	2	2
Dendrobates	—	—	—	—	—	1	—	—	—
Flectonotus				—	1	—	—	—	—
Gastrotheca	—			—	2	2	2	1	0
Hemiphractus	—	—	—	—	—	1	—	—	1
Anotheca	1	1	—	1	—	—	—	—	—
Hyla	6	2	2	7	—	1	1	4	3
Osteocephalus	—	—	-	-	—	—	—	1	—
Plectrohyla	—	2	3	—	—	—	—	—	—
Ptychohyla	2	2	2	—	—	—	—	—	—
Smilisca	1	1	1	1	—	—	—	—	—
Agalychnis	1	1	1	1	—	—	—	—	—
Phyllomedusa	—	—	—	—	1	—	-	2	—
Leptodactylus	—	—	—	3	2	—	—	—	1
Eleutherodactylus	2	3	5	8	8	22	8	7	7
Telmatobius	—	—	—	—	—	—	—	—	1
Hypopachus	-	—	1	—	—	—	—	—	—
Rana	1	1	2	1	—	—	—	—	—
Totals	17	16	19	30	20	39	20	25	23

TABLE 7. *Anuran species diversity at seven high montane sites in the Andes.*

Genus	RUSI	PRUA	ANGE	AZAM	AHUA	ACAN	SROS
Atelopus	1	1	1	1	—	—	—
Bufo	—	—	—	—	—	—	1
Osornophryne	—	1	1	—	—	—	—
Centrolenella	—	1	1	1	—	—	—
Colostethus	1	—	1	1	1	—	—
Gastrotheca	—	—	1	1	1	2	1
Hyla	1	—	—	—	—	—	—
Pleurodema	—	—	—	—	—	1	2
Eleutherodactylus	1	5	4	9	3	—	—
Phrynopus	1	—	—	1	2	2	—
Telmatobius	—	—	—	1	1	2	1
Totals	5	8	9	15	8	7	5

todactylines (Fig. 6). Telmatobiines (composed mostly of species of *Eleutherodactylus*) make up a significant part (21–35%) of the anuran fauna in the lowlands of the Chocoan region and lower Central America; this is about the same as their contribution (25%) to the anuran fauna of the Atlantic coastal forest in southeastern Brazil. In the Amazon Basin the number of species (and percentage contribution) diminishes rapidly from the equatorial part of the upper basin to the southern, middle, and lower parts of the basin. Telmatobiines are poorly represented in the Chaco and are absent from the Venezuelan llanos.

Although dendrobatids are represented by far fewer species, their pattern of diversity parallels that of the telmatobiines (Fig. 7). However, dendrobatids are absent from the Atlantic coastal forest in southeastern Brazil, the Chaco, and the llanos.

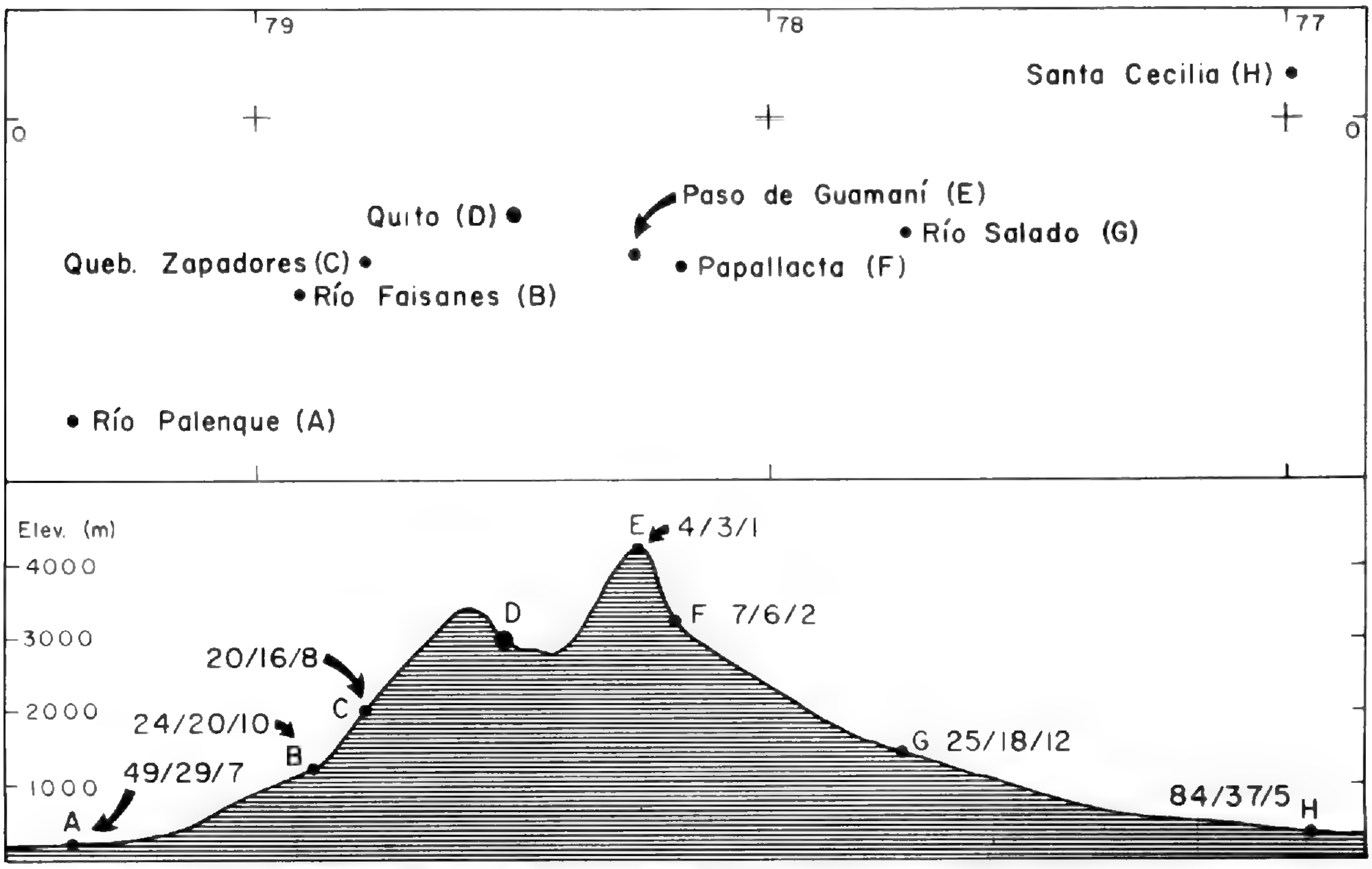

FIGURE 3. *Above, map of central Ecuador showing location of sites (A–H); below, equatorial transect of the Andes showing certain aspects of the anuran fauna at each site. Numbers are total number of species/percent with forest mode/percent with stream-dependent mode.*

FIGURE 4. *Hyline frogs in lowland sites in South America and lower Central America. Numbers are number of species/percentage of total at each locality.*

Bufonids are about equally abundant throughout the lowlands, but they tend to account for a higher percentage of the anuran fauna in the llanos (11–13%) and Chaco (3–9%) than elsewhere. Centrolenids make a large contribution to the anuran fauna in the Central American (10–17%) and trans-Andean (10–18%) lowlands; they are few in number or absent in the cis-Andean lowlands. Ranids are represented in South America by only one currently recognized species of *Rana*, which is absent from the southern and eastern lowlands. Pseudids are represented by only three species; these are restricted to the middle and lower Amazon Basin, the llanos, and the Chaco. Pipids are widespread in the cis-Andean lowlands and represented in eastern Panama by a single species. Three family groups have restricted distributions in the American tropics. The Allophrynidae occurs only in the Guianan forests. Brachycephalids and hylodines are restricted to southeastern Brazil, where they account for 1.5% and 6.2% of the anuran fauna, respectively.

In the Middle American lowlands, rhinophrynids and pelobatids make a minor con-

FIGURE 5. *Leptodactyline frogs in lowland sites in South America and lower Central America. Numbers are number of species/percentage of total at each locality.*

tribution to the anuran fauna in dry forests, and hylines and telmatobiines (mostly *Eleutherodactylus*) contribute significantly to the anuran fauna of the wet forests.

Taxonomic composition changes radically in the montane cloud forest and high Andean sites. A significant part of the anuran fauna in cloud forests is made up of telmatobiines (mostly *Eleutherodactylus*); these account for 28–56% ($\bar{X}$ = 38.8, N = 5) of the anuran fauna in South American cloud forests and 12–27% ($\bar{X}$ = 21.0, N = 4) in Middle American cloud forests. The most striking difference between cloud forests in Middle and South America is the number of species of hylines; in Middle America these make up 30–53% ($\bar{X}$ = 44.0, N = 4), as contrasted with 0–20% ($\bar{X}$ = 8.2, N = 5) in South America. Centrolenids are a major component of the anuran fauna in South American cloud forests (10–25%, $\bar{X}$ = 19.0, N = 5), whereas in Central America they account for no more than 10% of the fauna at any one site. Hemiphractines and dendrobatids each account for an average of 9% of the anuran fauna in South American cloud forests, whereas hemi-

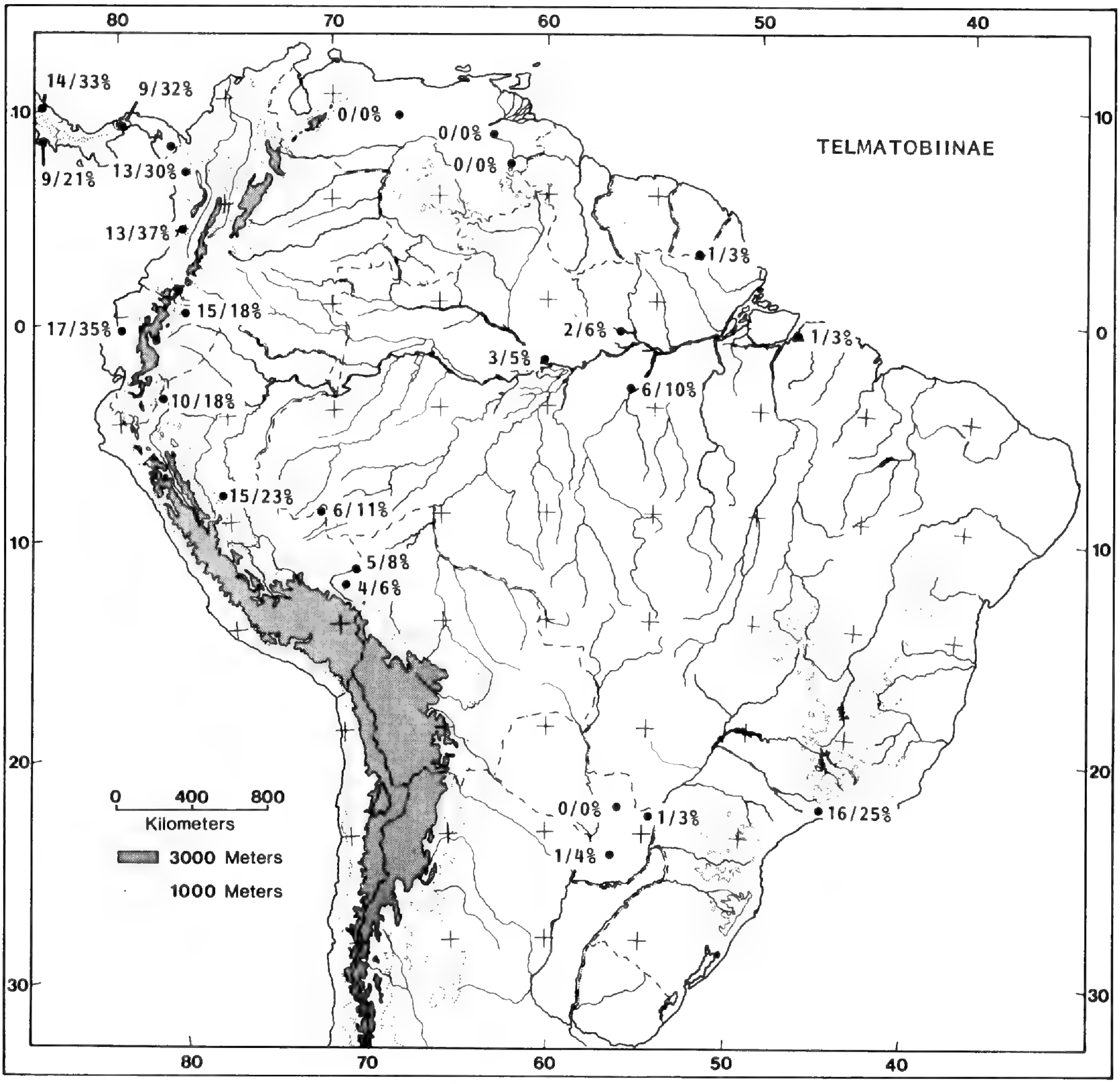

FIGURE 6. *Telmatobiine frogs in lowland sites in South America and lower Central America. Numbers are number of species/percentage of total at each locality.*

phractines are absent at all of the Middle American sites, and only one dendrobatid occurs at one of the sites. On the other hand, *Rana* makes up an average of 6.5% of the anuran fauna at Middle American sites, but the genus is absent in South American cloud forests.

In humid high Andean sites, telmatobiines (*Eleutherodactylus* and *Phrynopus*) account for the majority of the anuran fauna—45–74% ($\bar{X}$ = 62.0, N = 5). Bufonids are the other major component, accounting for as much as 22% of the fauna. The rest is composed mainly of dendrobatids (*Colostethus*) and hemiphractines (*Gastrotheca*). In the southern part of the Andes, aquatic telmatobiines (*Telmatobius*) and leptodactylines (*Pleurodema*) make significant contributions to the small anuran faunas.

From these data it is apparent that the patterns of diversity of various taxonomic components are not reflected in the overall diversity of anurans. This is especially noticeable in different patterns of diversity among taxonomic groups in Middle America and South America and suggests that the histories

FIGURE 7. *Dendrobatid frogs in lowland sites in South America and lower Central America. Numbers are number of species/percentage of total at each locality.*

of the family groups may play an important role in the geographic differences in species diversity.

HISTORICAL COMPONENTS

An overwhelming amount of data on plate tectonics and biogeography shows that (1) South America had a land connection with Middle America at the time of the Cretaceous–Tertiary boundary; (2) South America was isolated from other land masses throughout most of the Tertiary; and (3) the isthmian link providing a continuous land connection between Middle America and South America has persisted since the late Pliocene (Stehli & Webb, 1985). The early unification of the land masses provided an opportunity for interchange of Laurasian and Gondwanan biotas at the end of the Cretaceous. The interchange, followed by separation of the land masses, resulted in isolation of taxa in South America and Middle America and subsequent vicariance of taxa. Reunification of the land masses provided the opportunity for more recent dispersal.

TABLE 8. *Biogeographical components of the tropical American anuran fauna.*

NORTH AMERICAN
- Pelobatidae
- Ranidae
- Rhinophrynidae

MESOAMERICAN
- Bufonidae (pt)
    - *Bufo* (pt)
    - *Crepidophryne*
- Hylinae (pt)
    - *Anotheca*
    - *Hyla* (pt)
    - *Plectrohyla*
    - *Pternohyla*
    - *Ptychohyla*
    - *Smilisca*
    - *Triprion*
- Phyllomedusinae (pt)
    - *Agalychnis*
    - *Pachymedusa*
- Telmatobiinae (pt)
    - *Eleutherodactylus* (pt)
    - *Hylactophryne*
    - *Syrrhophus*
    - *Tomodactylus*
- Microhylidae (pt)
    - *Gastrophryne*
    - *Hypopachus*

SOUTH AMERICAN
- Allophrynidae
- Brachycephalidae
- Bufonidae (pt)
    - *Bufo* (pt)
    - All other South American genera
- Centrolenidae
- Dendrobatidae
    - Hemiphractinae
    - Hylinae (pt)
        - *Hyla* (pt)
        - All other South American genera
    - Phyllomedusinae (pt)
        - *Phyllomedusa*
    - Ceratophryinae
    - Hylodinae
    - Leptodactylinae
    - Telmatobiinae (pt)
        - *Eleutherodactylus* (pt)
        - All other South American genera
- Microhylidae (pt)
    - All South American genera
- Pipidae
- Pseudidae

The history of anurans with respect to the inter-American biotic exchange has been reviewed by Savage (1982) and by Vanzolini & Heyer (1985). Savage championed the idea of a Mesoamerican herpetofauna that evolved in isolation in Central America. Thus, the tropical American frog fauna is composed of three historical elements—North American, Mesoamerican, and South American (Table 8).

TABLE 9. *Biogeographic components of anuran faunas at 48 sites in the American tropics. Numbers in parentheses indicate number of sites. Numbers in columns are percentages.*

Sites	South American	Meso-american	North American
Middle American lowlands			
Dry forests (5)	20.3	63.6	16.1
Wet forests (6)	33.6	59.0	7.4
Middle American cloud forests (4)	13.6	79.9	6.5
South American lowlands			
Trans-Andean Chocó (3)	93.8	4.8	1.4
Upper Amazon Basin (6)	99.5		0.5
Middle and lower Amazon Basin (4)	100.0	—	—
Atlantic coastal forest (1)	100.0	—	—
Guianan forests (2)	98.5	—	1.5
Venezuelan llanos (2)	98.1	-	1.9
Chacoan forests (3)	100.0	—	—
South American cloud forests (5)	100.0	—	—
High Andean sites (7)	100.0	—	—

TABLE 10. *Anuran reproductive modes at 48 sites in tropical America. Numbers in parentheses in the first column indicate the number of sites; in the other columns the numbers are the range and mean percents.*

Sites	Forest	Stream
Equatorial upper Amazon Basin (3)	46.4–47.7 (47.1)	5.9–12.7 (8.3)
Southern Amazon Basin (3)	22.5–36.4 (29.2)	1.6–1.8 (1.7)
Middle and lower Amazon Basin (4)	18.8–28.8 (24.1)	0.0–8.5 (4.7)
Brazilian coastal forest (1)	30.8	23.1
Guianan forest (2)	24.1–25.7 (24.9)	0.0–8.6 (4.3)
Venezuelan llanos (2)	0.0–3.8 (1.9)	—
Chacoan forest (3)	3.4–9.1 (5.5)	—
Trans-Andean forest (3)	59.2–74.3 (67.2)	12.2–29.5 (23.4)
Lower Middle American wet forest (4)	55.6–60.7 (57.9)	14.3–26.2 (17.5)
Upper Middle American wet forest (2)	23.1–35.7 (29.4)	—
Middle American dry forest (5)	0.0–20.0 (11.6)	—
Middle American cloud forest (4)	23.5–50.0 (35.9)	33.3–52.9 (45.9)
South American cloud forest (5)	61.0–92.0 (76.4)	28.0–43.5 (38.1)
Wet high-Andean sites (6)	57.1–100.0 (81.2)	12.5–33.3 (22.8)
Dry high-Andean sites (1)	20.0	20.0

The North American anurans make only a minor contribution to the tropical anuran fauna. These include pelobatids (two species of *Scaphiopus*), rhinophrynids (one species of *Rhinophrynus*), and ranids (21 species of *Rana*) in Middle America; of these, only one species of *Rana* occurs in South America. There is no evidence that any North American anurans entered South America during the connection with South America at the Cretaceous–Tertiary boundary.

On the other hand, during the Cretaceous–early Tertiary connection, members of five family groups dispersed into Middle America from South America. These include some groups of bufonids (*Bufo*), hylines (*Hyla*), phyllomedusines (ancestor of *Agalychnis* and *Pachymedusa*), telmatobiines (*Eleutherodactylus*), and microhylids (ancestor of *Gastrophryne* and *Hypopachus*). During their isolation in the Tertiary, these groups differentiated into many species. The "*Hyla*" vicariant presumably was ancestral to the Middle American genera *Anotheca*, *Plectrohyla*, *Pternohyla*, *Ptychohyla*, *Smilisca*, and *Triprion*, in addition to the numerous Middle American and Holarctic frogs currently placed in the genus *Hyla*. Likewise, the "*Eleutherodactylus*" vicariant presumably was ancestral to the genera *Hylactophryne*, *Syrrhophus*, and *Tomodactylus*, as well as the many species of Middle American *Eleutherodactylus* placed in the subgenus *Craugastor* by Lynch (1986).

With the closure of the Panamanian Portal in the late Pliocene, a few groups of Mesoamerican taxa dispersed into South America (principally the Chocoan region), and many South American taxa dispersed into Central America. Mesoamerican dispersalists into South America include only *Agalychnis*, *Smilisca*, *Eleutherodactylus* (members of subgenus *Craugastor*), and *Rana*. Only *Rana palmipes* is widely distributed in the cis-Andean lowlands, where *Agalychnis* is represented by one species in the upper Amazon Basin, as contrasted with three species in the trans-Andean lowlands.

Twenty-one genera included in ten family groups have dispersed from South America into Central America since the late Pliocene. Two genera of bufonids (some groups of *Bufo* and *Atelopus*) have reached Costa Rica, and *Atelopus* has differentiated in Central America. *Centrolenella* has dispersed to southern Mexico and has undergone extensive speciation in Central America. All three genera of dendrobatids have dispersed to Costa Rica (*Dendrobates* to Nicaragua) and have differentiated in Central America. Among hemiphractines, one South American species each of *Gastrotheca* and *Hemiphractus* have

FIGURE 8. *Reproductive modes of anurans at lowland sites in South America and lower Central America. Numbers are percentages of species with forest modes/stream-dependent modes.*

reached Panama, and another *Gastrotheca* has dispersed to Costa Rica. The hyline genera *Hyla* and *Ololygon* have dispersed to Mexico and differentiated in Middle America, whereas the South American *Phrynohyas venulosa* extends throughout the tropical lowlands of Middle America. *Phyllomedusa* has reached Costa Rica, where a distinct species occurs; another South American species extends into eastern Panama. Although leptodactylines are widely dispersed in Middle America, they have not differentiated from South American populations; one *Leptodactylus* reaches Texas, and four other species have dispersed shorter distances in Middle America. *Physalaemus* reaches southern Mexico and *Pleurodema* extends only to central Panama. South American *Eleutherodactylus* extends northward to Nicaragua. Three South American species of microhylids have dispersed to Panama and one to Costa Rica. Pipids are represented by a distinct species in eastern Panama.

When the anuran diversity at the 48 sites is examined with respect to the histories of the component taxa, we see that slight differences exist among the South American sites but that these are notably different from the Middle American sites (Table 9). Moreover, North American and Mesoamerican elements play a minor role in the South American fauna, whereas at Middle American sites, a significant contribution is made by South American elements. The recent dispersal of South American taxa into Central America accounts for the greater species diversity in lower Central American lowland forests than in those in Mexico.

REPRODUCTIVE MODES

Mode of reproduction is a combination of ovipositional and developmental factors, including oviposition site, ovum and clutch characteristics, rate and duration of development, stage and size of hatchling, and type of parental care, if any. Duellman & Trueb (1986) recognized 29 reproductive modes in anurans worldwide. At the 48 tropical American sites analyzed here, 17 modes occur. These modes and the taxa exhibiting them are:

1. Eggs and tadpoles in lentic water.—All allophrynids, ceratophryines, ranids, and pseudids; most bufonids, hylines, and microhylids; telmatobiines (*Proceratophrys*), and some leptodactylines (*Paratelmatobius, Pseudopaludicola, Pleurodema marmorata*).
2. Eggs and tadpoles in lotic water.—Bufonids (*Atelopus, Bufo haematiticus* group), hylines (*Hyla bogotensis, H. callipleura, H. larinopygion, H. circundata* groups and most Middle American cloud forest groups, *Plectrohyla, Ptychohyla*), hylodines, and telmatobiines (*Paratelmatobius, Telmatobius*).
3. Eggs and tadpoles in water in basins constructed by males.—Hylines (*Hyla boans* group).
4. Eggs and tadpoles in tree holes or bromeliads.—Some hylines (*Anotheca, Nyctimantis, Phrynohyas resinifictrix, Hyla astartea, H. bromeliacia*).
5. Eggs in streams; tadpoles on rocks in spray zone.—Telmatobiines (*Cycloramphus* and *Thoropa*).
6. Eggs in aquatic foam nest; tadpoles in ponds.—Most leptodactylines.
7. Eggs in terrestrial foam nest; direct development into froglets.—Leptodactylines (*Adenomera*).
8. Eggs embedded in dorsum of aquatic female; tadpoles in ponds.—Pipids (*Pipa arrabali*).
9. Eggs embedded in dorsum of aquatic female; direct development into froglets.—Pipids (*Pipa pipa*).
10. Eggs terrestrial; tadpoles in streams.—Centrolenids (*Centrolene*).
11. Eggs terrestrial; tadpoles carried to water by adults.—All dendrobatids.
12. Eggs terrestrial; direct development into froglets.—Brachycephalids, bufonids (*Osornophryne, Rhamphophryne*), telmatobiines (*Barycholos, Eleutherodactylus, Holoaden, Hylactophryne, Ischnocnema, Phrynopus, Phyzelaphryne, Syrrhophus, Tomodactylus*), microhylids (*Myersiella, Synapturanus, Syncope*).
13. Eggs arboreal; tadpoles in ponds.—Hylines (*Hyla leucophyllata* and *H. parviceps* groups) and all phyllomedusines except *Phyllomedusa cochranae* group.
14. Eggs arboreal; tadpoles in streams.—Centrolenids (*Centrolenella*), hylines (*Hyla albosignata* and *H. lancasteri* groups), and phyllomedusines (*Phyllomedusa cochranae* group).
15. Eggs in dorsal pouch of female; feeding tadpoles in ponds.—Hemiphractines (some *Gastrotheca*).
16. Eggs on dorsum or in dorsal pouch of female; nonfeeding tadpoles in tree holes or bromeliads.—Hemiphractines (*Flectonotus, Fritziana*).
17. Eggs on dorsum or in dorsal pouch of female; direct development into froglets.—Hemiphractines (*Hemiphractus*, some *Gastrotheca*).

Lynch (1979) and Duellman (1982) noted the fidelity of certain reproductive modes to tropical forest environments and designated forest and nonforest reproductive modes. In the foregoing list, numbers 10–17 are considered to be forest modes. In these modes the eggs (and in some cases the tadpoles) are exposed to the air as they develop on the ground, on vegetation, or on the back of the female. Thus, egg development is dependent upon high humidity.

Modes 2, 5, 10, 14, and 11 (in part, *Colostethus*) are dependent on the existence of high-gradient streams for the survival of the tadpoles. Of these, modes 10, 11, and 14 also are forest modes, for the eggs are deposited on the ground or on vegetation.

Analysis of the reproductive modes at the 48 tropical American sites reveals great disparities in the proportions of nonforest, forest, and stream-dependent modes (Fig. 8, Table 10). The highest proportions of forest modes are in the equatorial part of the upper Amazon Basin, the trans-Andean forests, the lower Central American wet forests, and the humid montane sites. In Middle American dry forests, the Venezuelan llanos, and the Chacoan dry forests, the proportion of forest modes is less than 12%. Reproductive modes dependent on streams are most common in the humid montane forests (28–53%), the trans-Andean forests (12–30%), the lower Central American wet forests (14–26%), and the coastal forest of southeastern Brazil (23%). Stream modes are uncommon in the Amazon Basin (6–8%) and absent in the Venezuelan llanos, Chacoan dry forests, and Middle American dry forests.

Thus, we find that there is a trend from a high proportion of forest modes in aseasonally wet lowland forests to low proportions (or absence) of these modes in dry forests and llanos. Stream-dependent modes are uncommon or absent in most lowland sites, and these make up a larger proportion of the anuran faunas in montane sites (Fig. 3). Likewise, most montane sites have a high proportion of species having forest modes of reproduction (Fig. 3).

DISCUSSION

When all of the factors (environmental, historical, and reproductive) are viewed as a whole in attempting to provide an explanation for the patterns of species diversity in neotropical anurans, we find that each factor influences species diversity to varying degrees in different areas. The combined effects of these factors result in the existing patterns of diversity.

In the cis-Andean tropical lowlands of South America, Mesoamerican and North American components play a minor role. No taxa of Mesoamerican origin are found there, and one northern group (Ranidae) is represented by a single species, *Rana palmipes*, at sites primarily north of the Equator. Some South American family groups have restricted distributions; thus, *Allophryne ruthveni* is restricted to the Guianan forests, and *Brachycephalus* and hylodines are restricted to the coastal forests of southeastern Brazil.

Within the cis-Andean lowlands there is a decrease in annual rainfall and an increase in the seasonality of rainfall away from the equatorial part of the upper Amazon Basin. This trend is reflected in the diminution in overall anuran species diversity from the equatorial upper Amazon Basin to the lower basin in the east, the Chaco in the south, and the llanos in the north, and a concomitant trend in the reduction in forest modes of reproduction. Thus, in the cis-Andean lowlands, climatic factors seem to have an important effect on overall anuran species diversity.

In the cis-Andean lowlands stream-dependent modes of reproduction are poorly represented, but in southeastern Brazil, where high-gradient streams are numerous, 23.1% of the anurans have stream-adapted reproductive modes.

Compared with other lowland sites, those in the trans-Andean Chocó and lower Central America (Costa Rica and Panama) have a high percentage (61.9%) of forest modes of reproduction and also a high percentage (20.0%) of stream-dependent modes. The presence of high-gradient streams provides the necessary habitat for the stream-adapted reproductive modes. Overall diversity at these sites is less than in the upper Amazon Basin, and the high percentage of forest modes of reproduction is correlated with the few species of pond-breeding hylids and leptodactylids as compared with the upper Amazon Basin. The principal differences between the lower Central American and Chocoan sites are the historical components of their anuran faunas.

At the Chocoan sites more than 90% of the taxa are South American, whereas at the Central American sites 55% of the species are Mesoamerican. One North American species (*Rana palmipes*) occurs in the Chocó; the same species occurs with two other species of *Rana* in lower Central America.

There is a gradient in decreased annual precipitation and increased seasonality from the lower Central American rainforests to those in northern Central America and Mexico. This is reflected in a decrease in overall anuran species diversity. Furthermore, in the northern forests there is an absence of stream-dependent reproductive modes, a decrease to only 7.1% of South American taxa, and an increase to 14.2% of North American taxa. These trends are continued in contrasting Mesoamerican dry forests with the northern rainforests. In the dry forests there are no stream-dependent reproductive modes, and only 11.6% of the species (all Mesoamerican in origin) have forest modes of reproduction. In the dry forests, 16.1% of the species are North American in origin.

Comparison of Middle and South American cloud forests with one another and with adjacent wet lowland forests reveals that overall diversity is much less in the cloud forests in lower Central America and in South America than in the adjacent lowlands; however, in northern Middle American cloud forests the overall diversity is only slightly less than that in the lowlands. The scarcity of ponds in the montane cloud forests is reflected in the few pond-breeding species of anurans at these sites; this is the single largest group of anurans having low diversity in the cloud forests. In contrast, all cloud forests have a high percentage of stream-breeding anurans (45.9% in Middle America and 35.9% in South America) and species with forest modes of reproduction (35.9% in Middle America and 76.3% in South America). The major genera having forest modes are *Colostethus*, *Centrolenella*, and *Eleutherodactylus*, and the first two also are stream-breeding taxa. On the other hand, in Middle American cloud forests, the major stream-breeding genera are *Hyla*, *Plectrohyla*, and *Ptychohyla*. All species in South American cloud forests are members of groups having a South American origin, but in Middle American cloud forests 33.3% of the stream-breeders and 28.3% of the forest modes are species of Mesoamerican origin. No North American groups are represented in South American cloud forests, and North American groups (species of *Rana*) constitute only 6.5% of the anurans at sites in Middle American cloud forest.

All of the taxa at the high Andean sites are South American in origin. The major reproductive modes at wet páramo sites are forest modes (76.3%) or stream modes (38.2%), some of which are included in the forest modes. The anuran fauna of the wet páramos has been derived from that of the adjacent cloud forests, whereas that of the drier puna habitats in the central and southern Andes, which is less diverse and contains about 60% pond-breeding species, has been derived from the Patagonian region (Duellman, 1979b).

Our knowledge of the anuran fauna of tropical America is fragmentary. Of the sites included herein, only those at La Selva, La Planada, Barro Colorado Island, Palenque, Santa Cecilia, and Belém can be considered to have been studied thoroughly enough to provide a reasonably complete list of species and knowledge of their reproductive modes. In order to refine the patterns of anuran species diversity presented here, more data need to be accumulated from many other sites.

I have emphasized the role of reproductive mode in understanding anuran species diversity. The diversity of modes seems to be correlated with humidity and with stream gradients. Accurate microclimatic measurements and data on the physiology of anuran eggs and larvae are needed in order to quantify and refine these presumed correlations.

Much of the anuran fauna in tropical America is disappearing at a rapid rate. The wet lowland rainforest at Santa Cecilia, Ecuador, that provided data for the largest assemblage of anurans in the world has been destroyed. Other tracts of rainforest and especially cloud forest are being eliminated before their biotas are inventoried. Fortunately, many tracts of forest are being set aside as preserves, and data from some of them have been incorporated into this review. However, the establishment of reserves usually is based on the known or presumed existence there of high diversity of birds or primates, with little or no attention given to more poorly known groups such as anurans.

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MANAGEMENT OF HABITAT FRAGMENTS IN A TROPICAL DRY FOREST: GROWTH[1]

Daniel H. Janzen[2]

ABSTRACT

Tropical conservation biology is inescapably the biology of habitat fragments and has been focused on habitat decay. Habitat restoration is primarily the initiation, growth, and coalescence of habitat fragments. Management of a tropical wildland will become the art and science of arresting the decomposition of habitat fragments and promoting their growth and coalescence. Forces that determine accumulation of structure and species are significantly within human control. Today's management actions will determine the nature of wildland habitats for centuries to come. Tropical dry forest is the most threatened of all the major lowland tropical forest habitats, simply because it has always occupied some of the lands most easily farmed in the tropics, and because it is so susceptible to fire. When dry forest and fields are abandoned and therefore allowed to return to dry forest, there are two principal kinds of forest initiation (assuming that there are nearby seed sources). a. When large pastures are downwind of a relatively intact forest, the initial invasion is primarily by individuals of large wind-dispersed trees that will persist and characterize the site for hundreds of years. However, these tree species are a minority of the total flora. Such forests of wind-dispersed trees are relatively inhospitable to animals, highly deciduous, and relatively species-poor. b. When there is any kind of attraction for animals in an abandoned open area, they may perch in it or rest below it while crossing the open area. This results in accumulation of an entirely vertebrate-dispersed forest patch. Such patches may grow and coalesce to form a forest type as artificial as is a wind-generated forest. Vertebrate-generated forests contain more food items of interest to animals, are more species rich, and are more evergreen than are wind-generated forests. As large areas of abandoned low-grade farm and ranch land are returned to dry forest, the manager of national parks or other wildlands is confronted with the difficult decision of just which of the above, or other, forest types is to be promoted. The same will apply to rainforest when its restoration becomes a focus of concern.

Tropical conservation biology is inescapably the biology of habitat fragments. There are two kinds of fragments. First, much of what is worthy of conservation has already been broken into *decomposing habitat fragments* that are refugia and remnants. Even a large national park that is a solid block of pristine forest is a fragment. The biology of the decomposition process of these fragments is of intense contemporary interest to conservation planners and managers (e.g., Lovejoy et al., 1986; Diamond, 1986; Janzen, 1986a, c; Wilcove et al., 1986; Uhl & Buschbacher, 1985; Newmark, 1987). Second, habitat restoration is primarily the initiation and coalescence of *growing habitat fragments*. Management of a tropical wildland therefore becomes the art and science of arresting decomposition of habitat fragments and promoting their growth and coalescence. In such an arena, today's management actions will determine the nature of wildland habitats for centuries to come; forces that determine accumulation of structure and species are significantly within human control.

Here I examine the biology of habitat initiation and growth in a Costa Rican tropical dry forest. Dry forest is the most threatened of all the major lowland tropical forest habitats. It once covered more than half of the world's tropics (e.g., Brown & Lugo, 1982; Murphy & Lugo, 1986) but now supports a diverse array of breadbaskets, cotton fields, and pastures. In Pacific Mesoamerica, for example, less than 0.1% of the original tropical dry forest, which once covered an area the size of France (equal to five Guatemalas in area), has conservation status, and there

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TABLE 1. *Monthly precipitation (rounded to the nearest mm) in the administration area of Santa Rosa National Park, Guanacaste Province, Costa Rica (data collected by park rangers and extracted from the Meteorology Institute in San José).*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1980	1	0	5	0	184	175	139	159	331	417	240	9	1,660
1981	0	1	1	11	353	582	172	478	195	268	153	27	2,241
1982	16	2	0	41	919	129	117	34	328	197	37	1	1,820
1983	2	0	22	4	21	180	106	107	188	201	79	7	917
1984	6	8	0	0	118	218	278	162	613	261	52	7	1,723
1985	0	0	0	3	99	211	154	169	214	436	119	26	1,431

are no remaining large areas of even relatively pristine dry forest (Janzen, 1986a). This dry forest area exists almost entirely as habitat fragments and degraded patches, all of which are still shrinking if not in conserved areas. If there is ever to be a Pacific mesoamerican dry forest national park large enough to truly maintain the animals, plants, and habitats that greeted the Spaniards in the early 1500s, it will have to be grown rather than decreed (Janzen, 1986a).

The study site is the 108-km^2 Santa Rosa National Park and its immediate surroundings, the site of the proposed 800-km^2 Guanacaste National Park (GNP) (Janzen, 1986a). GNP is an approximate rectangle of variably damaged dry forest in northwestern Costa Rica, lying between Volcán Orosí and Volcán Cacao on the east and the Pacific Ocean to the west, with the Interamerican Highway cutting through the middle. From the ocean to the tops of the 1,500-m volcanoes is a moisture and elevational gradient that ranges from the driest part of Costa Rica (the sea level tip of the Santa Elena Peninsula, with less than 1 m of rainfall during its 5–6-month rainy season, Table 1) to seasonal rainforest on the volcano sides to ever-wet cloud forest on the volcano tops. The dry forest discussed here grows primarily within 10 km of the Administration Area of Santa Rosa National Park and is a mosaic of pristine forest, 0–400-year-old woody succession, and abandoned pastures of an introduced African pasture grass (jaragua, *Hyparrhenia rufa*). The Santa Rosa dry forest contains about 700 species of plants (Janzen & Liesner, 1980), 115 species of mammals (Wilson, 1983), 170 species of resident birds (Stiles, 1983), and 13,000 species of insects (including about 3,000 species of moths and butterflies, Janzen, 1988a, b).

The essay presented here is based on processes observed within the area of the proposed Guanacaste National Park. Space does not permit review of the pertinent literature from other habitats, but this will be done in a later publication.

WHAT ARE THE TRAITS OF THE TWO PRINCIPAL KINDS OF HABITAT FRAGMENTS?

DECOMPOSING HABITAT FRAGMENTS

As logging, burning, and clearing for pastures and agriculture have whittled away at Guanacaste Province's dry forest in northwestern Costa Rica (e.g., Uhl & Buschbacher, 1985; Janzen, 1986a), the large and multi-habitat dry forest expanses have been reduced to fragments ranging in size from a few hundred hectares to areas containing only a single remaining tree. Species richness in these fragments is decaying to substantially lower equilibrium densities than once existed, but many decades will pass before a stable equilibrium level is reached (if ever). The rate and depth of decay depends on at least three major variables:

1. How directly prejudicial is the forest fragmentation process to the organisms in the remaining fragments? This aspect of fragmentation cannot be separated from the simple effects of reducing the size of the habitat (and thus the sizes of the constituent populations). Except in experiments (e.g., Lovejoy

et al., 1986) and massive logging or resettlement schemes, habitat is almost never reduced in area as if a giant cookie-cutter had cut out a small relict piece in one fell swoop. For example, the fragmentation and decomposition of dry forest by repeated fires has a quite different effect on its species composition than if some of the forest is left standing and some is bulldozed for cotton fields that are then allowed to change to brushy pastures.

2. Are there other areas that continually generate incoming individuals? In other words, is the population of any given species in a habitat fragment maintained by internal recruitment, colonists, or both? Incoming individuals may originate in the same or different kinds of habitat as the recipient habitat (e.g., Janzen, 1986e).

3. What proportion of the species have what population decay rates and individual life spans? A tree species whose individuals have a 400-year life span may persist in a habitat fragment long after that fragment can support a breeding population of the species, while an insect population might well disappear within weeks of the time when its population no longer achieves recruitment. Whether the observer is left with a feeling of pending doom as a dry forest is increasingly fragmented depends in great part on which kinds of organisms are censused as indicators. Agroecosystems based on what once was tropical dry forest are especially rich in the living dead—individuals living out a physiological life span but no longer occupying a habitat in which recruitment occurs (Janzen, 1986b).

GROWING HABITAT FRAGMENTS

The second kind of habitat fragment is very different from the shrinking relict mentioned above. In the long view of tropical conservation, growing habitat fragments are extremely important and complex; while shrinking habitats may even be accepted as they stand, growing habitats require management technology and choices. As more tropical restoration projects take root, there will be more efforts at initiating habitats, reconstructing habitats from fragments, and even reinstalling species from distant habitats and geographies. Restoration will often initiate growing habitat fragments that accumulate species richness to equilibrium levels as yet unknown. As they grow and coalesce, the three variables mentioned above will generally apply, but with different relative importance.

1. The selection of ecological processes (e.g., fire, hunting, grazing) to be stopped will determine the species richness, life forms, and habitat structure. Stopping hunting but allowing fire to continue yields a very different kind of habitat fragment than does allowing hunting but stopping fires. Stopping anthropogenic fires has a very different effect than does stopping natural fires. While the site may initially have had an equilibrium array of species, for all practical purposes and for many centuries it can sustain many different kinds of habitats during the restoration phase. Which habitat occurs will depend on the initiation and management processes.

2. Proximity of source areas for incoming species, as measured by the ability of individuals of species to arrive, establish, and recruit once present, will be very important in determining whether a growing fragment quickly or slowly rises to an equilibrium value. Since different groups of organisms have extremely different abilities to colonize, and since the chance of establishment in a habitat depends at least on what species have colonized earlier and the environmental traits of the habitat, I expect the rate of species buildup to be very irregular, with long periods of relative stasis.

3. Species will appear in a fragment long before they have attained a density at which their population can survive through recruitment and/or persistence within the habitat. That is to say, the species richness of a growing habitat fragment can easily be greater than the equilibrium density for a fragment of that size and set of conditions.

Study of the decay of species richness within a fragment requires either actual or inferential knowledge of reference or benchmark habitat. This is becoming extremely difficult in dry forest because this forest type has already been thoroughly fragmented for decades or even centuries. On the other hand, there are numerous opportunities to study species accumulation in growing habitat fragments, even if there are not enough species in the region to completely restore the habitat.

INITIATION AND GROWTH OF HABITAT FRAGMENTS

The manner of initiation and growth of habitat fragments in Santa Rosa's dry forest is a novel process in the evolutionary and ecological history for these habitats and for this fauna and flora (just as it would be for other tropical restoration projects). Even though much of Santa Rosa has been cleared to bare ground by volcanic activity in the past, habitat restoration (primary succession) on such a site is different in many ways from the secondary succession that occurs when habitats are initiated and grow in old fields, abandoned pastures, or repeatedly burned forest. However, be they novelties or otherwise, understanding the biology of growing fragments is critical to survival and maintenance of Santa Rosa's tropical dry forest.

Growing habitat fragments in Santa Rosa are most commonly initiated in abandoned pastures. Even if land is lumbered or cleared for fields, it is usual for such areas to be converted to pastures before the restoration process is allowed. Most Santa Rosa pastures are almost pure jaragua (*Hyparrhenia rufa*) with a sprinkling of native herbs, though a few pastures of native grasses remain on the poorest, driest, and/or rockiest soils (e.g., Santa Elena Peninsula and Cerro El Hacha), and pastures of other introduced grasses occur on the moister volcanic slopes. The abandoned or lightly used pastures in Santa Rosa range from grass patches of less than a hectare to several km^2 in area.

Abandoned pastures initially range from virtually lacking trees and treelets to quite rich in sucker shoots from old and large root systems. Santa Rosa pastures are also dotted with the occasional seedling or sucker shoot from a sapling tree or treelet. The numbers, sizes, and kinds of large woody plants in a newly abandoned pasture depend on its age, frequency and timing of burning, timing of pasture "cleaning," proximity to forest (e.g., Purata, 1986), kind of livestock, stocking density, and numerous other variables (just as is the case in extratropical invasion of abandoned fields and pastures by forest, e.g., Olsson, 1984, and included references). All of the initially present woody plants are potential starting points for dry forest habitat initiation (see "nuclear trees" discussed below) and add to the composition of a growing habitat fragment without having to arrive by dispersal.

Expanding and filling habitat fragments range from being totally isolated to being expansions of an existing forest into an adjacent pasture. Placement of these fragments is not haphazard and often has clear relationships to fire patterns, wind direction, animal availability, soil moisture and contour, kinds of nearby forest, and other factors.

TWO PRINCIPAL KINDS OF HABITAT INITIATION

Almost all fires were stopped in abandoned pastures in Santa Rosa's dry forest through an active fire control program initiated in the 1984 dry season. All modern fires in the Santa Rosa area are set by humans or arrive as free-running wildfires that were set by humans. In some of the park pastures, fires even stopped at the time of park establishment in 1972 (or later, 1972–1983) because they were sufficiently isolated that only deliberately set fires got to them. There are even some old pastures or pasture remnants in the park that have not been burned for many decades because woody succession isolated them from the pastures that traditionally burned. As a general rule in Santa Rosa, when woody succession has proceeded to the point where the overstory canopy shades out the grasses and herbs, the forest does not carry a fire (though there are special circumstances, to be described elsewhere, in which enough dry forest can burn to initiate a return to grassland).

When livestock were finally removed from Santa Rosa in 1978–1979, an important ecological process was altered. Livestock had maintained the jaragua at a low level through heavy grazing. Grass fires had relatively little fuel, and a conspicuous equilibrium was maintained between forest/pasture edges; in dry years or when the fire was late in the dry season, it nibbled away the margins of the forest. In wet years or when there was an early burn, the forest margins moved slightly into the pasture. When the cattle were removed, the jaragua formed dense stands 1–2 m in height within a single rainy season. These stands shade woody plant seedlings and provide enough fuel to support very hot and thorough fires at any time in the dry season (such stands even support fires during droughts in the rainy season). This initiated a rapid decline in the area and quality of dry forest fragments surviving in the abandoned pastures and on their margins. This decline stimulated the fire control program initiated in the 1984 dry season.

The two processes of forest initiation described below are occurring in fire-free and cattle-free contemporary Santa Rosa. Were the park to be returned to either cattle-rich, fire-rich, or cattle- and fire-rich status, the details of these processes would undoubtedly be different.

Habitat establishment through seed dispersal by wind.

In many of Santa Rosa's abandoned pastures free of cattle and fire, a distinctive set of woody species has appeared as the forest moves into the pasture. At least 90% of the trees and treelets have wind-dispersed seeds. The vertebrate-dispersed initial colonizers, such as *Cecropia obtusifolia*, *Piper* spp., *Trema micrantha*, *Muntingia calabura*, *Spondias mombin*, and *Bursera simaruba*, are almost entirely absent. For example, the oldest explicit regeneration plot (CT Regeneration Plot, on soils derived from a flat, volcanic welded ashflow) in the park was last swept by fire in the 1979 dry season (it was a jaragua pasture that had been frequently burned pasture of some kind for several hundred years). Today (end of the 1986 rainy season), the following 12 species constitute at least 90% of the 5,000-plus individuals and biomass of trees and treelets in the 3-ha plot (all trees of all sizes in the plot are registered and mapped): *Ateleia herbert-smithii*, *Acosmium panamensis*, *Lysiloma auritum*, *Dalbergia retusa* (Leguminosae); *Rehdera trinervis* (Verbenaceae); *Cordia alliodora* (Boraginaceae); *Luehea speciosa* (Tiliaceae); *Swietenia macrophylla* (Meliaceae); *Tabebuia rosea* and *T. ochracea* (Bignoniaceae); *Cochlospermum vitifolium* (Cochlospermaceae); and *Hemiangium excelsum* (Hippocrateaceae). All plants in this plot arrived by their own means, and the vegetation was not manipulated.

All these species have wind-dispersed seeds. However, Santa Rosa has a native tree and treelet flora of 215 species (Janzen & Liesner, 1980) of which 25% are wind dispersed; 64% are vertebrate dispersed. More than 100 species of vertebrate-dispersed trees and treelets maintain breeding populations within 200 m of the CT Regeneration Plot. It is clear that habitat initiation in this plot is based on an ecologically distinctive subset of the species pool (cf. Beyer, 1975, for a curiously similar extratropical example).

There is one major reason why vertebrate-dispersed species are scarce in this restoration site. Among the many seed-dispersing vertebrates in the park, only white-tailed deer (*Odocoileus virginianus*) and coyotes (*Canis latrans*) encounter resources in a pure stand of jaragua. A deer sometimes uses it for cover when resting and spits out *Spondias mombin* (Anacardiaceae) and *Byrsonima crassifolia* (Malpighiaceae) nuts when chewing its cud (Janzen, 1985). Coyotes hunt there for cotton rats, *Sigmodon hispidus*, and defecate tree seeds such as *Manilkara chicle* (Sapotaceae) and *B. crassifolia*. Other vertebrates that disperse trees and treelets (e.g., collared peccaries (*Tayassu tajacu*), coatimundis (*Nasua narica*), magpie jays (*Calocitta formosa*), and tapirs (*Tapirus bairdii*)) only defecate in the pasture when they happen to cross it on their way from one forest to another; in addition to the two plants listed above, these animals have dispersed a few individuals of *Enterolobium cyclocarpum* and *Acacia collinsii* (Leguminosae), *Genipa americana* and *Alibertia edulis* (Rubiaceae), and *Annona reticulata* (Annonaceae) into the CT Regeneration Plot. This particular abandoned pasture did not have a tree that served as a nuclear tree (see below) though the single old *Acrocomia vinifera* palm could have served that role. Also, animal-rich forest only occurs along one side of the plot and so there is little reason for animals to cross it.

There are many places in Santa Rosa where patches of wind-generated forest have recently been initiated as major protrusions into abandoned pastures. Examination of these forest fragments (or peninsulas) over the past few years allows a number of generalizations:

1. Not only is an abandoned jaragua pasture initially unattractive to seed-dispersing animals because the grass usually does not represent food or other resources, but the growing forest made up predominantly of wind-dispersed trees offers no food for frugivory (by monkeys, bats, coatis, tayras, tapirs, peccaries, deer, numerous birds) compared with a forest fragment containing a more balanced mix of seed dispersal types. Since the wind-dispersed trees are first to colonize the site, they physically and numerically dominate it for many decades as they live out their life spans. While the site does offer shade and some foliage and seeds, it still lacks a major class of food.

2. The wind-dispersed initial colonizers are large trees (attaining heights of 15–25 m) and live for 50 to several hundred years. There is no wave of early successional, short-lived, and comparatively small species. It is even tempting to suggest that a wind-dispersed colonizing tree has to be tall in dry forest, or it won't be tall enough to have its seeds blow over the canopy and into tree falls and other gaps in the canopy. Put another way, in a climatic regime that grows a tall forest, only canopy-level or emergent trees (and high-climbing vines) will successfully colonize that forest via wind-dispersal or evolve wind-dispersal.

3. Not only does a wind-dispersed dry forest lack fruit, but all its seeds are well protected against vertebrate postdispersal seed predators. The species with big seeds in conspicuous fruits or other dispersal units (e.g., *Lonchocarpus* spp., *Acosmium*, *Swietenia*, *Hemiangium*, *Ateleia*) have very toxic seeds (e.g., Janzen, 1986d). Those with edible seeds (e.g., *Cochlospermum*, *Rehdera*, *Luehea*) have very small seeds that easily escape by self-burial in the litter.

4. As the first wave of wind-dispersed trees reaches maturity and begins bearing seeds, the dispersal process in the fragment does not change. By contrast, in a site that is invaded by vertebrate-dispersed tree species, the pattern of the dispersal process will change as the trees come into reproductive maturity and begin to attract animals. Some of these animals (e.g., agoutis (*Dasyprocta punctata*)) play no part in initiating the forest fragment. This attraction will increase the rate of accumulation of plant species in the habitat fragment.

5. The majority of the large trees in Santa Rosa (many with fruits eaten by vertebrate dispersal agents) require at least as much sunlight as is made available when a tree falls to grow into saplings (the evergreen *Manilkara chicle* is the only obvious exception). Once the habitat fragment is occupied by large wind-dispersed trees, the species composition of the canopy will not significantly change its composition until these wind-dispersed trees begin to die of senescence (and create tree falls) many decades later, even if there is a very heavy flow of vertebrate-dispersed seeds into the site during intervening years.

6. A wind-dispersed forest does not expand into a pasture from all compass directions. A pasture on the downwind side of a forest of mixed dispersal types receives a heavy inoculum of wind-dispersed seeds, but a pasture upwind of forest receives none. This process is especially critical to restoration efforts if the upwind margin of the pasture borders

on a park boundary with agricultural land, ocean, or other nonforest habitat. Vertebrate-dispersed seeds in a pasture may have come from any direction. In Santa Rosa, the dry season winds blow almost invariably from northeast to southwest; rainy season winds blow in many different directions, but there are no wind-dispersed trees or treelets that mature their seeds at this time (see 10 below).

7. The only parents of wind-generated fragments in pastures are trees near the forest–pasture interface. Even a few tens of meters of forest thoroughly filter out wind-borne tree seeds (e.g., Augspurger, 1986). On the other hand, the vertebrate-dispersed seeds falling into a growing habitat fragment in an abandoned pasture may have passed through forest expanses hundreds to thousands of meters wide.

8. Wind-dispersed seeds at Santa Rosa move up to about 200 m into pastures, but a more common distance is 0–100 m. The seeds move greater distances if the parents are maximally tall individuals that have grown up in competition with other forest trees (i.e., near forest margins) rather than shorter isolated trees in open pastures. This means that wind-generated growing habitat fragments will always be near another forest with adult trees in it.

9. Wind-generated seed shadows are often dense and very uniform compared with vertebrate-generated seed shadows (which have conspicuous heterogeneity associated with perches, waterholes, trails, shade, steep contour, tourist presence, and other factors). If there is one member of a wind-dispersed species of tree maturing in a growing habitat fragment, there are likely to be numerous others (unique individuals of vertebrate-dispersed trees are commonplace in growing habitat fragments, see below).

10. Forests of wind-dispersed species bear no ripe fruits or seeds throughout the rainy season (no Santa Rosa species of wind-dispersed tree or treelet ripens its fruits in the rainy season). Associated with this, the wind does not blow with equal intensity and pattern throughout the year. The highest average wind velocity occurs during the first half of the dry season (December through early March). The days with the strongest wind occur in late December and January. During the dry season the most intense winds occur during the central part of the day (when it is driest and fruits are most likely to be shed or broken off, and fruits are most likely to dehisce). During the rainy season, there are many nearly calm days, and winds often occur during rainstorms (when a wind-dispersed fruit or seed would have little or no chance of dispersal). Another barrier to wind-dispersal during the rainy season is that wind-dispersed units of dispersal lose weight at maturity by drying out, which does not occur readily in the rainy season.

Along the same lines, almost all wind-dispersed seeds at Santa Rosa appear to germinate within a few weeks of being wetted by the first rains. There is a major pulse of seedling appearance with the first rains (from seeds accumulated during the dry season) followed by no further seedling input or site colonization during the six-month rainy season. Vertebrate-dispersed seeds in Santa Rosa display many kinds of dormancy and new seedlings of many species appear at different times during the rainy season. Since many of these seeds are dispersed during the rainy season, a habitat fragment can be initiated at this time of year from dispersing seeds or from seeds in the soil.

Habitat establishment through seed dispersal by vertebrates.

Vertebrates play a much more complex role than does wind in initiation and growth of habitat fragments. This is because:

a) There are nearly three times as many species of vertebrate-dispersed than wind-dispersed trees and treelets in Santa Rosa, and they bring with them more life forms and kinds of ways to occupy a site than are found among the wind-dispersed species.

b) There are many more kinds of vertebrate-generated seed shadows than wind-dispersed seed shadows in Santa Rosa.

c) The pattern of forest initiation depends on the biology of the animals as well as on the biology of the plants. The wind has not evolved and coevolved with plants, and the plants can only evolve, not coevolve with the wind.

Here, I focus on one particular kind of vertebrate-generated forest initiation in Santa Rosa pastures, that which is associated with nuclear trees.

A nuclear tree is a single tree that appears in a pasture and is then attractive to animals that defecate or otherwise drop seeds in its vicinity (see McDonnell & Stiles, 1983; Beckwith, 1954; Debussche et al., 1982, for ornithological extratropical examples). The animals go to the tree as a perch, for shade, to eat its fruits, to mark ranges, and other reasons. Whether a nuclear tree and its associated seed rain actually becomes a growing fragment of forest habitat depends on numerous environmental variables ranging from the rate and kind of seed rain to the depth of the grass, soil conditions, species of nuclear tree, fire regime, and other factors. For example, many of the best contemporary examples of vertebrate-generated growing habitat islands in Santa Rosa are centered on guanacaste trees (*Enterolobium cyclocarpum*) on small rocky outcrops that protected the sapling from low grass fires (in the heavily grazed pastures). Within a few years after cattle were removed from Santa Rosa, the high grass fires swept across these small fragments and obliterated many of them and their nuclear guanacaste trees.

Representative nuclear trees in Santa Rosa are guanacaste, cenizaro (*Pithecellobium saman*, Leguminosae), guacimo (*Guazuma ulmifolia*, Sterculiaceae), jobo (*Spondias mombin*, Anacardiaceae) and figs (*Ficus* spp., Moraceae), but many other species can serve this function (some are remnant wind-dispersed trees standing as the sole survivors of a dwindled forest fragment).

A growing dry forest fragment that has been generated by vertebrates around a nuclear tree in the center of an abandoned pasture has a number of distinctive traits:

1. Wind-dispersed species of trees and treelets are absent (unless they were present as persistent suckers at the time of fragment initiation). That is to say, the species pool from which the fragment is potentially drawn is some subset of the 138 species of vertebrate-dispersed trees and treelets in Santa Rosa.

2. Certain vertebrate-dispersed species are missing because they are usually dispersed by vertebrates that either never cross pastures or are very unlikely to carry one of these seeds when they do. For example, agoutis and monkeys are very unlikely to carry the large seeds of guapinol (*Hymenaea courbaril*, Leguminosae), panamá (*Sterculia apetala*, Sterculiaceae), and tempisque (*Mastichodendron capiri*, Sapotaceae) across a pasture.

3. The species and age of the nuclear tree will influence the species composition of arriving seeds. If it bears edible fruits (which is very likely since wind-dispersed nuclear trees are almost nonexistent in large pastures), the species composition of the seed rain during fruiting will be strongly influenced by the assortment of animals attracted to its fruit. Additionally, different species of trees offer different kinds of perches and shade, which likewise will influence animal visitors and their seed cargoes.

4. The species and age of the nuclear tree will influence the survival of the seedlings below it through differential shade effects on grasses and woody seedlings, protection of seedlings from fire through shading out grasses and keeping the soil moist, and the duration of its deciduousness during the dry season.

5. The trees accumulating around a nuclear tree are usually smaller and shorter than the nuclear tree because they are younger than it and because they compete with it. The canopy is therefore dome-shaped with the nuclear tree near the center rather than flat-topped (as is the case in wind-generated habitat fragments).

6. The understory of a vertebrate-generated habitat fragment often contains reproducing treelets and shrubs, e.g., *Chomelia spinosa*, *Alibertia edulis*, *Psychotria* spp.

(Rubiaceae); *Piper* spp. (Piperaceae); *Erythroxylon havanense* (Erythroxylaceae); *Malvaviscus arboreus* (Malvaceae), *Hirtella racemosa* (Chrysobalanaceae); *Ximenia americana* (Olacaceae); *Casearia* spp. (Flacourtiaceae); *Ocotea veraguensis* (Lauraceae); and *Annona reticulata* (Annonaceae). Reproducing small plants are generally missing from the understory of a wind-generated forest fragment.

7. Owing to the larger species pool and area from which the species are drawn, species richness of trees and treelets is substantially greater in growing vertebrate-generated habitat fragments than in wind-generated ones. However, if there is frequent animal movement through a wind-generated habitat fragment, the sum of the wind-dispersed species and the animal-dispersed species gives the most species-rich habitats of all.

8. Except for the very large seeds that are not carried out into a pasture (see 2 above), all sizes of seeds arrive at a vertebrate-generated habitat fragment. However, there should be some sorting with distance as fragments get so far out into a pasture that small frugivorous birds are less likely to go to them. In contrast, a wind-generated growing forest fragment should also display sorting whereby the species with lighter seeds move further downwind in the initial invasion.

9. A vertebrate-generated habitat fragment can grow in any direction, rather than downwind as does a wind-generated habitat fragment; and a vertebrate-generated fragment can range from a distant island to a peninsula, while a wind-generated fragment is usually a peninsula from an established forest.

10. The seeds in a vertebrate-generated habitat fragment may come from as far as many thousands of meters from the fragment, and from any compass direction. The tree species in the fragment are thus likely to represent a much greater portion of their respective populations than is the case with a wind-generated patch (which is derived from the immediately adjacent forest). Associated with this process is the fact that vertebrate-generated habitat fragments often contain isolated representatives of a species; whether these individuals can reproduce (through long-distance pollination or by being self-compatible) varies with the species. However, it is quite likely that such species occasionally exceed the species carrying capacity of the fragment, since if it does not maintain itself in the fragment, it is not present in some senses.

11. Since there are some vertebrate-dispersed tree species in fruit throughout the year in Santa Rosa, there are likewise trees and treelets in fruit throughout the year in the vertebrate-generated growing habitat fragments.

12. As a habitat fragment grows by vertebrate input of seeds (and by internal recruitment), its margins become less likely sites of seed deposition. The rate of expansion of a habitat fragment noticeably declines as it becomes more than about 0.5–1 ha in area.

DISCUSSION

I have briefly described two prominent kinds of forest habitat initiation and growth in abandoned pastures in Santa Rosa's dry forests. There are also many other kinds of habitat initiation occurring in this park at present. It is evident that the initial processes in habitat initiation will determine the species composition and structure of the forest for many centuries on these sites. It is equally evident that the actions of park managers will determine the kinds of habitat initiation that occur. If the park is left completely to itself, one kind of mosaic will occur. If livestock are used to depress the grass in certain areas, a different kind of mosaic will occur. If nuclear trees are planted far out into pastures or seeded there in the dung of cattle (as occurs with guanacaste and cenizaro trees if the cattle have access to fruit crops), a third kind of mosaic will occur. If native timber trees are seeded in by air or hand, and then natural succession is allowed to continue (as an example for those who want to know how to return worthless dry forest pastures to timber production), the resultant forest will depend in great part on the particular species of timber trees used (fleshy fruit-bearing versus wind-dispersed, evergreen versus deciduous, fast- versus slow-growing). Pastures near forests rich in seed-dispersing mammals and birds will initiate quite different kinds of forest than will those in areas relatively free of vertebrates due to poaching, heavy tourist use, or experimental removal.

It is clear that the managed fate of the entire area of tens of km^2 of pasture in Santa Rosa or several hundred km^2 of pasture in Guanacaste National Park should not be the same from area to area. But whatever kinds of management of habitat fragment initiation and growth are to be applied, it will require basic research into the multiple pathways that secondary succession can follow in this species-rich situation. Whether these pathways will finally converge on a single kind of vegetation for any given site is almost irrelevant, since this will take thousands of years to occur and we have to deal with the situation at hand.

How broadly applicable is the philosophy espoused in this essay? Rainforest restoration has not been explicitly tried, but it is an integral part of traditional shifting agriculture in some areas and has occurred throughout the wet tropics where farms and homesteads have been abandoned when farmers have been relocated out of an area slated to become a rainforest national park. The details of rainforest restoration will obviously be different from those in dry forest, but there will be many similarities.

One difference is apparent even at this early stage of understanding. When a clean pasture is abandoned next to a pristine rainforest, the rate of rainforest tree and treelet movement into it appears to be much slower than in seemingly equivalent cases in dry forest. This is the case even in the wetter eastern end of Guanacaste National Park as compared with the central drier part. There are at least three possible causes. First, rainforest vertebrates may be even more reluctant to enter rainforest pastures and use nuclear trees, for example, than are dry forest vertebrates. Second, the general lack of strong directional winds in rainforest may impede movement of wind-dispersed species into pastures. Third, and I suspect the most likely case, a seedling from a dry-forest seed dispersed into a dry-forest pasture finds itself in a much more foreign environment than does a seedling from a rainforest seed dispersed into a rainforest pasture. The heat, sun, wind, dryness, and fluctuations of an open pasture are much more similar to the rigors of dry forest than they are to the understory of a rainforest (even in a tree fall). Additionally, dry-forest pasture soils are rich in spores of endomycorrhizal fungi while rainforest pasture soils are generally very poor in them (D. Janos, pers. comm.). Certainly at Santa Rosa there is no indication that the physical conditions of open pasture habitat are lethal to tree seedlings, even when they are species commonly associated with relatively moist habitats (e.g., *Hymenaea courbaril*, *Manilkara chicle*).

Blydenstein (1967) described the mosaic of Venezuelan grazed pasture and forest patches as the result of a dynamic interaction between dryness and fire, just as occurred in Santa Rosa before the fire and cattle were eliminated. In some ways, this dynamic is a fine-scale version of the global balance between the dwindling tropical wildlands and restoration systems such as that occurring in Santa Rosa National Park and the proposed Guanacaste National Park area. At present we are in a continuous drought and fire phase, with the forest patches shrinking very, very rapidly. If the dynamic is to have any significant balance, forest restoration is going to have to start up throughout the tropics. It must start not only in places like Guanacaste National Park, where remnants of the plants, animals, and habitats are still present, but also in the large expanses of the tropics where there is virtually nothing left. For example, in countries like Costa Rica, virtually all rainforest parks are on hilly to mountainous soils, with the true flatlands either cleared or almost cleared. The real challenge is whether with fencerow populations, woodlot populations, and living dead (Janzen, 1986f) one can put back together even a first approximation of the flatland rainforests that once stood on the enormous acreages of low-yield rainforest fields and pastures.

The question has been raised as to why Guanacaste National Park needs to be as large as 800 km², especially since about 90% of the habitat has been partly homogenized through partial destruction. The traditional answer is that a large area is needed to maintain even minimal populations of the wide-ranging large animals and the big trees. A less traditional, but nonetheless compelling, answer is that the area must be large to maintain intact wildlands *and* be extremely accessible to tourists, researchers, managers, and school groups; these are the people whose votes and long-term use will keep GNP alive. But there is also a less conventional biological reason that is especially pertinent to dry forest. Intact dry forest is a very complex mosaic of many small fragments of habitat types nestled in amongst each other, generated by soil type, drainage, wind exposure, slope, and rainfall. This mosaic of conditions and species is largely responsible for the many pathways that may be taken by secondary succession in an abandoned pasture; two pastures with identical conditions may easily be positioned next to two quite different source areas for the species that will colonize it. A given animal or plant species exists as a population supported by one or more of these habitat types, but the support base is highly fragmented. A dry forest wildland must be big so that the total area contains enough pieces of a given habitat type (e.g., dry ridges) to support healthy populations of the species that are supported by that habitat type. Yes, there are 800 km² of dry forest in GNP, but, for example, less than 100 km² supports the endemic population of the tree *Ateleia herbert-smithii*, the only legume in the world that is known to be wind-pollinated (Janzen, 1988c).

This worry applies to rainforest as well. Yes, it all appears to be just a sheet of green, but as soon as it is necessary to find any tree species, or any constellation of species, the biologist learns to search for the subtle differences in drainage, soil, and other factors that lead to the highly localized target. When the professional conservationists tell us that X% of the rainforest still remains, and that Y% of X is disappearing daily, it is imperative to remember that 0% of many of the habitat types of tropical rainforest remain. Furthermore, that Y% is not spread proportionately over the remaining types, giving us an equal amount of time to crusade for what remains. It is critical to identify those rainforest habitat types that are as threatened as is the tropical dry forest and focus restoration projects on them. The battle for mesoamerican tropical dry forest conservation should have been fought in the year 1800; don't wait until the year 2000 to begin to fumble with the rainforest pieces worth restoration.

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FACTORS CONTROLLING SPECIES DIVERSITY: OVERVIEW AND SYNTHESIS

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ABSTRACT

Factors controlling species diversity are usually presented as a laundry list without organization—for instance, "The tropics have more species than the temperate zones because of greater stability and *reduced seasonality* and *higher productivity* and *more diverse resources* and . . . ." *This paper instead proposes a fourfold grouping of factors, termed the QQID approach. Q = resource quality, consisting of the habitat and resource factors that determine the "number of niches." Q = resource and consumer quantity, consisting of factors determining the quantity of resources (i.e., area and productivity), and factors determining the number of consuming individuals (especially body size) that divide those resources. I = species interactions, which may boost or lower species diversity through effects on individual numbers or individual fitnesses. D = dynamic processes (e.g., extinction, immigration, and speciation), which affect species diversity in both equilibrial and nonequilibrial situations. I illustrate this approach by applying it to understand the famous gradients of species diversity over altitudinal and latitudinal gradients. A major problem for the future involves seeking generalizations as to which factors are likely to be most important under which circumstances. Another problem is to convert this empirical fourfold grouping into a natural hierarchy of factors, possibly based on a hierarchy of processes in space and time.*

INTRODUCTION: THE QQID APPROACH

This article aims to provide an overview of the many factors controlling species diversity. My minimum goal is to construct a simple, four-step checklist for analyzing the determinants of species diversity in any given case (Table 1). I shall also briefly suggest an approach by which this checklist, designed for practical purposes, might be converted into a natural hierarchy of the determinants of species diversity. My examples will be drawn mostly from the other papers of this symposium.

At the outset, let us be clear why the problem of understanding species diversity is complicated. In the first place, species diversity is surely not determined in all cases by the same single factor but is the outcome of many contributing factors. Secondly, while one can formulate "rules" about species diversity, each rule has many exceptions. For example, island species diversity usually increases with island area, but there are more frogs on little Barro Colorado Island than on the much larger Cuba (Duellman, this volume). Island species diversity generally decreases with distance from the mainland, but one of the world's most remote archipelagoes, Hawaii, has more species of *Drosophila* than do continents. Species diversity as one ascends a mountain generally decreases with altitude, but along the western slopes of the Andes above Chile's Atacama Desert it increases from middle to high elevations (Arroyo et al., this volume). Small-bodied species are generally more diverse than large-bodied species, but whale diversity exceeds insect diversity in the open ocean. These exceptions to rules based on single factors arise in part for the obvious reason that species diversity is the outcome of many factors, so that the effect of one factor may be overridden by others. Partly, too, the reason is that some of the determinants of species diversity, such as predation, herbivory, disturbance, seasonality, and environmental predictability, control diversity in a nonmonotonic way, so that an increase in those factors may yield either an increase or a decrease in diversity.

Do the factors controlling species diversity just constitute a laundry list, a catalog without organization? Discussions of the latitudinal

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TABLE 1. *The QQID formulation of factors controlling species diversity.*

Q = Quality

1. Diversity of niches or resources
    - E.g., habitat structural complexity, habitat diversity, resource species diversity, temporal variability, and diversity of consumer strategies.

Q = Quantity

2. Number of consumer individuals, N
    - $N = R/R_0 = AP/R_0$
    - where R = available quantity of resources
    - R_0 = resource requirements per individual (increases with body size)
    - A = area
    - P = productivity per unit area

I = Interactions

3. Species interactions
    - Effects on N
        - Increase of N
            - Predation or herbivory on competing species
        - Decrease of N
            - Resource competition
            - Predation or herbivory on the consumer itself
    - Effects on individual fitness
        - Increase of fitness
            - Mutualism
        - Decrease of fitness
            - Interference competition
            - Parasitism
            - Disease

D = Dynamics

4. Species dynamics
    - Effects of dynamics at equilibrium
        - Effects of extinction rates (decrease with N, etc.)
        - Effects of immigration rates (increase with proximity, vagility, larval settling rates, etc.)
        - Effects of speciation rates (decrease with vagility, etc.)
    - Nonequilibrium situations
        - Pulse disturbance
            - Transiently depressed species diversity
        - Recent pulse decrease in area
            - Transiently elevated species diversity

gradient in species diversity often read that way: "The tropics have more species than the temperate zones because of greater stability *and* reduced seasonality *and* higher productivity *and* more diverse resources *and* . . . ." In fact, life is full of multi-determined phenomena (e.g., whether to declare war, whom to marry, how many children to bear) that at first appear to be influenced by innumerable factors, but for which the factors actually prove to fall into just a few groupings. In some cases, the groupings may even define a natural hierarchy or decision path of factors.

For example, suppose you want to know what determines the number of children in any given candy store. The number obviously depends on the quality or variety of candy to be seen in the window. It is also heavily influenced by the quantity of candy or the size of the store. A little reflection also shows that the number of children in the store depends on interactions, such as those with attractive fairy godmothers beckoning at the door, or with bullies or hungry lions inside. Finally, there is also some role of dynamic or nonequilibrium factors, such as how long ago the doors opened, or how large is the pool of children available for colonizing the store, and where the store is (particularly relative to a school). Thus, the numerous determinants of the number of children in the store sort out into four sets of considerations: quality of resources, quantity of resources, interactions, and dynamics.

It seems to me that species diversity as well is determined by the same four sets of factors—quality, quantity, interactions, and dynamics (Table 1). As a simple mnemonic, I shall abbreviate this accounting as "QQID."

Q. Discussions of species diversity usually start out with an analog of the quality or variety of candy: namely, the diversity of niches or of resources. Hence my first, simplest approach will consider just the diversity of niches without taking into account the quantity of resources or the number of consumer individuals or species interactions. We shall pretend that the environment is constant and without temporal variation, that the world is at equilibrium, and that species dynamics are nonexistent or irrelevant.

Q. Next, I shall take account of the quantity of resources, which partly determines the number of consumer individuals.

I. Thirdly, I shall add consideration of species interactions.

D. Finally, I shall incorporate consideration of dynamics and shall allow for the possibility of nonequilibrium.

Q: Resource Quality

The ecological equivalent of the variety of candy is the number of niches or of resources. One of the basic findings of ecology is that species diversity increases with niche or resource diversity, as expressed in the statement that each species must occupy a distinct niche. This ubiquitous generalization is the outcome of two facts. First, any given genotype can do certain things (e.g., harvest certain resources by a certain method) better than other things. Second, a single gene pool (i.e., one species) can comprise only a certain diversity of genotypes because of the constraint that the individuals carrying those genotypes must be reproductively inter-compatible in order to remain members of the same gene pool. The combination of those two facts has the consequence that each species occupies a certain "niche," however defined, and that species diversity increases with niche or resource diversity.

Many familiar predictors of species diversity fall under this heading of niche diversity. Among the many examples of predictors that could be cited, I shall discuss five that are well illustrated by the papers of this symposium.

Habitat structure.

It is commonly found that habitats with a more complex or variegated structure contain more species than do simpler habitats. Thus, within any given group of taxa there are generally fewer species in a rock desert than in an adjacent grassland, fewer in the grassland than in an adjacent savanna, and fewer in the savanna than in an adjacent tropical rainforest. The symposium papers by Gentry, Erwin, and Duellman emphasized that peak diversities of plants, beetles, and frogs are achieved in tropical rainforest. For birds a rough quantitative measure of habitat structural complexity that serves to predict species diversity is the habitat's foliage height diversity: that is, a diversity measure of how foliage is distributed among different vertical layers of the habitat (MacArthur et al., 1966).

Habitat diversity.

Another expression of niche specialization is that a particular species tends to occur only in certain habitats and not others. Thus, as one proceeds along a habitat gradient, one accumulates more and more species, and the accumulated number of species increases with the diversity of habitats encountered. Familiar examples are that species accumulate as one goes along an elevational gradient on a mountain, a depth gradient in the sea, or a horizontal sequence of habitats on land or in the intertidal zone. One example from this symposium is that most neotropical wet forest tree species are confined to a single forest type or soil type (Gentry, this volume). Another example is that 83% of the beetle species at Manaus, Brazil, are similarly confined to a single forest type (Erwin, this symposium).

Species themselves as niches or resources. Species may constitute niches or resources for exploitation by other species. Thus, diversity of consumer species tends to increase with diversity of resource species. For instance, there are more stenophagous herbivorous beetle species in tropical rainforest than in a temperate woodland because the rainforest has many more tree species. An example is that many neotropical rainforest beetle species are confined to a single tree species; some may even be confined to the interface of a particular pair of tree species (Erwin, this symposium).

Temporal variability. Time also serves as a niche dimension that can be partitioned, so that temporal variability provides opportunities for differentiation absent in an environment that is constant with time. For example, the 24-hour solar cycle permits differentiation between nocturnal, crepuscular, and diurnal species exploiting similar resources in the same habitat. The annual cycle permits species to specialize by adopting various seasonal strategies, as exemplified by the coexisting insect species with different overwintering strategies, or by bird species that coexist in the breeding season but segregate in winter as a result of some being migratory, others resident. Still longer cycles in a variable environment permit the differentiation of *K* strategists from *r* strategists. A striking example from this symposium is the 97% turnover of beetle species in a single tree species of Barro Colorado Island between the wet season and dry season (Erwin, this symposium).

Consumer strategies. Species that harvest similar resources in the same habitat may coexist by employing different foraging techniques, or by adopting differing life-history strategies. Here, too, this symposium has provided a striking example: the 28 alternative reproductive modes by which frogs solve the common problem of producing offspring while protecting them from desiccation (Duellman, this volume).

These five sets of examples do not exhaust the axes along which coexisting species may segregate. Readers will undoubtedly be able to think of further biologically significant ways in which differences in resources or in other niche parameters are exploited by different species.

QQ: Quantity of Consumer Individuals or of Resources

In the preceding discussion we have ignored consideration of the quantity of resources. We have pretended that a resource is either present in sufficient quantity to support a species, or else the resource is absent. However, resource quantity is obviously important because species are packaged in discrete units (i.e., individuals), and a population consisting of too few individuals cannot survive. There is no hard rule as to how many constitutes "too few," but a population consisting of one individual of a species practicing sexual reproduction is clearly doomed to extinction within one generation, a population size of two (one male, one female) is extremely precarious, and only populations with an effective size above 500 are considered reasonably safe even in the short run (Frankel & Soulé, 1981; Soulé, 1986). Thus, the species diversity of any given group of taxa generally increases with the group's total population size.

However, population size, the number of consumer individuals, does not depend only on quantity of resources. More generally, population size equals the total quantity of resources available, divided by the quantity of resources required to sustain one individual. Resource quantity in turn equals the product of area times productivity per unit area, while quantity of resources required per individual increases with body size. Thus, the second "Q" in our "QQID" formulation groups three factors: the increase in species diversity with area, productivity, and decreasing body size.

Area.

The most familiar generalization of island biogeography is that species diversity on islands, mainland habitat patches, or arbitrarily defined mainland census plots increases with area. This species/area relation arises partly from the increase in habitat diversity with increasing area sampled, but also from the direct proportion between area on the one hand and resource quantity and thus consumer population size on the other hand. An example from this symposium is Janzen's (this volume) comment that conservation areas in Costa Rican dry forest should be at least 500–1,000 km^2 in extent, because smaller areas would contain too few individuals of important species to sustain their populations.

Productivity.

Productivity increases with increasing rainfall or temperature, hence with decreasing latitude or altitude. Since number of consumer individuals increases with productivity, species diversity also increases with productivity. This symposium has provided three clear examples. First, plant species diversity on the western slope of the Andes rising out of the Atacama Desert of Chile increases with rainfall (Arroyo et al., this volume). Second, neotropical plant species diversity, collectively or else of each life form considered individually, increases with rainfall up to an asymptotic value (Gentry, this volume). Finally, neotropical rainforest beetle species diversity is much higher in the forest canopy than in lower vertical strata, because the canopy intercepts most of the solar energy and is the most productive stratum (Erwin, this symposium). (Note that these arguments implicitly assume a more or less uniform increase in productivity across the resource spectrum. If production of only certain resources is increased, as in a eutrophic pond, the outcome may be reduction rather than increase in species diversity, because those consumer species specializing on the increased resource type will thrive and may eliminate other species by preempting their resources.)

Body size.

The product of area times productivity equals the total quantity of available resources, but the body sizes of the consumers determine among how many individuals those resources may be apportioned. Thus, for a given resource quantity and hence given consumer biomass (ignoring second-order effects from the variation in metabolic rate per gram of tissue with body size), consumer population size decreases with body size. Hence, all other things being equal (which they often are not), there tend to be more species of small-bodied animals than of large-bodied animals. In the canopy, Erwin (this symposium) encountered thousands of species of beetles but not of elephants. The whole neotropical region contains only 1,545 species of frogs (Duellman, this volume), a number exceeded by the beetle species in a single tree canopy (Erwin, this symposium). Even among beetles, species diversity is highest in Erwin's smallest size class of beetles.

All these examples illustrate that species diversity increases with the quantity of resources and, more generally, with consumer population size.

QQI: SPECIES INTERACTIONS

In our discussion of resource quality and quantity so far, we have ignored species interactions and have implicitly lumped all resource species together simply as "food." However, species interactions may boost or lower species diversity in comparison with the value that one would predict by ignoring species interactions. Some of these effects of species interactions on species diversity are mediated by effects of species interactions on population numbers (the second "Q" of "QQID"), while other effects require instead consideration of individual fitnesses.

Effects on number of individuals.

A familiar example of how species interactions may lower species diversity is that certain consumer species may competitively lower diversity of other consumer species at the same trophic level by preempting resources and hence lowering the population sizes of their competitors. An example of resource competition on a gigantic temporal and spatial scale is that the evolutionary history of vascular plants has involved a parade of successive dominants, starting with the rhyniophytes and proceeding through pteridophytes and gymnosperms to the angiosperms. The rhyniophytes disappeared completely, but the pteridophytes and gymnosperms continue to survive today, albeit represented by many fewer species than formerly. The most likely explanation is that each new evolving group of vascular plants preempted resources that would otherwise have been utilized by previously evolved groups, thereby reducing their numbers of individuals and consequently of species, or even driving them to extinction (Knoll, 1986; Niklas, this volume).

Species interactions may have the opposite effect—boosting species diversity by boosting the quantity of available resources, these supporting greater numbers of consumer individuals. This situation arises when predators or herbivores reduce the numbers of individuals of their prey or plant species, thereby making more resources available for other consumer species at the same trophic level and thus increasing the numbers of individuals and hence species diversity of those other consumers (Paine, 1966). However, predators or herbivores can also reduce species diversity of consumer species by greatly reducing numbers of individuals. Thus, predation and herbivory can either increase or decrease species diversity, depending on circumstances such as the intensity of predation or herbivory. By analogy with the intermediate disturbance hypothesis, one might speculate that a community's species diversity initially increases with increased community-wide intensity of predation or herbivory, then decreases with further increase in intensity. (The intermediate disturbance hypothesis proposes that low levels of physical disturbance also increase species diversity by removing some consumer individuals, thus reducing competition for resources, while an increase in disturbance that more severely reduces consumer population sizes decreases species diversity. (See Yodzis (1986) for further discussion.)

Effects on individual fitness.

The species interactions of interference competition (e.g., physical aggression), parasitism, and disease tend to decrease species diversity by decreasing individual fitness. Conversely, the species interaction of mutualism tends to increase species diversity by increasing individual fitness. Effects on fitness merge into effects on population size as the effects on fitness become strong enough to kill individuals or else to permit them to survive where they otherwise could not.

QQID: DYNAMICS

Our discussion so far has ignored dynamic considerations. The final step in our QQID analysis takes species dynamics into account. We first retain the implicit assumption of equilibrium that we have made up to this point. Even at equilibrium, consideration of dynamics predicts trends in species diversity that one could not interpret without considering dynamics. We shall then relax our assumption of equilibrium and thereby encounter still further trends in species diversity. There are three dynamic processes underlying species diversity: extinction, which tends to decrease species diversity; immigration, which tends to increase it; and speciation, which also tends to increase it.

Effects of dynamics at equilibrium.

Effects of extinction dynamics. All else being equal, the probability (per unit time) of extinction increases with decreasing population size, hence with decreasing area. That inverse dependence of extinction rates on area provides the major reason why species number on islands increases with area. In this instance, dynamic considerations do not predict a new trend in species diversity that we have not already considered; instead, they provide the basis of a trend that we had already noted.

Effects of immigration dynamics. The second rule of island biogeography, after the species/area relation, is that species diversity tends to be higher on islands close to a colonization source than on distant islands, even if the close and distant islands are identical in area and in resources. In this case the phenomenon cannot be discussed at all without reference to dynamic considerations: immigration rates from the mainland source to a nearby island are higher than to a distant island, with the result that equilibrium species diversity is higher on the nearby island. Another consequence of immigration dynamics is that species groups with high immigration rates (high dispersal ability) are represented on islands by a higher fraction of the mainland species pool than are species groups with low immigration rates. Thus, compared with mainlands, oceanic islands have more species of birds and bats than of flightless mammals. As a final example of the effects of immigration dynamics on species diversity, high larval settling rates increase the diversity of barnacles, coral reef fish, and other marine organisms with planktonic dispersal (Roughgarden, 1986).

Effects of speciation dynamics. Anything that increases speciation rates will tend to increase species diversity. Speciation rates depend on numerous factors, such as frequency of chromosomal rearrangements, ease of developing reproductive isolation, and dispersal rates. I shall provide a few examples involving dispersal, which is important in speciation since reproductive isolation is more likely, even over shorter distances, for taxa with poor dispersal ability than for others with great dispersal ability. In part for that reason, there are many more species of flightless beetles and land snails than of tardigrades, which are readily wafted in the aerial plankton and are virtually panmictic and cosmopolitan. Because tropical species of birds and possibly of other taxa tend to be more sedentary than temperate species, considerations of dispersal and speciation rates also contribute to the higher species diversities in the tropics. Note that dispersal has opposing effects on species diversity: with increasing dispersal, the fraction of the regional species pool that reaches a given site increases (increasing the species diversity at that site), but the frequency of speciation and thus the size of the regional species pool itself decreases.

This symposium provided several examples of the sensitivity of species diversity to dispersal through its effects on immigration and speciation rates. As an example of the effect on immigration rates, the plant diversity and composition of Costa Rican dry forests depend on the relative opportunities for seed dispersal by wind and by animals (Janzen, this volume). As an example of the effect of dispersal on speciation rates, the roles of biotic vectors both for pollination and for seed dispersal were a decisive factor in the diversification of angiosperms (Niklas, this volume). Biotic vectors can carry out pollination between conspecific individuals separated by a much greater distance than can be effectively bridged by wind, thus permitting angiosperms to live at much lower population densities than other plants and hence to evolve high diversities of relatively rare species. Biotic seed dispersal permits angiosperms to reach sites accessible only with greater difficulty to other plants.

Nonequilibrium situations.

All out discussions so far have referred to species diversity at equilibrium. However, it is a debated question whether it is frequent or exceptional for species communities to be at equilibrium. There is no doubt that many communities have species diversities below equilibrium values, while other communities have species diversities above equilibrium values (Janzen, this volume). Subequilibrial diversities are a transient result of pulse disturbances, while supraequilibrial species diversities are a transient result of pulse decreases in area.

Pulse disturbances leading to subequilibrial species diversity. If populations or resources are decreased or wiped out by disturbance at a site, species diversity at the site will transiently be below the equilibrium value until the resources are restored, or until the consumer populations are restored by immigration or by speciation. The time constants or relaxation times for species communities to recover from disturbance vary enormously. It may be a few months or years after a storm batters a coastline until resources have been replenished and consumer species have returned. When a volcanic explosion destroys the biota of an island, as happened on Krakatau, it may be decades or centuries before immigration has restored the original species diversity. As a result of Pleistocene glaciations that backed populations of many northern European tree species against the Alps and exterminated them, tree species diversity in Europe today, 10,000 years after the end of the Pleistocene, is still below North American levels. It will presumably take much longer than 10,000 years for European tree species diversity to be restored by a combination of immigration and speciation. Finally, for many millions of years after an asteroid collision caused mass extinctions at the Cretaceous/Tertiary boundary—if indeed there was such a mass extinction, and if it was caused by an asteroid—species diversity of large terrestrial vertebrates remained low until it was eventually restored and surpassed by speciation of mammals.

Pulse decrease in area, leading to supraequilibrial species diversity. Because equilibrial species diversity tends to increase with area, a decrease in area eventually leads to a decrease in species diversity. However, the greater the area after the pulse decrease, the slower the "relaxation time" required for species diversity to decay to the new lower equilibrial value (because "relaxation time" depends on extinction rates which are inversely proportional to area according to Diamond, 1972). Immediately after the pulse decrease in area, species diversity equals that prevailing at the site immediately before the pulse decrease in area. If one looked at the site immediately after the pulse area decrease and did not know that there had been such an area decrease, one would be puzzled to find species diversity higher than the site would support if it had not just suffered such a pulse area decrease. This "supersaturation effect" lasts only for a century or so in the case of birds in a forest fragment of one km^2, but lasts for many millenia for birds or mammals on large land-bridge islands such as Java and Borneo, or on a large mountaintop with Pleistocene habitat connections to other mountaintops, such as the mountains rising out of the Great Basin (Brown, 1971; Diamond, 1984). Islands that lie today in shallow water near continents were connected to those continents at Pleistocene times of lower sea level by land bridges and were finally severed from those continents 10,000 years ago by rising sea levels. The larger land-bridge islands, which include Trinidad, Sri Lanka, Fernando Po, and Formosa, as well as Java and Borneo, are still supersaturated with bird and mammal species (Terborgh, 1974). It will presumably require many tens of thousands of years before their species diversities have declined back to the equilibrial values appropriate to their modern areas.

These considerations of how relaxation times of supersaturated habitat fragments increase with area have interesting implications for understanding continental biotas. Relaxation times for birds and mammals on islands of a few thousand square kilometers, and for insects, lizards, plants, and other species living at higher population densities than birds and mammals on still smaller islands, are in excess of 10,000 years. We must therefore expect that relaxation times for the world's continents are far longer, perhaps hundreds of thousands of years. As the continental tropical rainforests expanded in concert with Pleistocene climatic fluctuations, rainforest species diversity must also have tended to expand and contract. However, the expanses of rainforest in South America, Africa, or Asia are so large that species relaxation times for the rainforest biota may be longer than the interval between Pleistocene climatic optima. Thus, when the continental rainforests contracted during dry periods of the Pleistocene, the rainforest biotas may still have been supersaturated at the time when the next wet phase arrived. Species diversity on the major continents may never have a chance to decline to "equilibrium values" and may be chronically supersaturated.

The decreases in species number after habitat fragmentation, and their relaxation times, are of great significance in the worldwide extinction spasm that is now under way. This accelerating extinction wave is due partly to the habitat fragmentation and reduction in habitat area that humans are producing by destroying natural habitats. The habitat fragments thus created start off with their pre-fragmentation species diversity and are gradually losing populations at rates that depend on their area. We have already launched a process that, if it is not miraculously reversed, must result inevitably in a massive extinction wave, even though the wave itself has not yet reached massive proportions. Some economists ignorant of biology question those extinctions that have already occurred, note that massive extinction has not yet occurred, and on this basis belittle predictions of an impending extinction spasm. This reasoning reminds me of the story of the man who fell off the top of the Empire State Building and who had a friend working on the 20th floor. The worker on the 20th floor looked out the window, saw his friend plunging past, and shouted out in concern, "My God, what is happening?" to which the falling man shouted back as he plunged past, "Nothing much is happening, everything is okay so far." As stewards of the world's biota, we have already pushed most of the world's species off the top of the Empire State Building. Those who deny the impending extinction crisis demand to see bodies smeared on the pavement before they will discuss erecting a safety net.

SPECIES DIVERSITY GRADIENTS ALONG ENVIRONMENTAL GRADIENTS

Discussions of species diversity often focus on the famous changes of diversity over environmental gradients, such as habitat gradients, altitudinal gradients, and especially latitudinal gradients. All too often, ecologists seek to identify "*the* cause" of such a gradient. We should be suspicious of any such attempt. Since species diversity depends on many factors, diversity changes over such gradients are also likely to arise from gradients in multiple controlling variables. What we should seek instead is to provide a quantitative *partitioning* or *accounting* to tell us how the various factors that control species diversity vary along the environmental gradient and to tell how much each of the factors contributes to the species diversity gradient. Even along a given environmental gradient, the accounting will surely differ for different groups of species. For example, the form of the latitudinal gradient for birds is very different from that for salamanders, and these two gradients must be explained by different mixes of contributing factors.

To illustrate how the "QQID" approach provides a checklist of factors that may contribute to species diversity gradients, let us consider two of these famous gradients: the altitudinal gradient and the latitudinal gradient.

Altitudinal gradients in species diversity.

As one ascends from sea level towards the summit of a high mountain, species diversity tends to decrease with elevation, as exemplified in this symposium by the decrease in Andean tree species diversity (Gentry, this volume) and frog species diversity (Duellman, this volume) with altitude. However, this pattern is by no means universal. For example, the diversity of plant species along the western Andean slopes of northern Chile is extremely low at sea level, increases from middle to high elevations, and decreases only from high elevations onwards (Arroyo et al., this volume). In the Mediterranean zone of California the species diversity of birds reaches a maximum at middle elevations (Cody, 1975). How can we account for any one of these gradients, and why does the form of the gradient differ from case to case? Consideration of the QQID checklist suggests at least three important contributing factors that vary along the altitudinal gradient, one of them involving resource quality, the other two involving resource quantity.

Changes in habitat structural diversity. Habitat physiognomy varies dramatically along an altitudinal gradient. For example, in the moist tropics habitat structural complexity decreases monotonically along the altitudinal gradient, from tropical rainforest at the base through montane forest and then alpine elfin scrub at higher elevations, to alpine grassland and eventually rocky slopes and glaciers at the highest elevations. This continuous decrease in habitat structural complexity and consequently in "number of niches" contributes to the continuous decrease in plant and frog species diversity with elevation in the wet tropics. In the Mediterranean zone, however, scrub formations such as chaparral at sea level yield to forest at higher elevations before finally yielding to alpine habitats on the highest summits, and this intermediate maximum in habitat structural complexity contributes to the intermediate maximum in species diversity.

Productivity gradient. Temperature generally decreases with increasing altitude, while the altitudinal gradient of rainfall (and hence of productivity, which depends both on rainfall and temperature) varies from site to site. In the moist tropics, productivity decreases with elevation, or there may be a slight increase in productivity from sea level up to a gentle maximum at medium-low elevations, followed by a decrease in productivity thereafter. This productivity gradient reinforces the effect of the gradient in habitat structural complexity and also contributes to the decrease in species diversity with altitude in the moist tropics. However, in the Mediterranean zone of California and in the Atacama Desert there is a marked maximum in productivity at middle elevations (owing to the marked maximum in rainfall there), and this contributes to the species diversity maximum at middle elevations.

Area gradient. The distribution of available area with altitude depends on the form of the mountain. On conical mountains, area decreases continuously with altitude, tending to cause a monotonic decrease in species diversity with altitude. However, Tibet and the Peruvian/Ecuadorean Andes have a more trapezoidal shape, with a broad plateau at high elevations, so that the maximum area may actually be at high elevations rather than at sea level. These area considerations may contribute to the fact that species diversity at high elevations on the Tibetan Plateau and on the Andean Altiplano is much higher than in structurally similar habitats of New Guinea, whose mountains more nearly approximate steep narrow ridges with only tiny areas at high elevations. Quantitative analysis of the altitudinal distribution of area contributes to understanding the relative numbers of montane and lowland bird species on various islands of the Solomon Archipelago (Mayr & Diamond, 1976).

Thus, to account for the altitudinal gradient of species diversity in any particular case, one should at minimum consider that site's altitudinal gradient of habitat structural complexity, productivity, and area. Terborgh (1977) has shown that the quantitative accounting falls out differently for different trophic groups of birds (insectivores, frugivores, and nectarivores) along the altitudinal gradient of the Peruvian Andes. The same three variables—habitat structural complexity, productivity, and area—are also likely to be major contributors to species diversity gradients along horizontal habitat gradients such as the gradients of desert, grassland, scrub, and woodland in the Mediterranean zone, as illustrated by Cody's (1975) analysis.

Latitudinal gradients in species diversity. No discussion of species diversity would be complete without consideration of the latitudinal gradient. Species diversity of most broadly defined groups of plants and animals is maximal in the tropics and decreases towards the poles. Examples considered in this symposium are the high tropical diversity of plants (Gentry, this volume), beetles (Erwin, this symposium), and frogs (Duellman, this volume). In the analysis of plant species diversity in northern Chile by Arroyo et al. (this volume), a steep species diversity gradient arising from the rainfall gradient is superimposed on a gentler species diversity gradient associated with latitude itself. However, some plant and animal groups, such as sandpipers and Old World salamanders, do not exhibit a diversity peak in the tropics. Again using the QQID checklist, we can identify at least five factors with major contributions to the latitudinal gradient. Two of these factors involve resource quality, one involves resource quantity, and two involve dynamics.

Habitat structural diversity. Habitat structural diversity tends to decrease from the equator to the poles, the extreme ends of the gradient being equatorial tropical rainforest as contrasted with the polar ice caps. This environmental gradient contributes to the polewards decline in species diversity.

Gradient of resource types. The variety of resources, or of resources available year-round, tends to decrease with latitude. For example, the proportion of insect species with very large bodies decreases polewards, with the result that bird species (e.g., coucals) specializing on very large insects are mainly tropical. Nectar and fruit are available year-round in the tropics but not in the Arctic, contributing to the decrease in diversity of obligately frugivorous and nectarivorous bird species with latitude.

Productivity gradient. Productivity on land tends to decrease with latitude, reinforcing the polewards decline in species diversity. This latitudinal gradient in productivity is less regular in marine environments, because latitudinal effects of temperature changes in productivity are overridden by effects of nutrient upwelling in some high-latitude marine areas.

Disturbance gradient. One reason often proposed for the latitudinal gradient in species diversity is that disturbances on a geological time scale are supposedly more violent and produce more extinctions at high latitudes than at low latitudes. In particular, glaciations have periodically wiped out species diversity at high latitudes. This argument, if valid, would involve a contribution of species dynamics to the latitudinal gradient of species diversity. In recent years there has been increased appreciation of the historical importance of environmental disturbances in the supposedly stable tropics. The Pleistocene involved alternate wet and dry periods that caused large-scale habitat changes in the tropics. It is nevertheless probably still true that environmental changes over geological times have been more devastating of habitats and more destructive of species diversity at high than at low latitudes.

Gradient in dispersal and speciation rates. Tropical species of birds, and possibly of some other taxa, tend to be much more sedentary than temperate species. Practically all bird species of North America and Europe are known to have crossed water gaps of at least several miles in modern times, while most species of the continental tropics apparently do not cross water gaps (Diamond, 1976; Diamond & Gilpin, 1983). These low dispersal rates in the tropics may have contributed to tropical species diversity by making it possible for formerly conspecific populations to achieve reproductive isolation over shorter distances, and thus by enhancing speciation rates.

Thus, the latitudinal gradient in species diversity involves multiple factors, but these factors are not infinite in number. What is now required is to attempt to partition the contributions of these various factors to latitudinal gradients of species diversity in particular cases.

SUMMARY AND OUTLOOK

We have seen that determinants of species diversity can be grouped into four sets of factors that may be remembered by the mnemonic "QQID": (resource) quality, (resource) quantity, (species) interactions, and dynamics. This is not to say that all four sets of factors are equally important in explaining species diversity of different taxa, or at different sites. For example, an interesting interpretation of neotropical tree diversity within tree guilds dispenses almost entirely with considerations of niche differentiation and segregation by resource utilization, and instead stresses the dynamics of speciation, immigration, and extinction (Hubbell & Foster, 1986). A general explanatory theory of species diversity must ultimately tell us under what sorts of circumstances each factor is likely to be important and what factors contribute to species diversity gradients along various environmental gradients. At present, I doubt there is a single case where we have an adequate accounting that considers all four possible sets of factors for a given group of taxa at a given site. Thus, we shall have to obtain such analyses for many individual cases before we can begin to compare those cases and arrive at generalizations about species diversity. I view the gathering of such accountings as one of the two major tasks for future studies of species diversity.

The other major task is to attempt to convert empirical groupings of factors controlling species diversity, such as the one that I have proposed, to natural hierarchical groups. The QQID grouping is offered just as a convenient empirical checklist; it does not necessarily correspond to any scheme in nature. Must we always content ourselves with such an arbitrary laundry list, or is there any natural organization to the laundry list? I suggest that it may be possible eventually to account for species diversity by a hierarchy of processes in space and in time. The spatial hierarchy would begin or end with an understanding of species diversity at a single point in space, then within a single type of habitat (so-called alpha diversity), then diversity from end to end of a habitat gradient (species turnover along this gradient being termed beta diversity), and finally species diversity over areas large enough to permit geographic replacement (gamma diversity), or over whole biogeographic regions, or over the whole world. A hierarchy in time might begin with the rapid increase in species diversity during recovery from a storm, then the much slower increase following a glacial period with its attendant fluctuations in sea level, and finally the slow generation of species over geological/evolutionary time scales. In this way, it may eventually be possible to obtain not just a convenient checklist, but a natural explanation for the number of biological children in the world's candy store.

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A CONTRIBUTION TO THE POLLEN MORPHOLOGY OF NEOTROPICAL LAURACEAE[1]

Bhoj Raj[2] *and Henk van der Werff*[3]

ABSTRACT

The present study is a pollen-morphological investigation of 80 species belonging to 17 of the 22 known neotropical genera of Lauraceae. Observations were made with light and scanning electron microscopes. An ultrastructural study of the pollen wall of 11 genera was also undertaken by transmission electron microscopy. The pollen grains of most of the genera are easily identifiable by their sizes and by the number and organization of spinules. The pollen grains of all the species investigated are apolar, spheroidal, and inaperturate. The exine is very thin and coherent due to loosely or densely packed globular to variously shaped bodies. The surface of exine is scattered with pointed or blunt, monomorphic or dimorphic spinules. The spinules are made up of numerous tightly woven strands; their bases are encompassed by a thick, circular, cushionlike form. The intine was found to be the dominant layer of the pollen wall and to show varied composition and structural details. It is remarkable that a similar type of intine has been encountered in the inaperturate pollen grains belonging to such disparate genera as Canna, Heliconia, Hernandia, *and* Palmeria. *The taxonomic implications of the palynological observations are discussed.*

TAXONOMIC REVIEW AND CLASSIFICATION

Lauraceae form a large, predominantly tropical family of trees and shrubs. The sole exception is the genus *Cassytha*, which consists of leafless, twining parasites much like *Cuscuta* (Convolvulaceae). *Cassytha* is sometimes treated as a separate family, but since it differs only in habit from the woody Lauraceae, we maintain it in the Lauraceae. Centers of species richness are tropical Asia and tropical America. Lauraceae are rather poorly represented in Africa, are rather diverse in Madagascar, and occur in Australian rain forests, the Pacific Islands, and in New Zealand (two species).

The family is easily recognized by its flowers. The perianth consists of two cycles of three tepals each, which are usually equal. By far the most common flower colors vary from white to green or yellowish; very rarely does one encounter reddish flowers (*Kubitzkia*). The stamens are also arranged in cycles of three each, and in principle there are four staminal cycles. The fourth or innermost cycle is nearly always reduced to staminodes or is entirely lacking. Three cycles are usually present but can be reduced to two or one fertile cycle in some genera. The three stamens of cycle three have nearly always two glands attached at or near their base. In the genus *Pleurothyrium* these glands become greatly enlarged and surround all nine fertile

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stamens. The ovary is superior (except in the monotypic African *Hypodaphnis*), has one locule, and develops into a drupe, which may be subtended by the enlarged floral tube. The flowers can be perfect or unisexual.

Although the Hernandiaceae and Monimiaceae are frequently mentioned as close relatives of the Lauraceae, flowers of Lauraceae are rarely confused with other families.

The Lauraceae are of considerable economic importance. *Persea americana* is widely cultivated for its edible fruit, the avocado. Most species of Lauraceae possess varying amounts of aromatic oils, some of which are economically important. Examples are camphor oil from *Cinnamomum camphora*; rosewood oil from *Aniba rosaeodora*; and Brazilian sassafras oil from *Ocotea odorifera*.

The bark of *Cinnamomum verum* yields cinnamon. Leaves of *Laurus nobilis* and *Umbellularia californica* are used as spices (bay leaves); in Central America, *Litsea glaucescens* is used for the same purpose. Several other species are used on a local basis, for instance *Sassafras albidum* for the preparation of root beer and *Dicypellium caryophyllatum* (now supposedly very rare due to excessive exploitation) for its spicy fruits. The wood of many species of Lauraceae is valuable. Some species have unusually hard or decay-resistant wood used for construction, and the wood of other species is excellent for making furniture (Richter, 1981).

CLASSIFICATION

A workable generic classification of the Lauraceae does not yet exist. Several reasons lie behind the poor understanding at generic level. The most important reason is that, with very few exceptions (*Cassytha*, *Hypodaphnis*), the genera do not have exclusive characters, that is, characters restricted to one particular genus. As a consequence, the genera are separated by combinations of characters. Very often both floral and fruit characters are used, and, because specimens only rarely have flowers and fruits (fruits usually require one or two months to mature), keying specimens to genus is frequently impossible. A second difficulty is that in some cases the characters separating genera are weak or difficult to interpret. Thus, even perfect specimens cannot always be unambiguously assigned to a genus.

Results of these difficulties are that many generic identifications are suspect and that species are frequently transferred between genera or described in incorrect genera. It seems that the Lauraceae are the only family in which every botanist who seriously worked on the family has redescribed an already published species in a genus different from the one in which it was previously described.

Tables 1, 2, and 3 present three recent generic classifications of Lauraceae. Tables 1 and 2 are abbreviated versions of classifications by Kostermans (1957) and Hutchinson (1964) based on flower and fruit characters. Table 3 shows Richter's (1981) generic groupings and is based on studies of secondary xylem and bark. *Cassytha*, not being woody, is excluded from Richter's groupings.

Kostermans (1957) recognized five tribes in the woody Lauraceae, which are separated on inflorescence and cupule characters. One tribe consists solely of the African *Hypodaphnis*, which has an inferior ovary. The other four tribes occur in the New World. They are the Perseae (inflorescence exinvolucrate, cupule lacking), subdivided into two subtribes; the Cinnamomeae (inflorescence exinvolucrate, cupule present), likewise subdivided into two subtribes; the Litseae (inflorescence with decussate bracts, cupule present), subdivided into two subtribes; and the Cryptocaryeae (inflorescence exinvolucrate, drupe fully enclosed in floral tube), also subdivided. The subdivisions in each of these four tribes are based on numbers of anther cells.

Kostermans (1957) postulated an evolutionary trend in the Lauraceae from genera with a very shallow floral tube, where the fruit is not subtended by a cupule (tribe Perseae), through genera with a deeper floral tube, where the mature fruit is subtended by a cupule up to one-third the size of the fruit

TABLE 1. *Classification (after Kostermans, 1957) of the neotropical genera of Lauraceae.*

	Subfamily Lauroideae
Tribe	**Perseeae**. Inflorescence paniculate, exinvolucrate. Cupule absent.
Subtribe	Perseineae. Anthers four-celled.
Genera	*Persea, Phoebe, Caryodaphnopsis*
Subtribe	Beilschmiediineae. Anthers two-celled.
Genera	*Beilschmiedia, Mezilaurus*
Tribe	**Cinnamomeae**. Inflorescence paniculate, exinvolucrate. Cupule present.
Subtribe	Cinnamomineae. Anthers four-celled.
Genera	*Ocotea, Nectandra, Pleurothyrium, Sassafras, Umbellularia, Dicypellium*
Subtribe	Anibineae. Anthers two-celled.
Genera	*Aiouea, Aniba, Endlicheria, Licaria, Urbanodendron, Kubitzkia, Phyllostemonodaphne*
Tribe	**Litseae**. Inflorescence involucrate with decussate bracts. Cupule present.
Subtribe	Litseineae. Anthers four-celled.
Genus	*Litsea*
Subtribe	Lauriineae. Anthers two-celled.
Genus	*Lindera*
Tribe	**Cryptocaryeae**. Inflorescence paniculate, exinvolucrate. Fruit fully enclosed in flower tube.
Subtribe	Eusideroxylineae. Anthers four-celled.
Genus	*Eusideroxylon* (not neotropical)
Subtribe	Cryptocaryineae. Anthers two-celled.
Genus	*Cryptocarya*
Tribe	**Hypodaphneae**. Ovary inferior.
Genus	*Hypodaphnis* (African)
	Subfamily Cassythoideae
Genus	*Cassytha*

(tribe Cinnamomeae), and through genera with a deep floral tube, where the fruit is fully enclosed in the floral tube (tribe Cryptocaryeae), to the tribe Hypodaphneae, where the fruit is fully enclosed in and becomes fused with the floral tube. This is a stimulating theory, although it is not certain whether it is phylogenetically accurate, that is, whether the Perseae are indeed the most primitive tribe. The position of the Litseae, recognized by their inflorescence type, is not clear in this theory.

Hutchinson (1964) also recognized five tribes of woody Lauraceae but defined his tribes quite differently. His Apollonieae are characterized by exinvolucrate inflorescence, two-celled anthers, and fruit not fully enclosed by floral tube. His Cryptocaryeae are as his Apollonieae except for the fruit being enclosed by the floral tube. Tribe III, the Sassafrideae, is of doubtful value; its single New World species, *Sassafridium veraguense*, has been placed by nearly all botanists during the last century in *Ocotea*. This tribe is characterized by having all anthers with introrse cells. The Cinnamomeae (exinvolucrate inflorescence, at least one anther row extrorse, all anthers four-celled) differs from the Sassafrideae only in having some anthers extrorse. *Hypodaphnis* is placed in this tribe. The fifth tribe, the Litseae, is also separated based on its involucrate inflorescence.

The third recent classification of Lauraceae (Richter, 1981) is not based on floral or fruit characters, but on wood and bark. It should therefore not be surprising that it differs in several features from Kostermans's and Hutchinson's classifications. Richter recognized three main groupings of genera without giving them taxonomic status. Each group includes primitive and more advanced genera (as defined by wood and bark characters). Ancestral genera from which these groups were derived are not yet known. The first group includes mostly palaeotropical genera—from this group only *Beilschmiedia*,

TABLE 2. *Classification of Lauraceae—Hutchinson (1964), neotropical genera.*

- Tribe 1. **Apollonieae**. Inflorescence exinvolucrate; anthers two-celled; fruit not or partly enclosed by cupule.
  - Flower bisexual.
    - Fertile stamens 9; calyx usually persistent.
      - *Beilschmiedia, Kubitzkia, Aniba, Nobeliodendron, Urbanodendron*
    - Fertile stamens 6–3.
      - *Aiouea, Licaria, Phyllostemonodaphne, Misanteca, Mezilaurus*
  - Flowers dioecious or polygamo-dioecious.
    - *Aniba, Endlicheria*
- Tribe 2. **Cryptocaryeae**. Inflorescence exinvolucrate; anthers two-celled; fruit enclosed in floral tube.
  - *Cryptocarya*
- Tribe 3. **Sassafrideae**. Inflorescence exinvolucrate; anthers four-celled; all anther cells introrse.
  - *Sassafridium* (now included in *Ocotea*)
- Tribe 4. **Cinnamomeae**. As tribe 3, but at least one row of anthers with extrorse cells.
  - Flowers bisexual.
    - *Nectandra, Persea, Phoebe, Pleurothyrium, Caryodaphnopsis, Synandrodaphne* (= *Rhodostemonodaphne*)
  - Flowers bisexual or polygamous
    - *Ocotea, Dicypellium*
- Tribe 5. **Litseae**. Inflorescence involucrate; flowers umbellate or solitary within the involucre.
  - Anthers four-celled.
    - *Litsea, Umbellularia*
  - Anthers two-celled.
    - *Lindera, Laurus*
- Tribe 6. **Cassytheae**. Parasitic, leafless herbs.
  - *Cassytha*

Caryodaphnopsis, and *Cryptocarya* are represented in the New World, albeit with few species. The second group includes most of the genera occurring in the subtropics of the Northern Hemisphere (*Persea* is the exception), but several of the genera are best represented in tropical areas. This group is represented in the New World by *Litsea*, *Lindera*, *Sassafras*, and *Umbellularia*. The third group includes all other (15 or 16) neotropical genera plus a few paleotropical segregates of *Persea* and *Phoebe/Cinnamomum* (*Alseodaphne*, *Dehaasia*, *Neocinnamomum*, and *Nothaphoebe*). Within this group, *Persea*, *Cinnamomum*, *Phoebe*, and allies can be separated from the remaining endemic neotropical genera (*Ocotea* is also present in Africa and Madagascar), but the remaining genera do not fall in distinct groupings based on wood or bark characters.

The classifications by Kostermans and Hutchinson show that our knowledge of the relationships among the genera of Lauraceae is still limited. Essentially, these classifications are only keys to genera, often based on readily observable but artificial characters such as the number of fertile stamens and number of anther cells on the stamens. The genera, defined with the help of these characters, often include species that do not possess the required characters but are placed in a certain genus due to general resemblance to other

TABLE 3. *Genera groups according to Richter (1981), neotropical genera.*

Group I	Group III
Beilschmiedia	*Persea*
Cryptocarya	*Phoebe*
Caryodaphnopsis	*Pleurothyrium*
	Endlicheria
Group II	*Aiouea*
Lindera	*Nectandra*
Litsea	*Ocotea*
Umbellularia	*Urbanodendron*
Sassafras	*Kubitzkia*
	Dicypellium
	Licaria
	Aniba
	Anaueria
	Mezilaurus
	[*Rhodostemonodaphne*]

species in that genus. Needless to say, this frustrates the efforts of the botanists who are not familiar with the group but try to key specimens to genus. A good example of these problems is found in the genus *Persea.* One of its characters is the presence of nine four-celled anthers and three staminodes. However, Kopp (1966), who monographed the genus, included in *Persea* also species with six four-celled anthers and six staminodes, and Kopp included species with some or all anthers two-celled, largely because of similarities in fruit and vegetative characters. In *Persea* the staminal configurations seem to be constant for a given species, but there are a few cases where the number of anther cells varies between flowers of the same inflorescence (*Aiouea lundelliana, Kubitzkia macrantha*). Normally, when flowers have both two- and four-celled anthers, the outer six anthers are always of one type and the inner three anthers the other; for instance, in *Endlicheria anomala* the outer six anthers are two-celled, the inner four-celled, while in *Phoebe* subg. *Heteranthera* the outer six are four-celled and the inner three are two-celled. Mez (1889) realized this and restricted the couplet in his generic key "anthers 4-celled or anthers 2-celled" to the outer six anthers. This greatly reduced the number of species that did not fit in any of the genera and made identifications easier. It is regrettable that this has been overlooked by later workers.

The differences in treatment of the genera with two-celled anthers show the lack of understanding of the generic relationships. In Hutchinson's classification, two-celled anthers characterize two tribes, the Apollonieae and Cryptocaryeae; the Cinnamomeae consist of four-celled genera, and the Litseae include both two- and four-celled genera. Thus, Hutchinson regarded the difference in number of anther cells as very important. Kostermans considered this difference as secondary, as all of his tribes include both two- and four-celled genera (except the monotypic Hypodaphneae), and accepted that the transition from four-celled to two-celled genera occurred several times. Richter found that wood and bark characters do not support the idea that genera with two- and four-celled anthers form distinct groups, and it seems likely that the two-celled genera have been independently derived from four-celled genera. This theory is strengthened by the observation that in some two-celled neotropical genera the upper two cells have been lost, while in other genera the lower pair has disappeared. There are also indications that some two-celled genera (*Aiouea, Endlicheria*) are not monophyletic, but contain groups of species that were independently derived from four-celled ancestors; on the other hand, other two-celled genera of comparable size (*Aniba, Licaria*) seem to be monophyletic.

In addition to the differences in treatment of the two-celled genera, the three classification systems differ in many other details. Hutchinson and Richter recognized some neotropical genera that Kostermans did not accept. Examples are (from Hutchinson): *Sassafridium,* now accepted as belonging in *Ocotea*; *Nobeliodendron* and *Misanteca,* both now included in *Licaria* (Kurz, 1983); and *Synandrodaphne,* included in *Ocotea* by Kostermans (1957), also frequently included in *Nectandra* but recently recognized as *Rhodostemonodaphne* by Rohwer & Kubitzki (1985). Richter also recognized several genera that Kostermans had treated as synonyms: *Caryodaphnopsis, Nectandra, Pleurothyrium,* and *Anaueria.* More differences exist in the placement of the genera, largely because Kostermans and Hutchinson used different characters to define their tribes. For instance, Hutchinson placed most two-celled, exinvolucrate genera in the tribe Apollonieae, whereas in Kostermans's system these genera are divided between the Perseae and Cinnamomeae. Kostermans's Perseae are divided between Hutchinson's Apollonieae and Cinnamomeae. Although both classifications need to be modified, incorporating results from Richter's work, it seems that Kostermans's system needs fewer changes and has the major groups better defined than Hutchinson's system.

Both Kostermans's and Hutchinson's classifications are essentially keys and aimed at easing the identification of specimens to generic level. Information needed for an understanding of the phylogeny was (and is) not available. As has been mentioned earlier, workable keys to the genera are still not available and a large obstacle is that both floral and fruit characters are important for the definition of the genera although rarely specimens include flowers and fruits. This difficulty is not likely to be solved in the near future. It is possible to write a generic key based on floral characters with which most specimens can be identified. Fruiting material can be recognized either by cupule shape or leaf venation; cupules are likely to offer important characters for defining phylogenetically sound genera.

Difficulties in resolving the phylogenetic relationships should be viewed as distinct from difficulties involving identifications. Analyses of flower and fruit types have shown an extensive reticulate pattern of variation within the Lauraceae, and it is not known which taxa are primitive and which are derived, nor where the family originated. Raven & Axelrod (1974) postulated that, based on present patterns of distribution and endemism and on the fossil record, in the New World some taxa migrated from South America northward, while others, of Laurasian origin, were present in North America and moved southward. Gentry (1982) supported the hypothesis that the Lauraceae are a tropical Gondwanaland family. Richter's (1981) work on wood and bark anatomy has shown that the mostly small genera found in temperate and subtropical parts of the Northern Hemisphere (*Apollonias, Laurus, Lindera, Litsea, Sassafras,* and *Umbellularia*) have a similar wood structure. Because these genera occur in different continents, and because two other genera, now largely represented in the tropics, also occur in northern subtropical/temperate areas (*Ocotea* in the Canary Islands; *Persea* in North America and the Canary Islands), it is tempting to regard the Lauraceae as a Laurasian family that has very successfully spread into the tropics. The fact that *Ocotea* is much better represented in the tropics than in the temperate zones does not imply a tropical origin. Accepting the dioecious species as derived from species with hermaphrodite flowers, one should note that most *Ocotea* species in the South American lowlands are dioecious, whereas nearly all Central American *Ocotea* species and most Andean species have perfect flowers. Further, in Central America *Ocotea* is much more weakly separated from its closest allies (*Nectandra, Phoebe*). These observations do not support the view that in the New World *Ocotea* and its allies originated in South America and moved north, but rather the reverse (Rohwer, 1986).

Much more information is needed for making secure claims about the phylogeny of the Lauraceae. First of all, our knowledge about the distribution of the genera is incomplete. Recently *Caryodaphnopsis,* previously known as an Asian genus of seven species, was found in South America (van der Werff & Richter, 1985); recent collections show that this genus includes six to eight neotropical species and occurs in Costa Rica, Panama, Colombia, Ecuador, Peru, and Brazil. Also during the last few years, four genera previously not known from Central America have been discovered there (*Aniba, Caryodaphnopsis, Mezilaurus,* and *Pleurothyrium*; pers. obs.).

Characters beyond flowers and fruits should be investigated. An excellent example is the work by Richter (1981) on wood and bark anatomy; studies of pollen, such as here reported, are very promising, and a study of leaf venation (Klucking, 1987) will appear soon. Other areas worthy of investigation are the chemical constituents and the structure of the cuticles. Results of such studies will be of much help in assessing the importance of the various morphological characters and in determining which characters should be used to define monophyletic genera and which are important on the species level.

PALYNOLOGICAL REVIEW

Extensive palynological investigations have been few. These were based mostly on observations with light microscopes. Pollen-morphological studies have been made by classical and by recent workers. The former generally included information on pollen as a matter of secondary importance.

The history of pollen descriptions probably began with Kölreuter (1811), followed by Purkinje (1830), Fritzsche (1832), Mohl (1834), Schnizlein (1843–1870), Berg & Schmidt (1858), Griffith & Henfrey (1875), Edgeworth (1877), Mez (1888), Knell (1914), Armbruster & Oenike (1929), Wodehouse (1932, 1965), Zander (1935, 1937, 1941), Cranwell (1942, 1953), Selling (1947), Kasapligil (1951), Erdtman (1952), Veloso & Barth (1962), and Pal (1976). The general descriptions given by the said authors is that the pollen grains are devoid of furrows and pores. Likewise, the sculpture spoken of by Wodehouse, as well as Mez, Knell, Zander, and Selling, to mention a few, are matters of controversy.

Short pollen descriptions and illustrations have also found a place in many regional floras: see Cranwell (1942, 1953), Ikuse (1956), Zinderen Bakker (1956), F. H. Wang (1960), J. L. Wang (1962, 1969), Rao & Lee (1970), Heusser (1971), Huang (1970, 1972), Markgraf & D'Antoni (1978), Lieux (1980), and Lewis et al. (1983).

Casual reference to pollen morphology mainly from an embryological standpoint has also been made by Schroeder (1952), Sastri (1958, 1962), Mitroiu (1970), and Pal (1975).

Recent noteworthy palynotaxonomic and phylogenetic studies are those of Agababian (1969, 1973), Ghosh (1977), Suryanarayana & Deodikar (1978), and Datta & Chanda (1980).

Of late the specialized wall structure of pollen grains has attracted the attention of many workers such as Takeoka (1965), Walker (1976), Rowley & Vasanthy (1980), Kubitzki (1981), Hesse & Kubitzki (1983), Hesse & Waha (1983), and Sohma (1985). The pollen wall is characteristic because of the extreme thinness of exine and the massive nature of the intine. A similar type of sporoderm stratification has been encountered in Cannaceae, Heliconiaceae, Hernandiaceae, Strelitziaceae, and Monimiaceae (Erdtman, 1952; Kress et al., 1978; Kress & Stone, 1982, 1983a, b; Stone et al., 1979, 1981; Stone, 1987; Rowley & Skvarla, 1974, 1975, 1986; Foreman & Sampson, 1987).

There is a scanty pollen record of fossil lauraceous genera. The few recorded are those of Macko (1959) and Macphail (1980). It is interesting that Selling (1947) stated that it is not "as if it [lauraceous pollen] had been overlooked, nor do I think that the possibility of the pollens being easily destroyed and therefore rarely preserved in peat (as was suggested by Rudolph 1936, p. 297, with regard to the pollens of this family) is of importance for the interpretation of their absence."

The present study is a broadly based pollen-morphological investigation of the apparently eurypalynous family. The aim is to present detailed morphological descriptions based on light microscopy (LM) and scanning electron microscopy (SEM), as the previous works are limited to very brief, sometimes incorrect accounts, depending mostly on light microscope observations. The complicated exine structure, sculpture, and ultrastructural details can be adequately studied with scanning electron microscopy and transmission electron microscopy (TEM) only.

The present investigation is aimed not only at giving a better understanding of pollen morphology but also at determining the correctness of the grouping of different genera under different tribes, subtribes, and their subfamilies respectively. The deflections of the palynological compass needle, at times oversimplified, have been taken into account to see whether it points towards better grouping, rearrangement, affinities, or evolutionary tendencies among the genera investigated.

MATERIALS AND METHODS

Polliniferous material of all the species investigated (except one sample each of *Kubitzkia mezii* and *Mezilaurus navalium*, obtained from Kew) was collected from the herbarium of the Missouri Botanical Garden

(MO), St. Louis, Missouri, U.S.A. Permanent slides were made from unacetolyzed, fuchsine-stained pollen grains. Acetolysis easily disintegrates the pollen grains because of the extreme thinness of exine (Erdtman, 1943).

A total of 80 species belonging to 17 out of the known 22 neotropical genera have been investigated. The LM studies were made using a Leitz Wetzlar Dialux microscope with apochromatic oil immersion objective (×100, N.A. 1.32) and periplan eye pieces (GF ×10). Measurements were made under oil immersion and are based on 30 or more pollen grains per species. Exine thickness was measured in the center of mesocolpia of pollen grains lying in equatorial view and includes spinules and other exinous excrescences. The maximum and minimum numbers of spinules per species were calculated using a programmable computer (Texas Instruments II Programmable 59; for details see Christensen, 1986) and and are presented in Table 1.

Pollen descriptions are based on LM and SEM observations. A general description is given for each genus, followed by a TEM description of the taxa sectioned. Pollen morphological data of the species are compiled in Table 1. The classification and order of genera follows that of Kostermans (1957), and the species are arranged in alphabetical order. The arrangement of photographs is according to the classification.

For scanning electron microscopy, unacetolyzed pollen grains were suspended in a drop of absolute alcohol and transferred to brass stubs. The pollen grains were coated with gold palladium for seven minutes using a Fine Coat ION Sputter JFC-1100. Scanning micrographs were taken with a Jeol JSM 25S-II microscope using Ilford FP4 film.

For transmission electron microscopy, unacetolyzed anthers were fixed in TAG solution (Rodewald & Karnovsky, 1974), buffered in sodium cacodylate buffer, postfixed in osmium tetroxide, and embedded in Spurr. Ultrathin sections were cut with a diamond knife using an LKB ultratome and poststained with uranyl acetate and lead citrate. The terminology follows that of Erdtman (1969).

GENERIC DESCRIPTIONS

The pollen grains of all the species investigated are inaperturate and spheroidal. The exine consists of an extremely thin, continuous or interrupted layer with an ornamentation consisting of pointed or blunt spinules made up of numerous twisted strands or of minute processes of varying shape (except *Cryptocarya*, where the exine is thin and smooth). The thinness of the exine makes it exceedingly difficult to distinguish the sexinous layer from the nexinous layer. Ultrastructural study of the pollen wall leads to the conclusion that the exine is totally ectexinous. The dominant massive layer is the intine. It is stratified, and its composition can be fibrillar, lacunar, lamellated, or granular. The intinous nature of this layer has been verified by acetolysis. It is uniformly thick throughout and does not show special thickenings that indicate possible germinal exits or germinative zones at any place. Instead, the entire wall may be equally suited for pollen tube egress.

Persea. Figure 1.

Diameter of pollen grains 29–44 μm. Exine 0.5–1.5 μm thick, scattered with spinules 1–3 μm apart of faintly discernible twisted strands. Spinules < 0.5–ca. 1 μm long, pointed or blunt, monomorphic or dimorphic with a basal cushionlike form of irregular shape; spinule surface devoid of processes but surrounded by a ring of densely spaced processes of varying shape and size. Intine 3–4 μm thick, appearing homogeneous.

In *P. americana* and *P. mutisii* the spinules are dimorphic; blunt and pointed spinules are intermingled. In *P. caerulea* and *P. schiedeana* the pollen grains are dimorphic; one type of pollen grains has monomorphic spinules and the other dimorphic. In *P. veraguasensis* neither the pollen grains nor the spinules are dimorphic.

Persea fulva. Figure 1C. TEM observation: pollen wall 4 μm thick, its outer, very thin electron-dense layer consisting of globular elements or in places baculalike elements

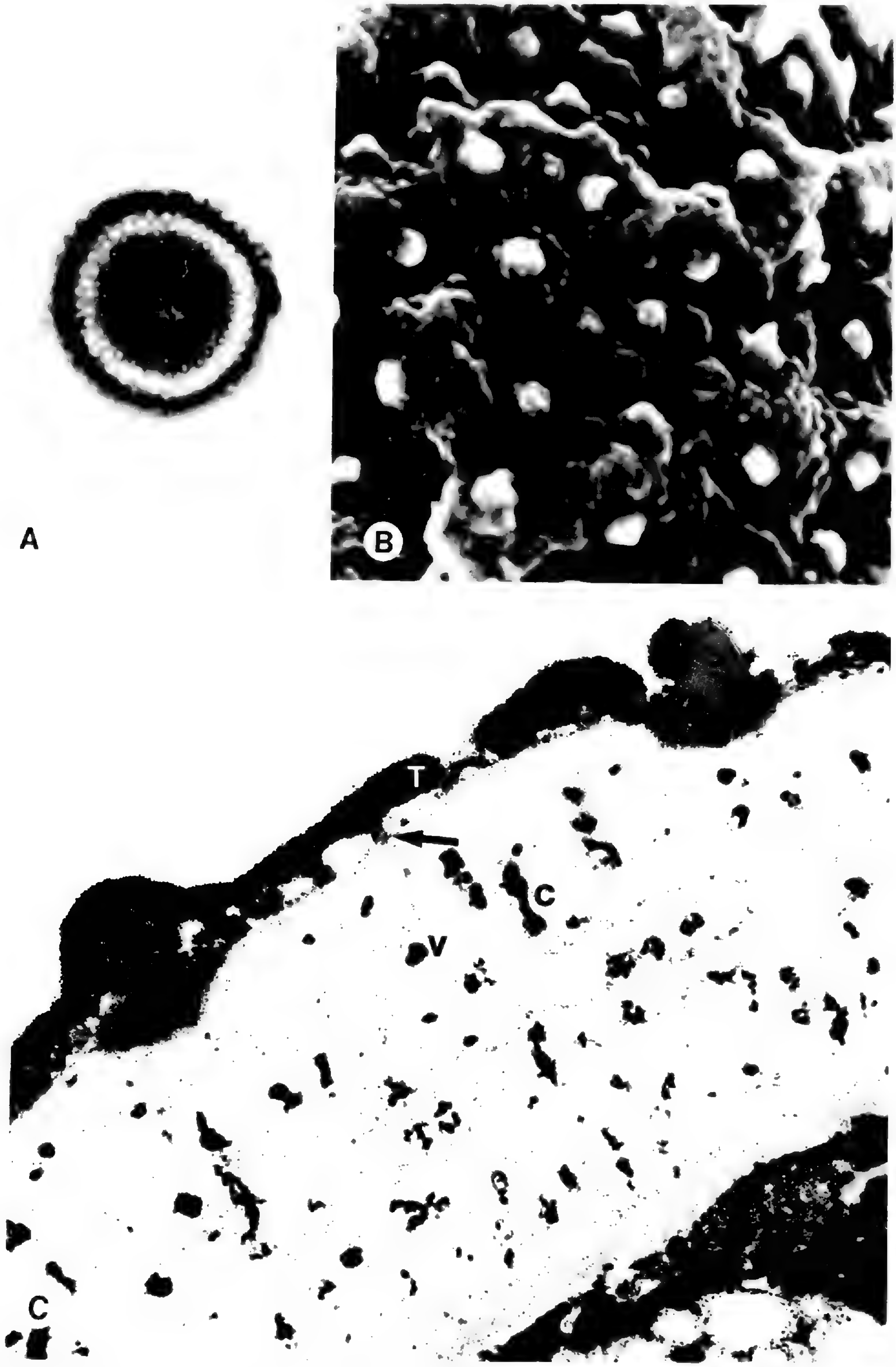

FIGURE 1. *A, B.* Persea americana.—*A. Entire pollen grain; spinules appear as white dots in the peripheral region; at a lower focus in the middle they appear as dark dots. LM ×1,000.—B. Part of exine showing spinules and the cushionlike bases studded with minute processes. SEM ×11,000.—C.* P. fulva. *Part of pollen wall showing the outer thin, electron-dense layer made up of globular or in places baculalike elements (arrow) supporting a discontinuous tectum (T). The underlying intinous layer shows channels (c) and vacuoles (v). TEM ×20,000.*

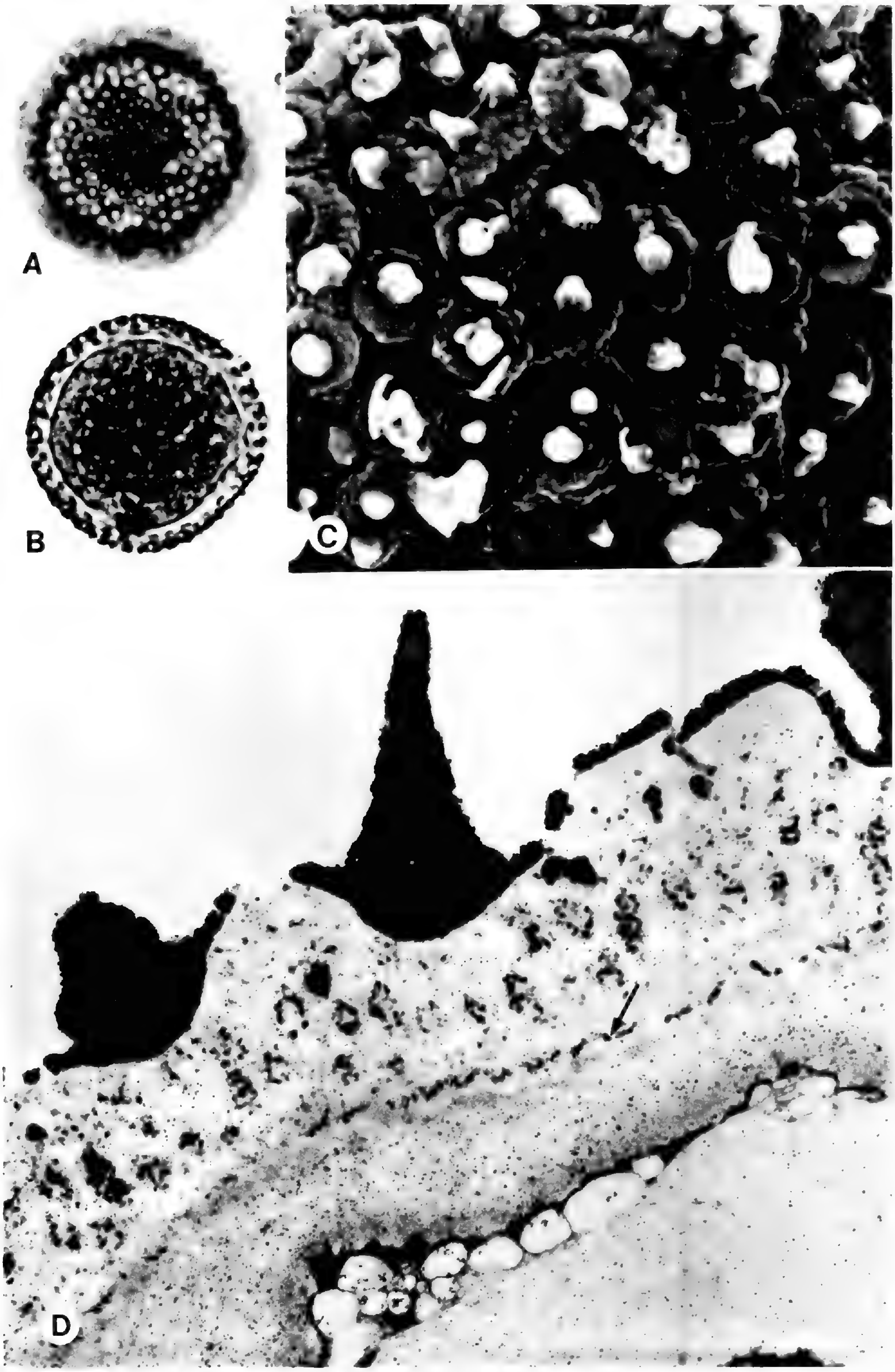

FIGURE 2. *A–C.* Phoebe porphyria.—*A. Entire pollen grain, surface view showing densely spaced spinules as white dots.—B. The same in optical cross section. LM ×1,000.—C. Part of exine showing spinules and their basal, circular cushion, its surface scattered with a few minute granular processes. SEM ×11,000.—D.* P. helicterifolia. *Part of pollen wall showing details of stratification. TEM ×20,000. Note the thin, interrupted commissural line (arrow) demarcating the outer and inner intine layers.*

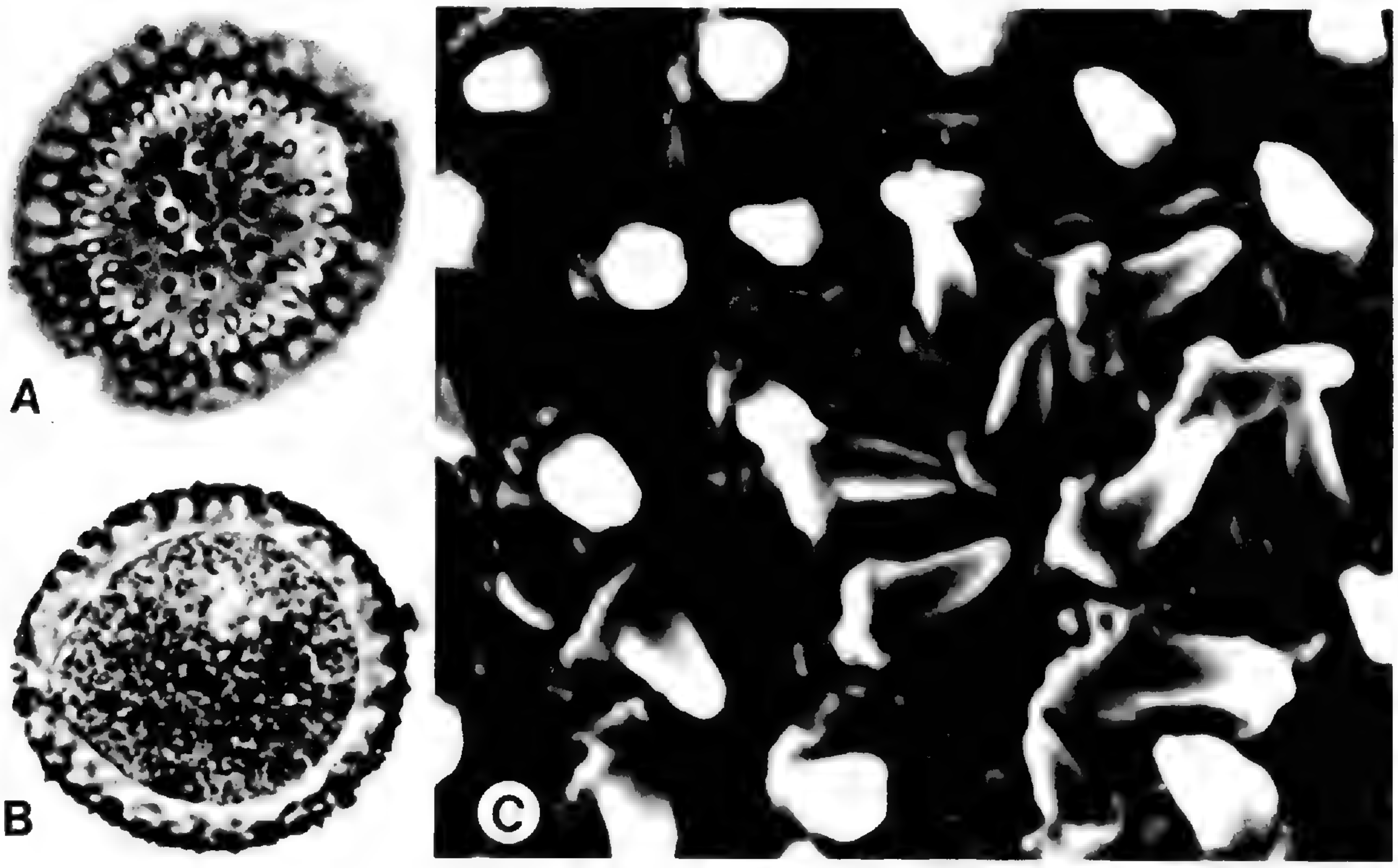

FIGURE 3. Caryodaphnopsis fosteri.—*A. Entire pollen grain; spinules appear as white dots in the peripheral region; at a lower focus in the middle they appear as dark dots.—B. The same in optical cross section. LM × 1,000.—C. Part of exine showing spinules and their basal cushion, the surface covered with granular processes. SEM × 11,000.*

supporting a discontinuous tectum and minute, pointed, solid spinules 3 μm apart, with a prominent, circular basal cushion intruding into the intinous layer, surrounded by densely spaced globular elements. The spinules and exinous surface covered with a "fuzzy coating" of granular composition. The underlying massive intinous layer distinguished into an outer, thick fibrillar layer with irregularly oriented narrow channels and vacuoles filled with osmiophilic material and into an inner, thin, electron-dense granular layer with a slightly undulating inner margin.

Phoebe. Figure 2.

Diameter of pollen grains 21–33 μm. Exine 1–2 μm thick, scattered with spinules 1–2.5 μm apart of easily discernible twisted strands. Spinules < 1–2 μm long, pointed, with a prominent basal, circular, cushionlike form. These cushionlike forms densely spaced, their surface and the general surface of exine scattered with sparsely spaced, minute, granular processes.

Phoebe helicterifolia. Figure 2D. TEM observation: pollen wall 5 μm thick, differentiated into an outer, thin, electron-dense ornamented exinous layer composed of closely packed granular elements and minute, pointed, spinules 2 μm apart, with a distinct, circular basal cushion intruding deeply into the intinous layer and making its distal surface distinctly undulating. Spinules and exinous surface covered with a "fuzzy coating." The underlying massive intinous layer distinctly demarcated into an outer, relatively thick, distally undulating layer beset with usually radially oriented cavities, these partly filled with osmiophilic material, and into an inner, unevenly thickened, electron-dense fibrillar layer, its inner margin uneven. The outer and inner layers of intine clearly separated by a thin, discontinuous electron-dense commissural line.

Caryodaphnopsis. Figure 3.

Diameter of pollen grains 27–33 μm, rarely 41 μm. Exine 2 μm thick, scattered with simple spinules 2–3 μm apart (rarely the spinules show faintly discernible twisted strands). Spinules about 1.5 μm long, pointed, with a basal cushionlike form, this circular to irreg-

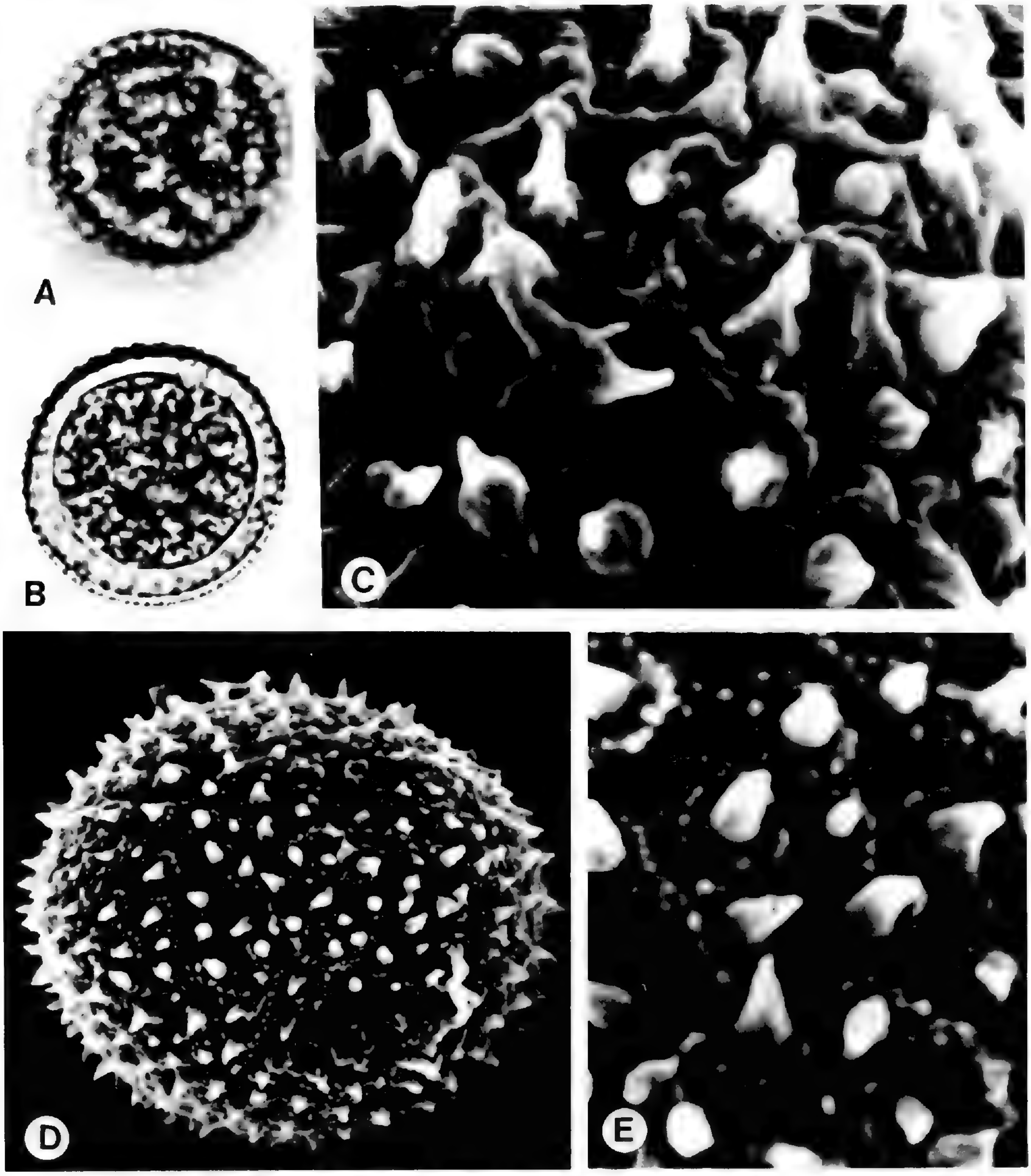

FIGURE 4. *A–C.* Beilschmiedia pendula.—*A. Entire pollen grain showing spinules as white dots.—B. The same in optical cross section. LM ×1,000.—C. Part of exine beset with spinules, their basal cushionlike form devoid of granular processes. SEM ×11,000. D, E.* Mezilaurus navalium.—*D. Entire pollen grain showing spinules, their basal cushions beset with minute processes. SEM ×3,300.—E. Part of the same at a higher magnification. SEM ×11,000.*

ular in shape, its surface devoid of processes. The general surface of exine sparsely covered with minute processes. Intine 2 μm thick, appearing homogeneous.

Beilschmiedia. Figure 4A–C.

Diameter of pollen grains 23–38 μm. Exine 1–2 μm thick, scattered with spinules 2–3 μm apart of easily discernible twisted strands. Spinules 1–1.5 μm long, pointed, with a basal cushionlike form of irregular shape; its surface and the general surface of exine devoid of processes. Intine 2.5–5 μm thick, appearing homogeneous.

Mezilaurus. Figure 4D, E.

Diameter of pollen grains 22–26 μm. Exine > 1 μm thick, scattered with spinules 2 μm apart of easily discernible twisted strands. Spinules < 0.5 μm long, pointed, with an ill-defined basal cushionlike form; its surface and the general surface of exine beset with densely spaced processes. Intine 2 μm thick, appearing homogeneous.

Ocotea. Figure 5.

Diameter of pollen grains 17–39 μm. Exine 1–2.5 μm thick, scattered with spinules 1–4 μm apart of distinctly discernible twisted strands. Spinules < 0.5–2 μm long, pointed or blunt with well-defined, thick, basal, circular, cushionlike form, its surface uneven. The cushionlike forms densely spaced and each surrounded by a ring of partially fused elements of varying size and shape. The general surface of exine beset with small processes of varying size and shape.

In a few species, such as *O. cernua* and *O. ira*, transparent porelike or colpuslike areas devoid of spinules occur. In *O. cuprea* the pollen grains are dimorphic; one type of pollen grain has pointed spinules made up of twisted strands, with a prominent, circular, basal cushionlike form. These cushionlike forms are densely spaced and appear as small islands surrounded by partially fused, small, globular processes. In places five or six spinules are grouped on a single cushion. In the second type of pollen grain, the spinules are pointed and broad basally but without a basal cushionlike form. The intine is 2–5 μm thick and homogeneous to many layered.

Ocotea puberula. Figure 5C. TEM observation: pollen wall 4 μm thick, differentiated into an outer, very thin, electron-dense ornamented exinous layer composed of minute, closely packed globular elements and minute, pointed, solid spinules, 3 μm apart with a distinct, circular basal cushion slightly intruding into the intinous layer and surrounded by densely spaced globular elements. The spinules and general exinous surface covered with a "fuzzy coating." The underlying massive intinous layer clearly distinguished into an outer, relatively thick layer beset with narrow, radially oriented channels in contact with the surface, these partly filled with bead-shaped osmiophilic material, and into a relatively thin, electron-dense, rather homogeneous layer of varying electron density, its inner margin irregular.

Nectandra. Figure 6.

Diameter of pollen grains 18–33 μm. Exine 0.5-1.5 μm thick, scattered with spinules 1–4 μm apart of faintly discernible twisted strands. Spinules 0.5–1.5 μm long, pointed, with a distinct, basal, circular to irregular cushionlike form, its surface and the general surface of exine devoid of processes.

In *N. ambigens* the spinules are crowded in places to form a rosettelike pattern or are sometimes found in pairs on a common basal cushion. In *N. falcifolia* the spinules are frequently crowded in places or are dimorphic. In *N. grandis* they are blunt and vestigial. The intine 1–4 μm thick and homogeneous or apparently bizonal or lamellated.

Nectandra gentlei. Figure 6E. TEM observation: pollen wall 5 μm thick, its outer, very thin, electron-dense, ornamented exinous layer composed of closely packed granular to globular elements and minute, pointed, solid, spinules 1 μm apart with a distinct, circular, basal cushion intruding into the underlying layer. The underlying massive intinous layer made up of an upper, relatively thick layer beset with ill-defined narrow channels partly filled with osmiophilic material and of an inner, relatively thin, many-layered granular stratum of varying electron density, its inner margin very irregular.

Pleurothyrium. Figure 7.

Diameter of pollen grains 21–30 μm. Exine 0.5 μm thick, scattered with spinules 1–2 μm apart of easily discernible twisted strands. Spinules < 0.5 μm long, pointed, with a prominent, basal, circular cushionlike form, totally or partially surrounded by a ring of densely spaced, partially fused minute processes. The general surface of exine beset with sparsely

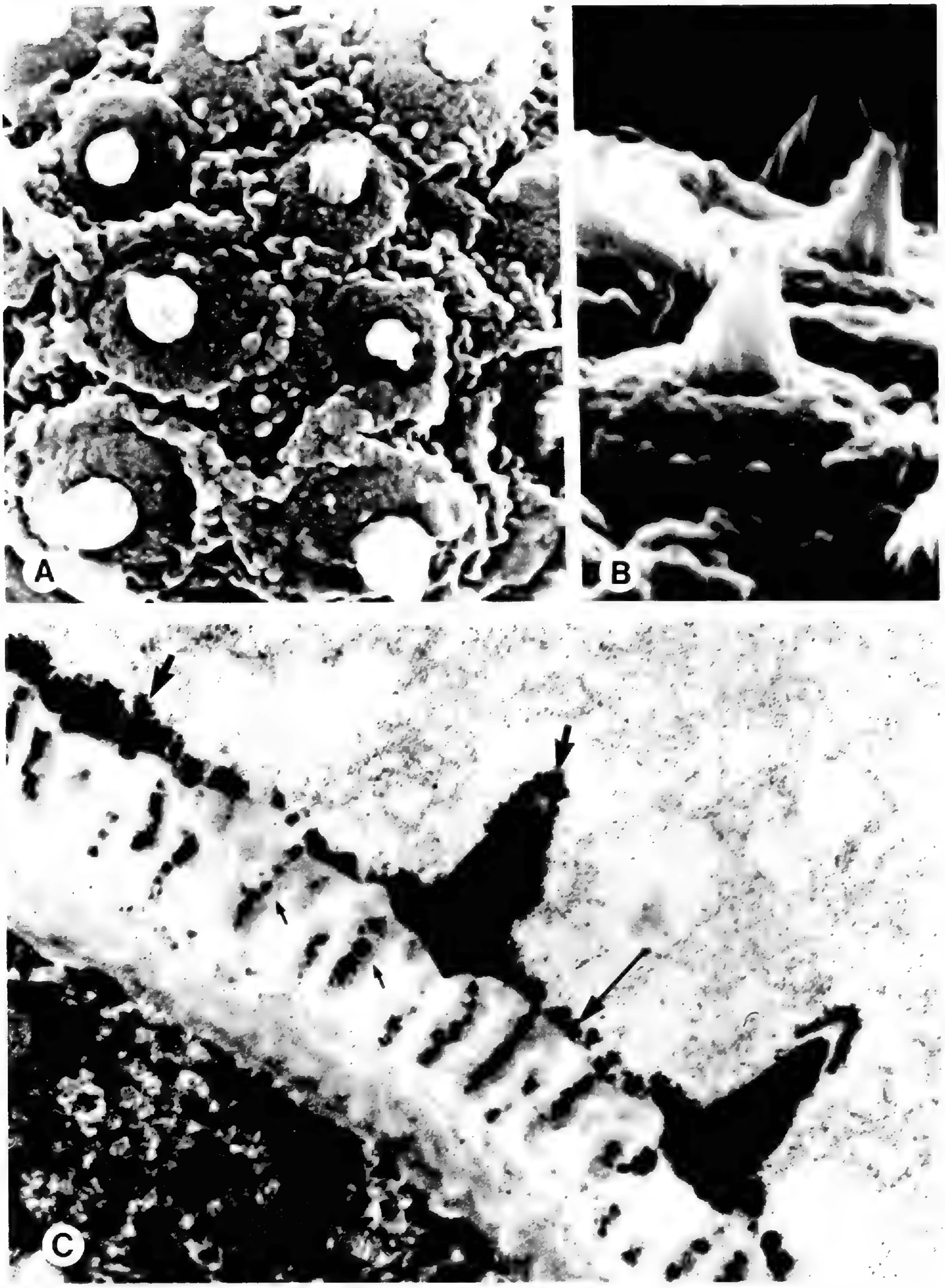

FIGURE 5. *A, B.* Ocotea cuprea.—*A. Part of exine showing spinules, circular, cushionlike smooth form, surrounded by densely spaced minute processes. SEM ×11,000.—B. Part of the same showing a few spinules and details of their basal part. Note the twisted strands of the spinules. SEM ×22,000.—C.* O. puberula. *Part of pollen wall differentiated into an outer thin, electron-dense layer, composed of globular elements (long arrow). Note the spinules and exine covered with a "fuzzy coating" (thick, short arrows); radially oriented channels filled with bead-shaped osmiophilic material (small, thin arrows). TEM ×20,000.*

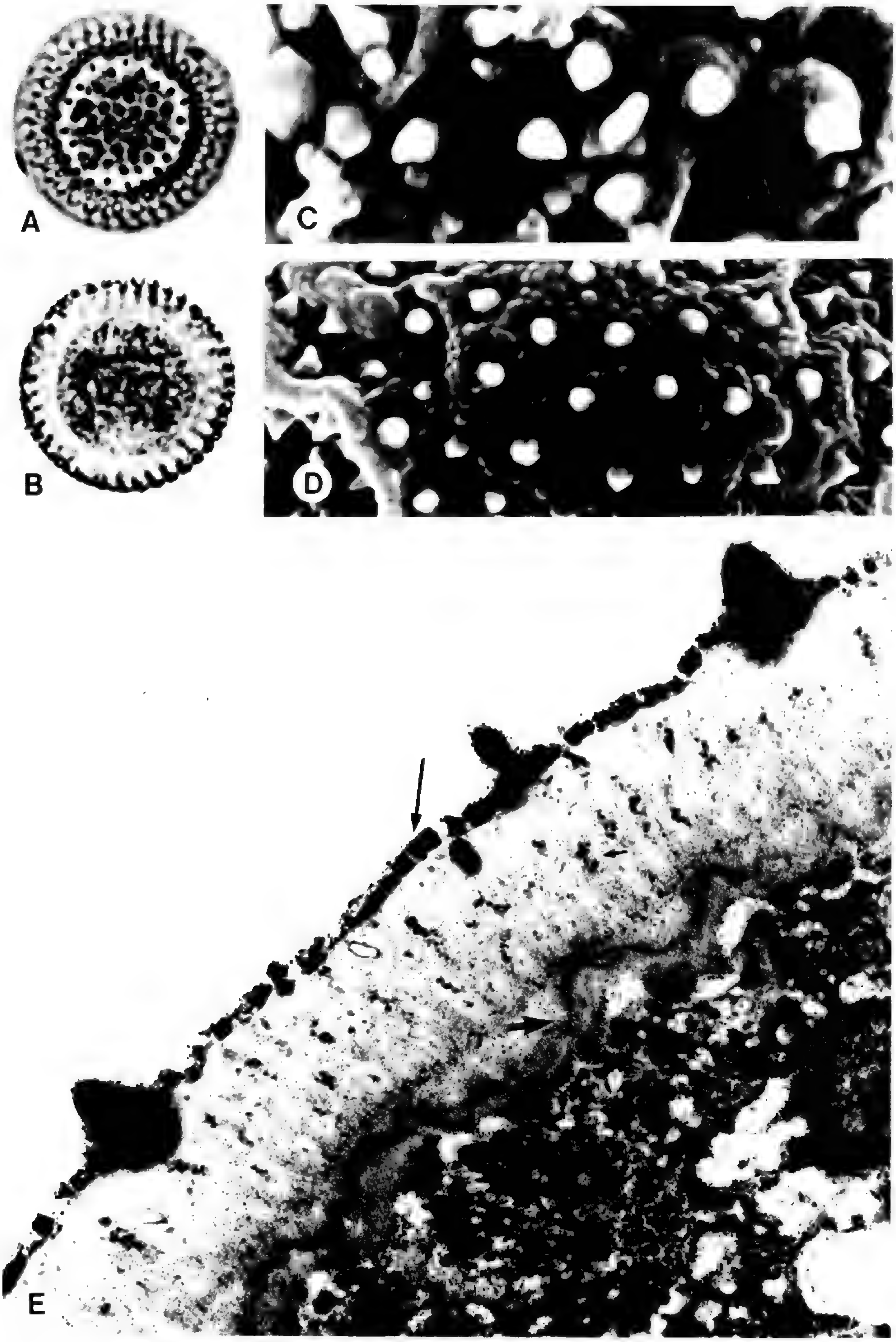

FIGURE 6. *A–C.* Nectandra reticulata. *A. Entire pollen grain showing spinules as white dots in the peripheral region and as dark dots in the middle.—B. The same in optical cross section. LM ×1,000.—C. Part of exine showing spinules and their smooth, basal cushionlike form. SEM ×11,000.—D.* Rhodostemonodaphne grandis. *Part of exine showing a surface pattern dissimilar to* N. reticulata. *SEM ×11,000.—E.* Nectandra gentlei. *Part of pollen wall showing the outer thin, electron-dense layer made up of granular to globular elements (arrow).*

spaced, minute processes. Intine 1.5 μm thick, appearing homogeneous.

Pleurothyrium zulianense. Figure 7D. TEM observation: pollen wall 2 μm thick, its outer thin, electron-dense ornamented exinous layer made up of granular to globular elements and minute, pointed, solid spinules 1 μm apart with a distinct, circular, basal cushion intruding into the intinous layer. The underlying massive intinous layer distinguished into an outer thick, structurally loose, granular stratum bearing closely packed, narrow, radially oriented channels filled with osmiophilic material and into an inner, thin, granular layer, its margin irregular.

Umbellularia. Figure 8.

Diameter of pollen grains 31–36 μm. Exine 1 μm thick, scattered with spinules 3 μm apart of faintly discernible twisted strands. Spinules < 1 μm long, pointed, with a prominent, basal, circular cushionlike form, partially surrounded by a ring of densely spaced, partially fused minute processes. The general surface of exine studded with densely spaced, minute processes of varying size and shape. Intine 2.5 μm thick, appearing homogeneous.

Umbellularia californica. Figure 8D. TEM observation: pollen wall 6 μm thick and consisting of an outer, thin, electron-dense ornamented exinous layer composed of densely spaced clavate to globular elements of varying size and of minute, solid, spinules 3 μm apart with a distinct, circular basal cushion intruding deeply into the intinous layer, and surrounded by densely spaced globular elements of varying size. The spinules and general exinous surface covered with loose "fuzzy coating." The underlying massive intinous region clearly distinguished into an outer, relatively thick stratum with scattered, radially oriented, ill-defined channels partly filled with osmiophilic material and into an inner, relatively thin, granular layer of varying electron density, its inner margin smooth.

Aiouea. Figure 9.

Diameter of pollen grains 19–29 μm. Exine 0.5 μm thick, scattered with spinules 1–3 μm apart of very faintly discernible twisted strands. Spinules 0.5 μm long, pointed, with a basal, thin, circular to irregularly shaped cushionlike form, frequently surrounded by a ring of densely spaced, partially fused, minute processes. Cushionlike forms usually fused, their surface uneven, devoid of processes. General surface of exine beset with sparsely spaced, minute processes. Intine 1.5–3 μm thick and appearing homogeneous.

In *A. costaricensis* the pollen grains exhibit in places porelike transparent areas devoid of spinules.

Aiouea trinervis. Figure 9D. TEM observation: pollen wall about 4 μm thick, differentiated into an outer, very thin, electron-dense ornamented exinous layer made up of compact granular elements and spinules. The spinules minute, pointed, solid, 1–3 μm apart with a distinct, circular basal cushion intruding into the subtending layer, and surrounded by densely spaced globular elements of varying size. The underlying massive intinous stratum consisting of an outer, relatively thick, structurally loose fibrillar layer made up of vacuoles and channels filled with osmiophilic material and of a denser inner, 2–3-layered granular zone of varying electron density, its inner margin slightly irregular.

Aniba. Figure 10A–C.

Diameter of pollen grains 16–27 μm. Exine 0.5 μm thick, scattered with spinules 1 μm apart of faintly discernible strands. Spinules < 0.5 μm long, pointed, without dis-

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The upper part of the intinous layer is beset with ill-defined channels partly filled with osmiophilic material (thin arrow); in the lower part undulating layers of varying electron density are seen (thick arrow). TEM ×22,000

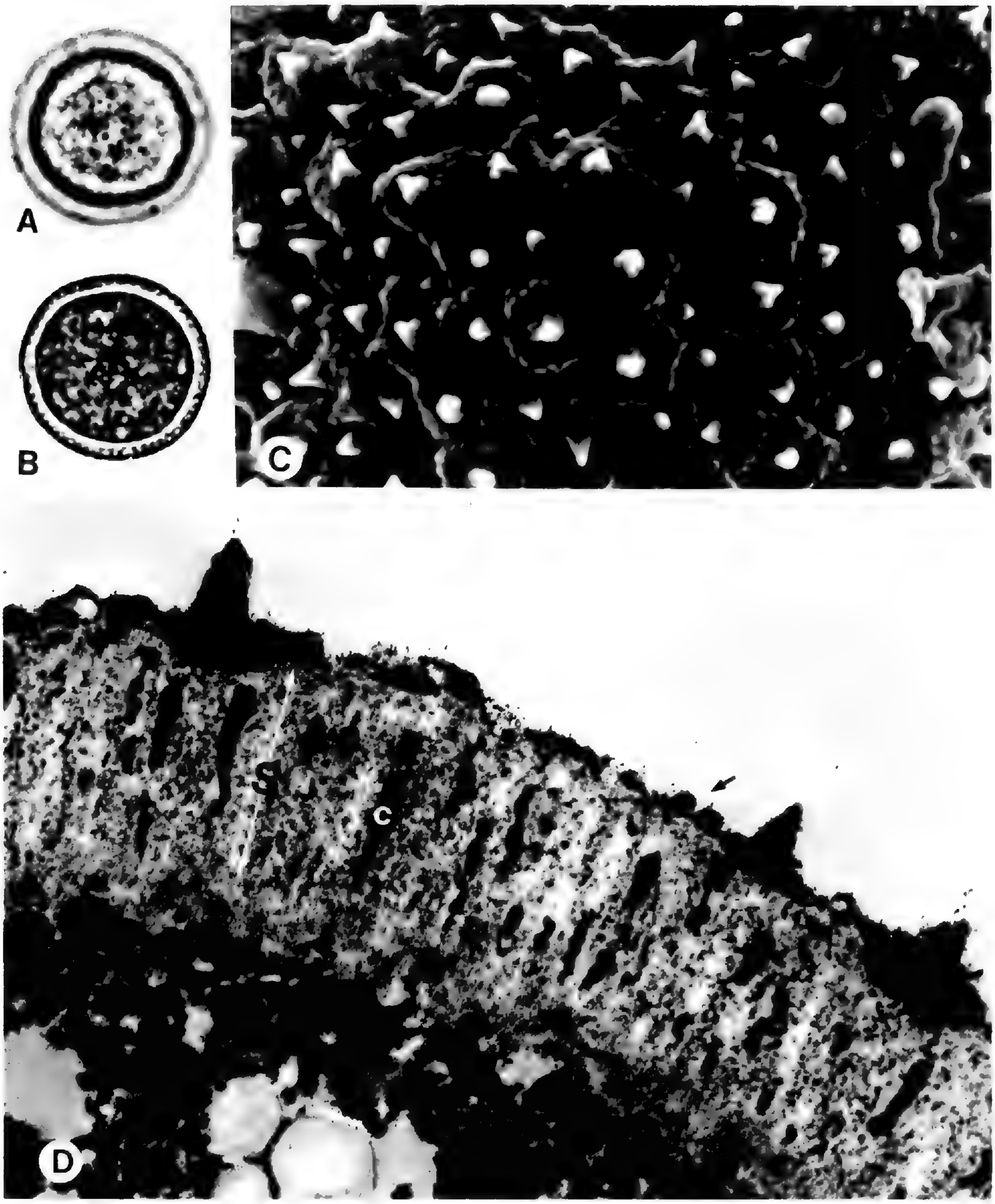

FIGURE 7. *A–C.* Pleurothyrium densiflorum.—*A. Entire pollen grain showing spinules, white and dark dots.*—*B. The same in optical cross section. LM ×1,000.*—*C. Part of exine showing surface details. SEM ×11,000.*—*D.* P. zulianense. *Part of pollen wall showing the outer thin, electron-dense exinous layer made up of granular to globular elements (arrow) and showing the outer thick, structurally loose, granular stratum of intine (S) and an inner thin, granular layer (L). Note the radially oriented channels in the outer intine filled with osmiophilic material (c). TEM ×20,000.*

tinct, basal cushionlike forms. The general surface of exine densely spaced with granular processes. Intine 1.5–2 μm thick and appearing homogeneous. In pollen grains of *A. firmula* 2–3 porelike or irregular openings encountered.

Endlicheria. Figure 10D–F.

Diameter of pollen grains 15–27 μm. Exine 0.5–1 μm thick, scattered with spinules 0.5–2 μm apart of faintly discernible strands. Spinules < 0.5–1 μm long, densely or sparse-

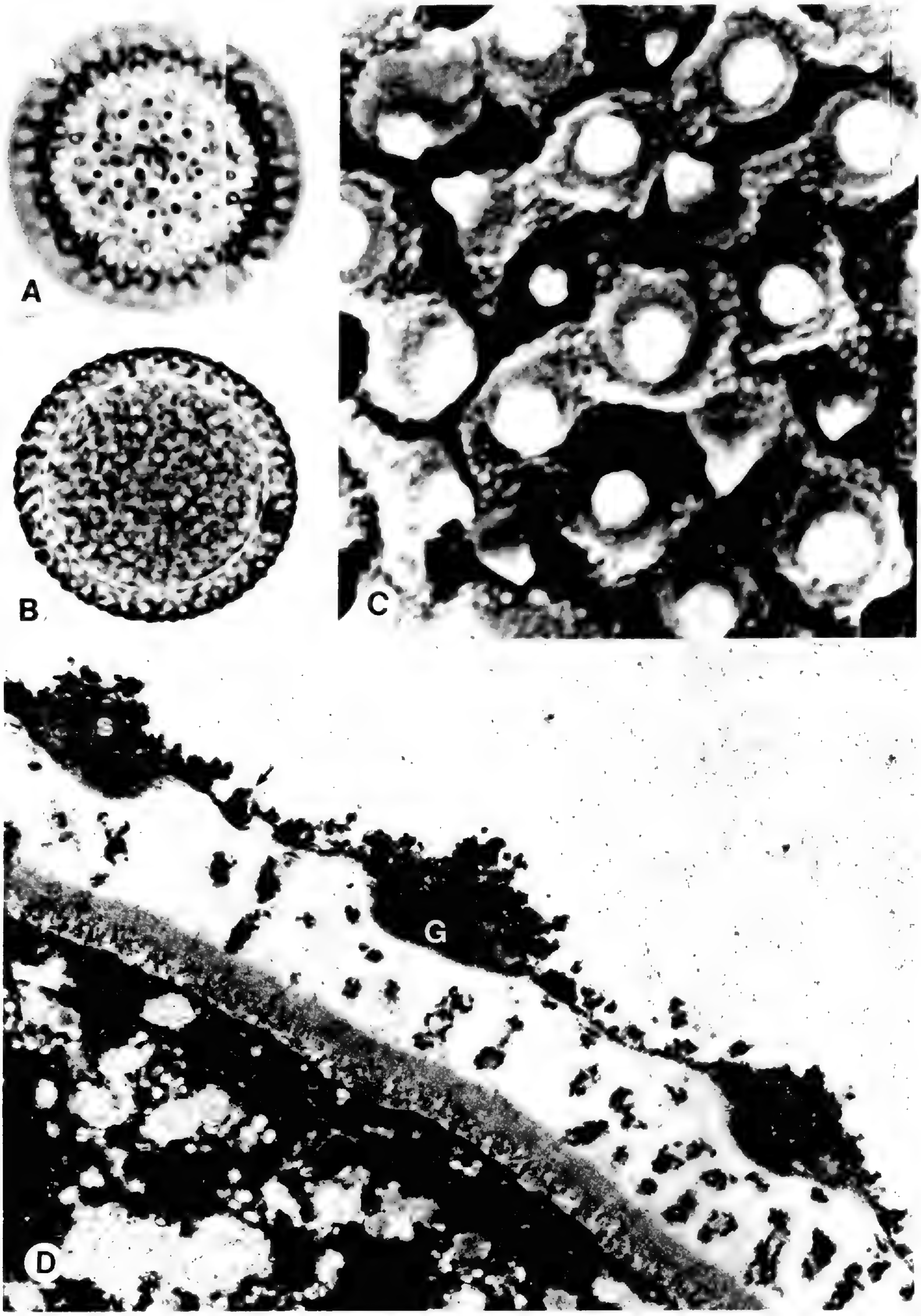

FIGURE 8. Umbellularia californica.—*A. Entire pollen grain, showing spinules as white dots in the peripheral region and as dark dots in the middle.—B. The same in optical cross section. LM ×1,000.—C. Part of exine showing spinules, their basal, circular, cushionlike form and the surrounding densely spaced, granular processes. SEM ×11,000.—D. Part of pollen wall showing the outer, thin, electron-dense layer composed of clavate to globular elements (arrow) and spinules (s), their bases deeply intruding into the intine and surrounded by globular elements (G); spinules and exine surface covered with loose "fuzzy coating." The underlying thick, outer intine scattered with ill-defined channels partly filled with osmiophilic material; inner intine thin, granular, and of varying electron density. TEM ×20,000.*

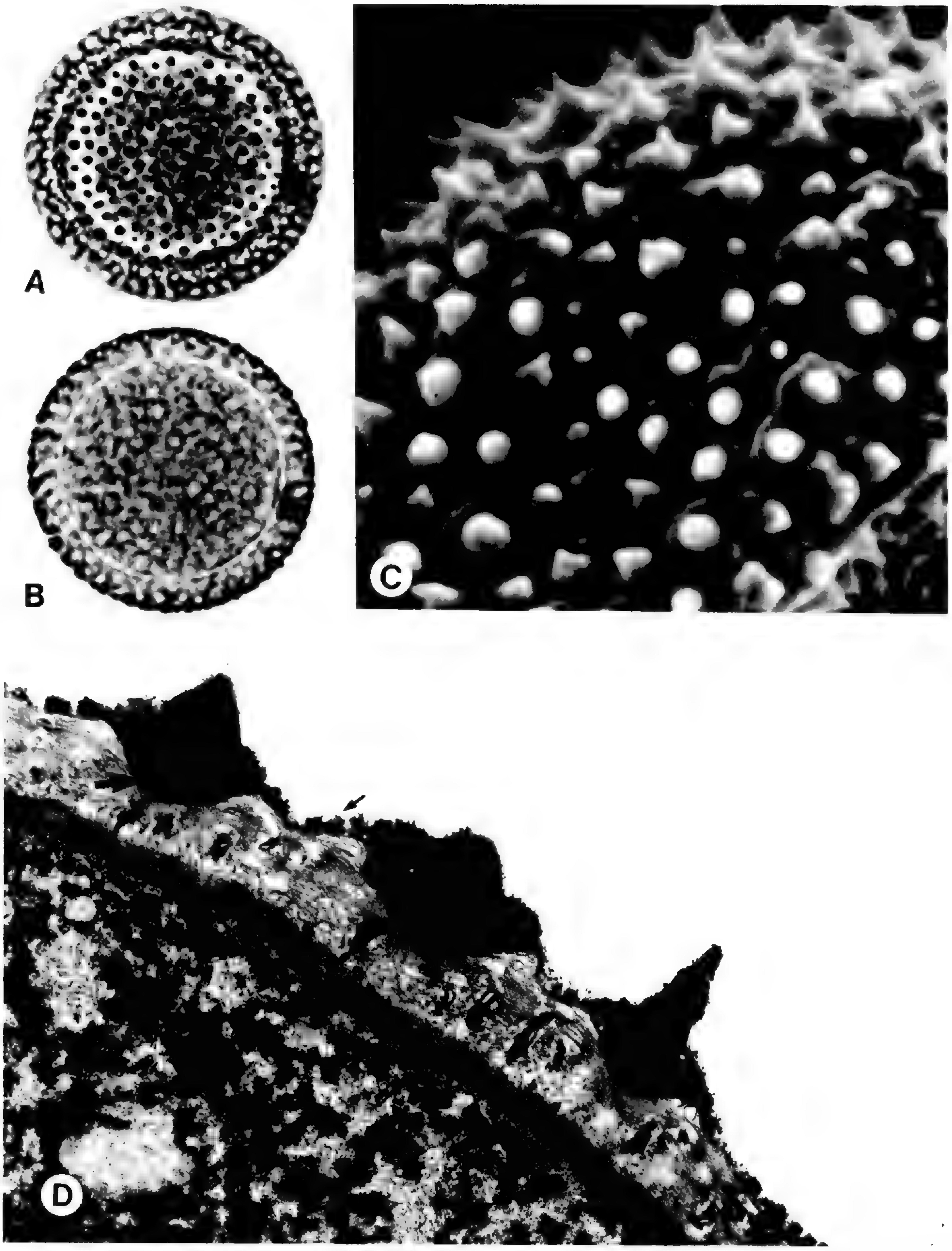

FIGURE 9. *A, B.* Aiouea costaricensis.—*A. Entire pollen grain showing spinules as white dots in the peripheral region and as dark dots in the middle.*—*B. The same in optical cross section. LM ×1,000. C, D.* A. trinervis.—*C. Part of exine showing surface details. SEM ×11,000.*—*D. Part of pollen wall showing thin, electron-dense exinous layer made up of granular elements (thin arrow) and spinules, their bases intruding into the intine and surrounded by globular elements (thick arrow). Outer layer of intine fibrillar in composition and beset with radially oriented channels filled with osmiophilic material; inner layers denser, of varying electron density. TEM ×20,000.*

ly spaced, usually pointed, frequently vestigial. The basal cushionlike form of the spinules not easily discernible due to the surrounding densely spaced processes of varying size and shape. General surface of exine beset with densely spaced, minute processes. Intine 1.5–2.5 μm thick, appearing stratified.

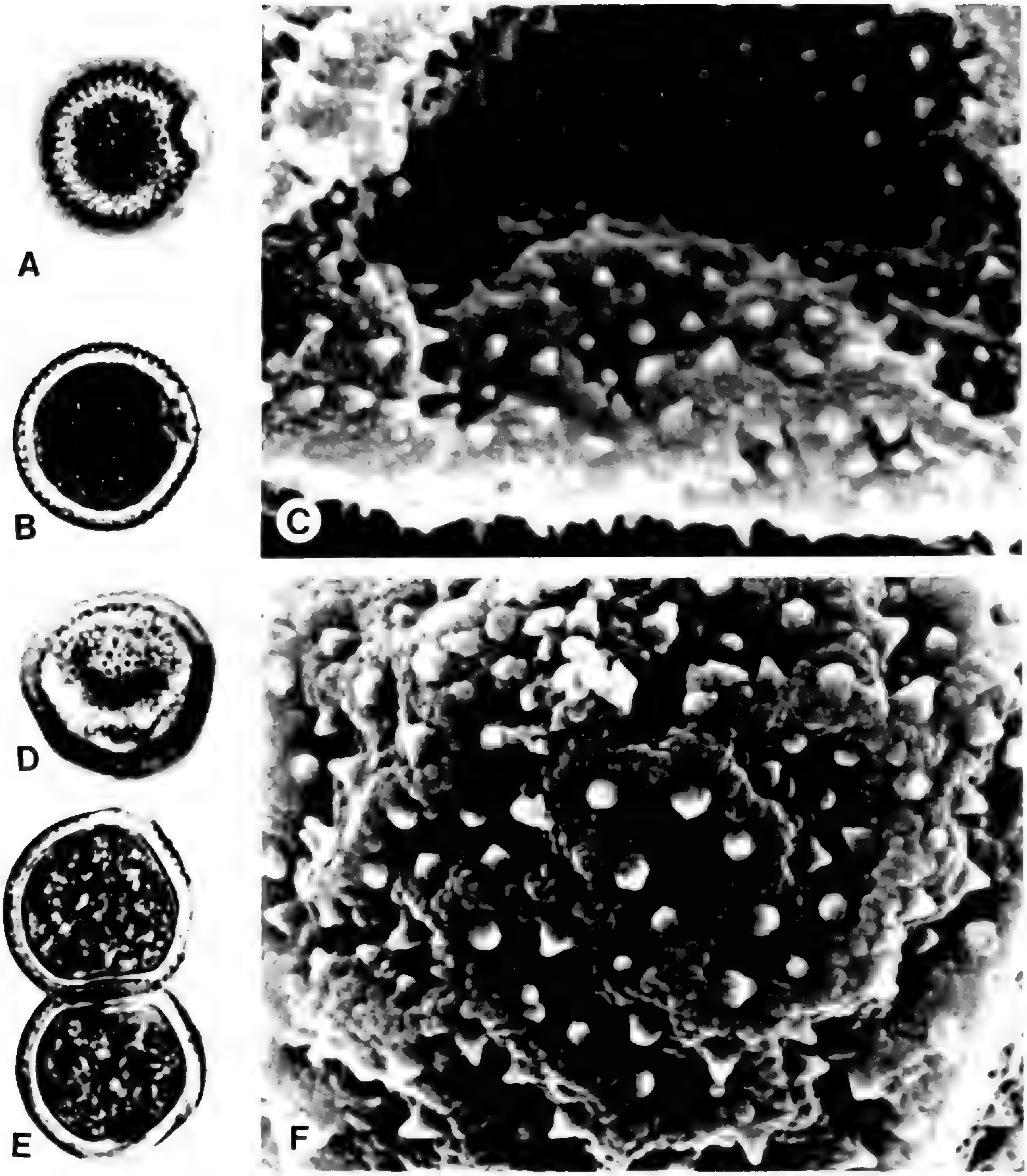

FIGURE 10. *A, B.* Aniba burchellii.—*A. Entire pollen grain showing spinules as white dots in the peripheral region and as dark dots in the middle.—B. The same in optical cross section. LM ×1,000.—C.* A. riparia × A. kappleri. *Part of exine showing surface details. SEM ×11,000. D–F.* Endlicheria endlicheriopsis.—*D. Entire pollen grain showing spinules as white dots in the peripheral region and as dark dots in the middle.—E. Two pollen grains in optical cross section. LM ×1,000.—F. Part of exine showing spinules and the surrounding densely spaced processes. SEM ×11,000.*

Endlicheria serica. Figure 11A. TEM observation: pollen wall about 3 µm thick, differentiated into an outer, very thin, electron-dense ornamented exinous layer composed of globular to granular elements, these appearing to fuse to form a thin tectum, and of minute, pointed, solid spinules 2 µm apart with a distinct basal cushion intruding deeply into the underlying layer. The subtending massive intinous layer loosely granular throughout, densely spaced with radially oriented channels partly filled with osmiophilic material, its inner margin more or less smooth.

Licaria. Figure 11B–D.

Diameter of pollen grains 17–33 µm. Exine 0.5–1 µm thick, scattered with spinules

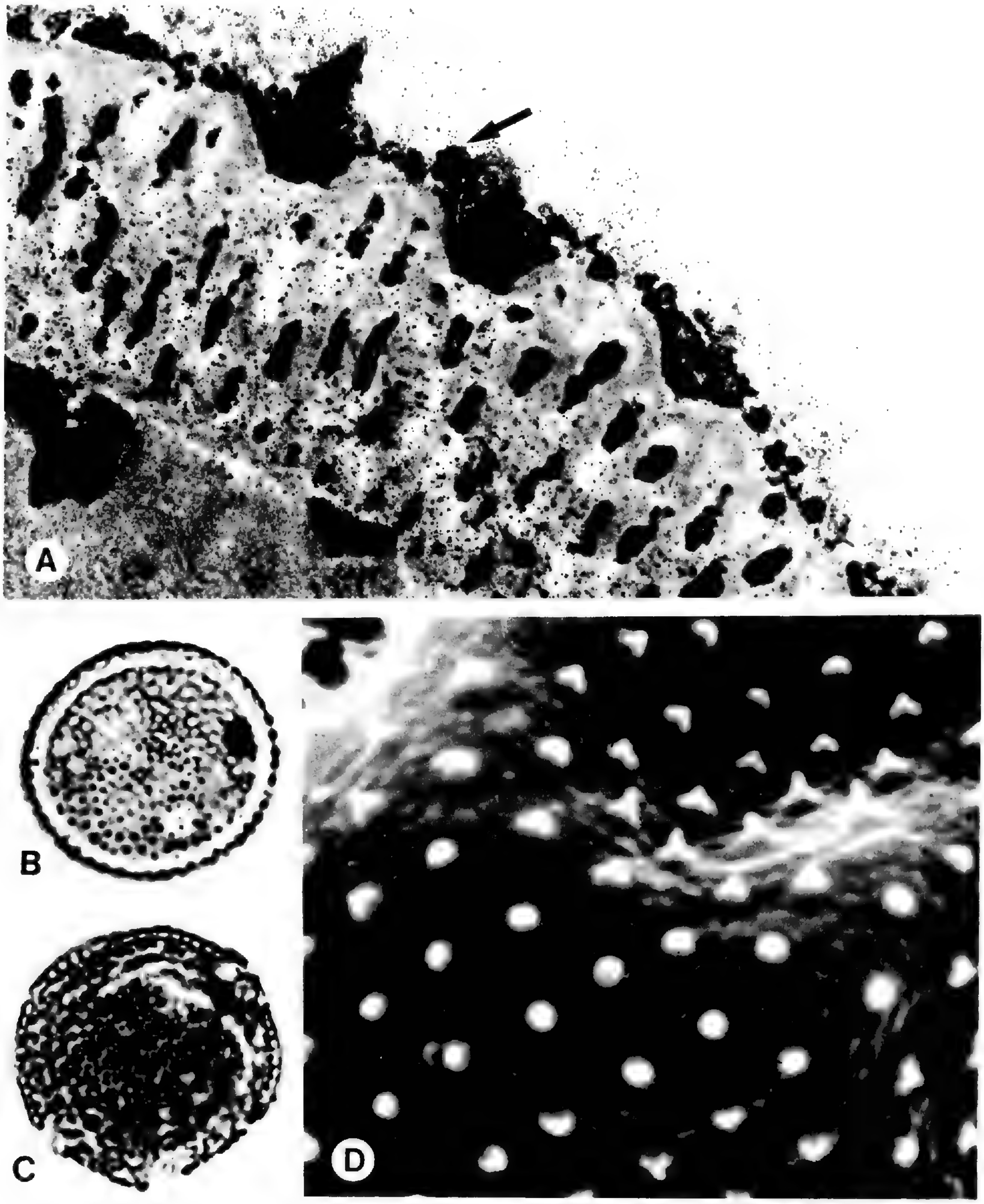

FIGURE 11.—*A.* Endlicheria serica. *Part of pollen wall showing an outer thin, electron-dense exinous layer composed of granular to globular elements, which appear to form a thin tectum. Note traces of "fuzzy covering" on the surface of spinules and exine (arrow). Intine loosely granular throughout, beset with radially oriented channels, partly filled with osmiophilic material. TEM ×20,000. B, C.* Licaria armeniaca.—*B. Entire pollen grain showing spinules as white and dark dots.—C. The same in optical cross section. LM ×1,000.—D.* L. capitata. *Part of exine showing spinules and granular processes. SEM ×11,000.*

1–2 μm apart of faintly discernible twisted strands. Spinules < 0.5 μm long, pointed, with a basal, circular, cushionlike form, surrounded by a ring of densely spaced, partially fused processes of varying size and shape. The general surface of exine beset with minute processes. Intine 1–3.5 μm thick, appearing homogeneous.

Licaria triandra. Figure 12A. TEM observation: pollen wall 2 μm thick, consisting of an outer, very thin, electron-dense, ornamented exinous layer composed of scattered or irregularly clustered granular elements and minute, pointed, solid spinules 1 μm apart with a distinct basal cushion intruding into the underlying layer. The subtending massive

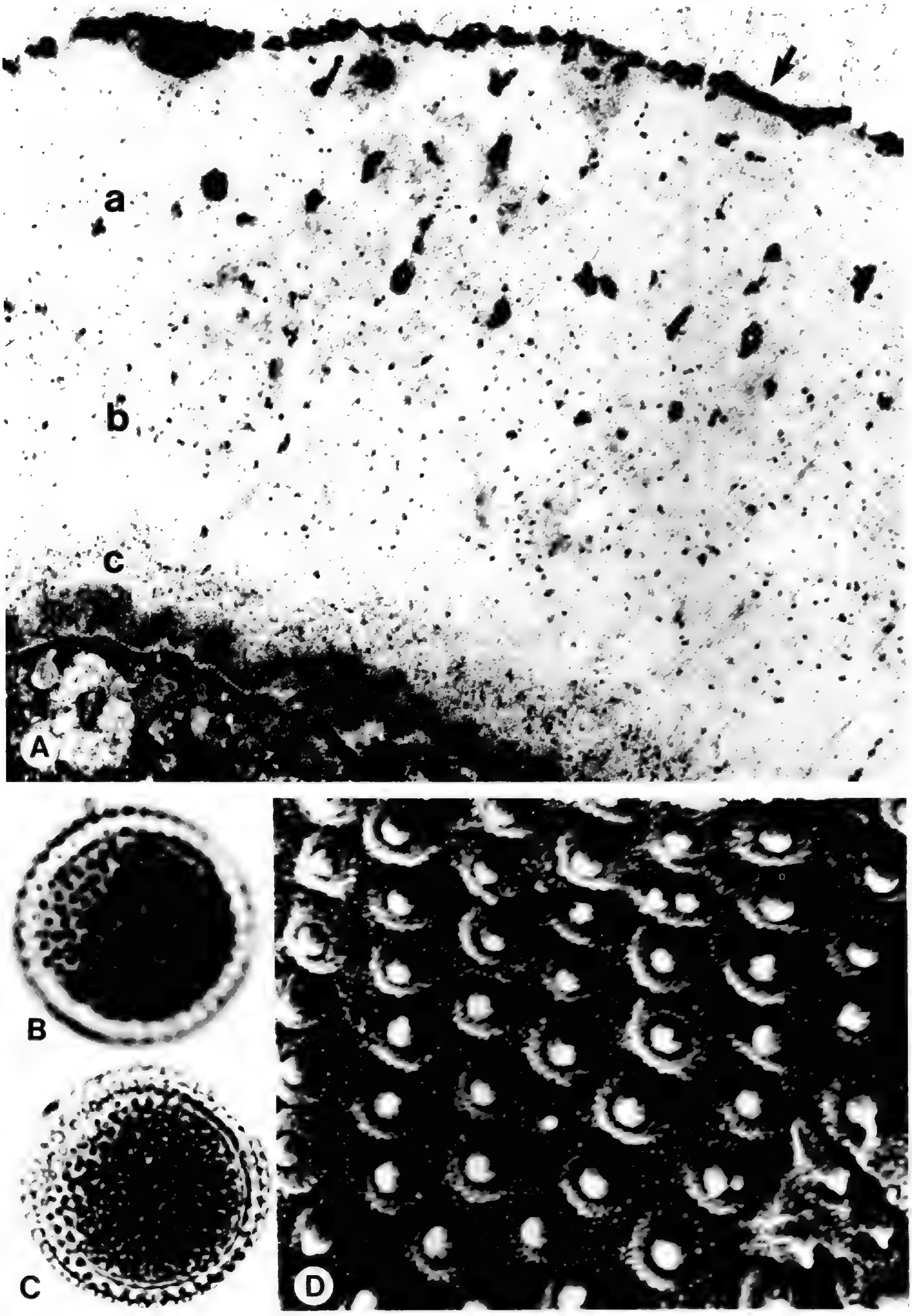

FIGURE 12. *A.* Licaria triandra. *Part of pollen wall showing an outer thin, electron-dense exinous layer (arrow). The underlying massive intinous layer differentiated into an outermost thick stratum, this fibrillar in composition with scattered narrow channels and with vacuoles filled with osmiophilic material (a); the second layer structurally loose and fibrillar, sprinkled with osmiophilic material (b); the third layer densely granular and sprinkled with osmiophilic material (c); the innermost layer denser than the other layers, extremely irregular in outline, structurally compact and granular (d). TEM ×20,000. B–D.* Kubitzkia mezii.—*B. Entire pollen grain, spinules appear as dark dots (lower focus).—C. The same in optical cross section. LM ×1,000.—D. Part of exine showing spinules and the surrounding granular processes. SEM ×11,000.*

intinous stratum made up of 4 distinct layers of varying composition. The outermost relatively thick, transversely organized, compact fibrillar layer with scattered, narrow channels and vacuoles partly filled with osmiophilic material. The second layer equally thick, less electron dense, structurally loose and fibrillar, sprinkled with osmiophilic material. The third layer is thinner, densely granular in composition, much more electron dense, and sprinkled in places with osmiophilic material. The layer next to the cytoplasmic boundary extremely irregular in outline, in places very thin or absent, and also much denser than the other layers, structurally compact and granular.

Kubitzkia (*Systemonodaphne*). Figure 12B–D.

Diameter of pollen grains 24–27 μm. Exine 1 μm thick, scattered with spinules 2 μm apart of easily discernible twisted strands. Spinules 0.5 μm long, pointed, with a prominent basal, circular cushionlike form surrounded by a ring of densely spaced, partially fused processes of varying size and shape. The general surface of exine beset with densely spaced minute processes. Intine 3 μm thick, appearing homogeneous.

Litsea. Figure 13.

Diameter of pollen grains 27–35 μm. Exine 1 μm thick, scattered with spinules 3 μm apart of not easily discernible strands. Spinules < 1 μm long, pointed with a basal cushionlike form, circular to irregular in shape and devoid of processes, partially surrounded by a ring of densely spaced, minute processes. Intine 4 μm thick and appearing homogeneous.

Litsea glaucescens. Figure 13D. TEM observation: pollen wall 5 μm thick, its outer, very thin, electron-dense, ornamented exinous layer composed of scattered or irregularly clustered granular to globular elements and of minute, pointed, solid spinules 3 μm apart with a distinct basal cushion intruding into the intinous layer. The underlying massive intinous layer distinctly distinguished into a thicker outer layer inlaid with channels and vacuoles filled with osmiophilic material and into a thinner, denser, homogeneous layer with a slightly uneven inner margin.

Cryptocarya. Figure 14.

Diameter of pollen grains 30–33 μm. Exine 0.5–1 μm thick, appears disrupted in optical cross section (in LM), its outer surface much wrinkled. Intine 2.5–4 μm thick, appearing stratified.

Cryptocarya aschersoniana. Figure 14D. TEM observation: pollen wall about 4.5 μm thick, its outer very thin, electron-dense stratum consisting of an uneven tectum supported by densely spaced clavatelike to globular elements and of a supratectal thin coating of compact material. The subtending massive intinous layer distinctly distinguished into an outer thick, less electron-dense, structurally loose, transversely organized fibrillar layer inlaid with scattered vacuoles, these partly filled with osmiophilic material, and into an inner electron-dense, structurally compact, transversely organized fibrillar layer interrupted by long, narrow channels filled with osmiophilic material. These channels traversing the entire thickness of the layer, conical in shape, and having an outlet into the layer above. The intinous layer next to the cytoplasmic boundary denser than the other layers and in places beset with narrow, short channels filled with osmiophilic material.

Cassytha. Figure 15.

Diameter of pollen grains 22–28 μm. Exine 0.5 μm thick, its surface scattered with minute, spinuloid excrescences. Intine 4 μm thick, appears homogeneous.

DISCUSSION

GENERAL POLLEN-MORPHOLOGICAL FEATURES

The pollen grains of Lauraceae are inaperturate and more or less spheroidal. Kasapligil (1951), however, found monocolpate pollen

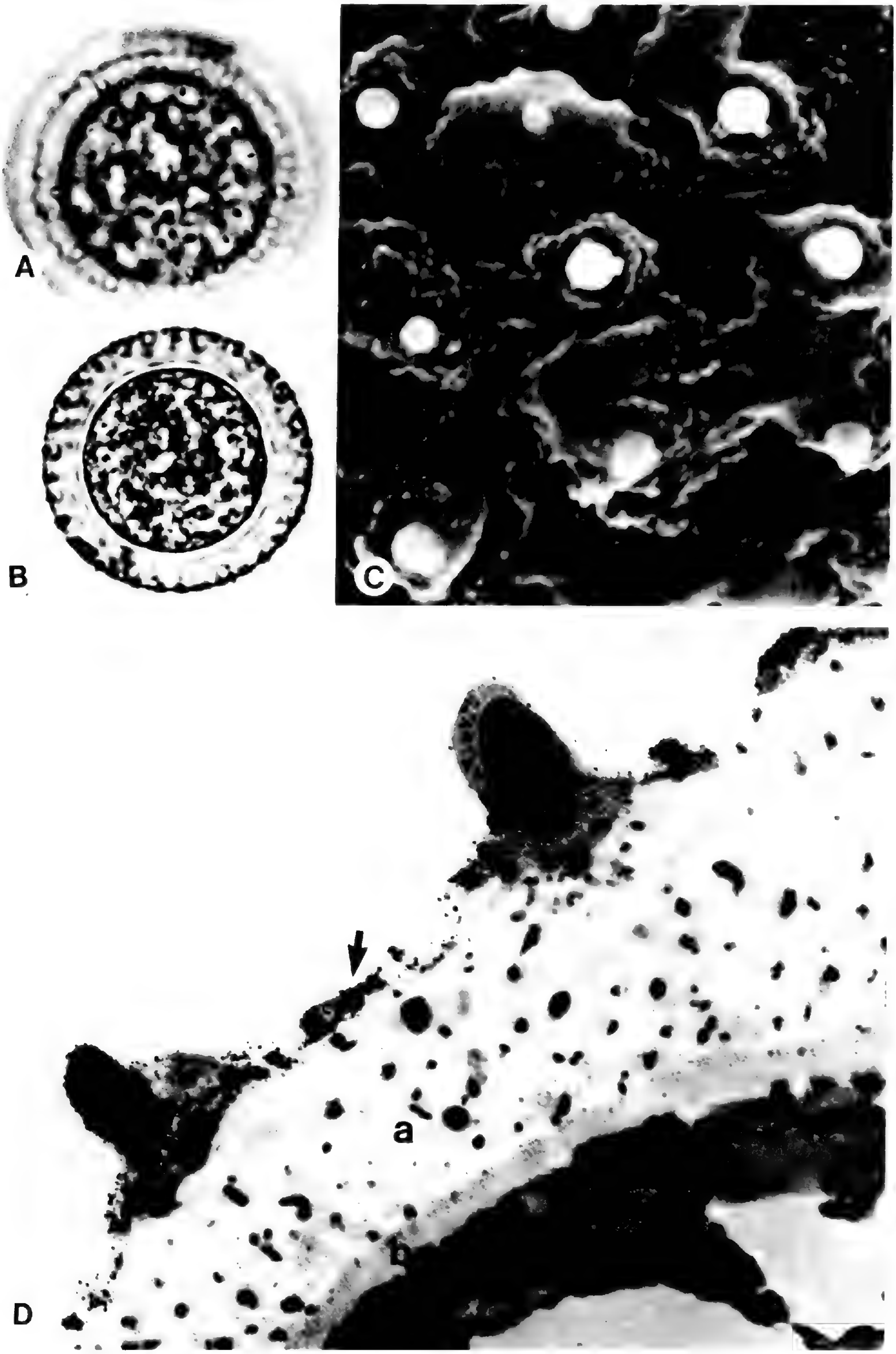

FIGURE 13. Litsea glaucescens.—*A. Entire pollen grain showing spinules as white and dark dots.—B. The same in optical cross section. LM ×1,000.—C. Part of exine showing spinules and their basal cushions. SEM ×11,000.—D. Part of pollen wall showing an outer very thin, electron-dense exinous layer composed of scattered or irregularly clustered granular to globular elements (arrow). Intine distinctly differentiated into an outer, thick stratum inlaid with channels and vacuoles filled with osmiophilic material (a) and an inner thin, denser, homogeneous layer (b). TEM ×20,000.*

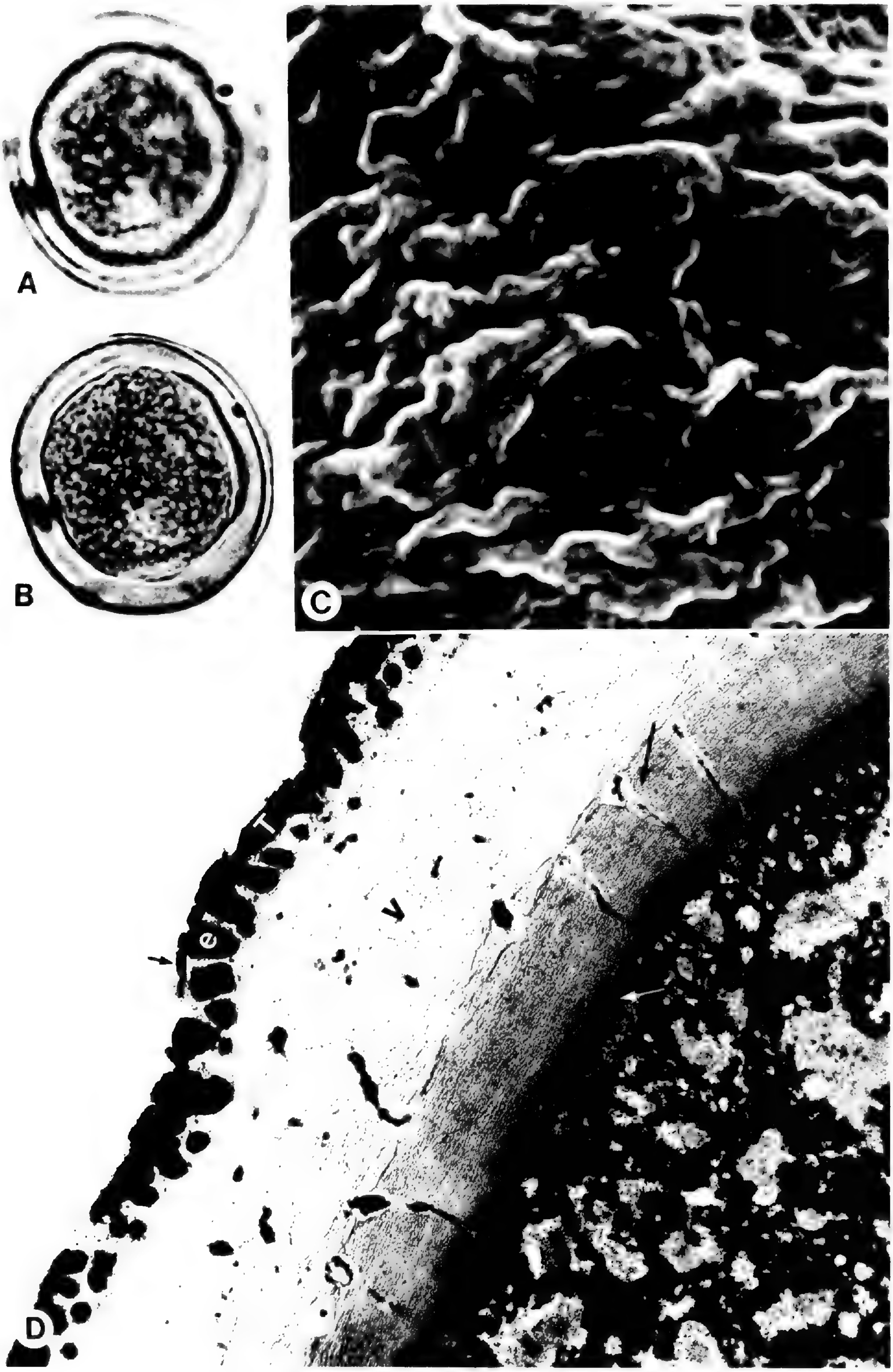

FIGURE 14. Cryptocarya aschersoniana.—*A. Entire pollen grain showing the smooth exinous surface.—B. The same in optical cross section. LM ×1,000.—C. Part of exine showing the smooth and wrinkled surface. SEM ×11,000.—D. Part of pollen wall showing a thin, electron-dense layer consisting of tectum (T), supported by clavatelike to globular elements (e), and covered by a thin coating of compact material (arrow). The subtending intinous layer distinguished into an outer thick, fibrillar layer inlaid with vacuoles (v), followed by*

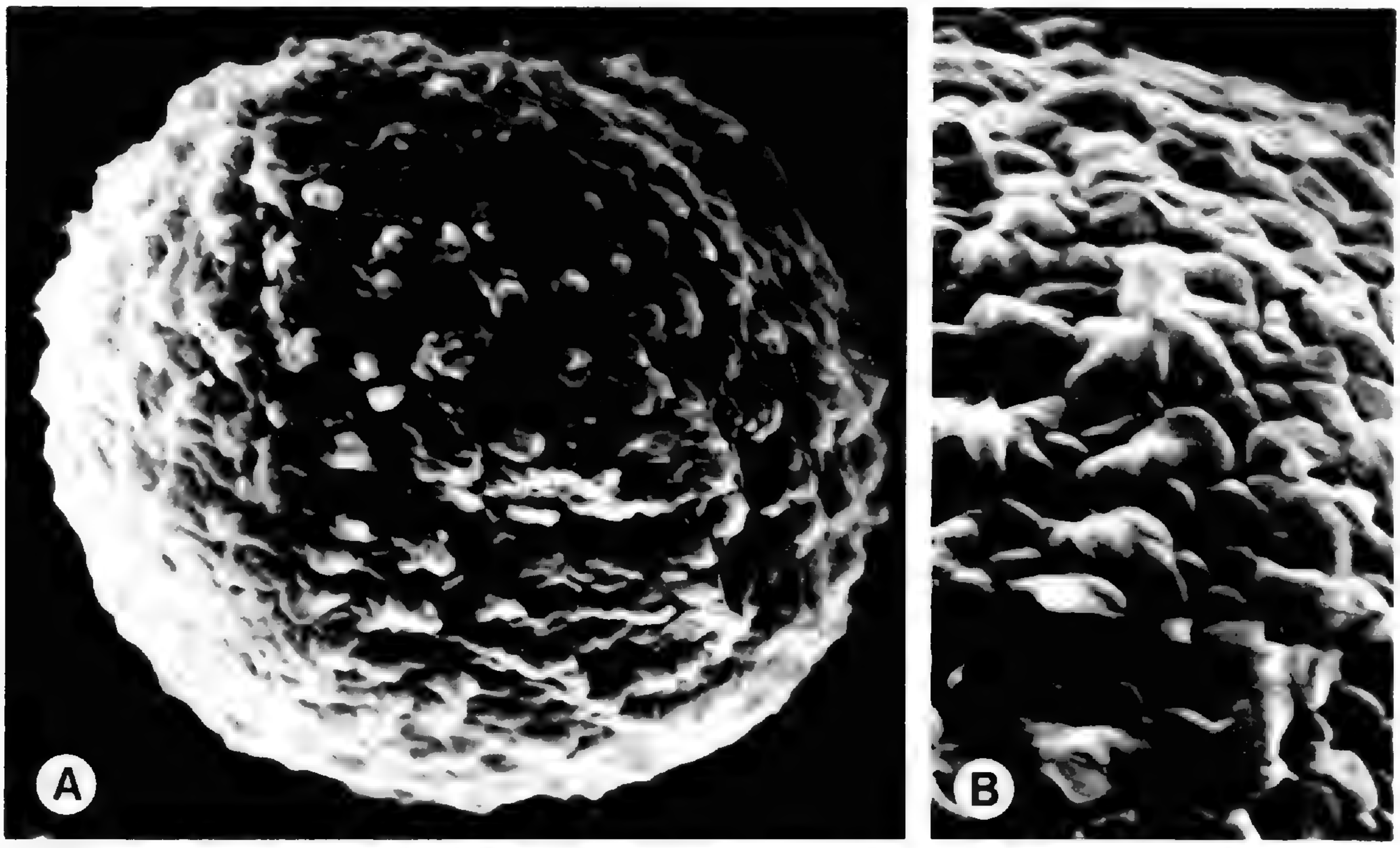

FIGURE 15. Cassytha filiformis.—*A. Entire pollen grain showing uneven exinous surface beset with spinuloid processes. SEM ×5,200.—B. Part of the same at a higher magnification. SEM ×10,000.*

grains in *Umbellularia californica* (not confirmed by the present investigation) and acolpate grains in *Laurus nobilis* (not included in the present study). Also Markgraf & D'Antoni (1978) described the pollen grains of *Nectandra angustifolia* as tricolpate, prolate spheroidal (not included in the present study).

The pollen grains of this family are considered to be "delicate" since they disintegrate readily or come out in a more or less shriveled and wrinkled condition after acetolysis. They are tenui-exinous and, as TEM observation shows, entirely ectexinous. The exine is provided with spinules or spinuloid projections, or rarely the exine is smooth as in *Cryptocarya aschersoniana* (Heusser, 1971, described the exine of *Cryptocarya alba* as foveolate). The intine represents the dominant, massive layer of the pollen wall.

Out of the 80 taxa investigated, the largest pollen grains are those of *Beilschmiedia miersii, Cryptocarya aschersoniana, Ocotea calophylla, O. spixiana, Persea americana, P. caerulea, P. fulva,* and others (over 30 μm in diameter); while the smallest belong to *Aniba burchellii, Endlicheria glomerata, Nectandra purpurea, Ocotea cernua,* and *Persea veraguasensis* (under 20 μm in diameter). In the remaining taxa the diameters are 20–30 μm. The grains are usually monomorphic; however, dimorphic grains occur in *Persea caerulea* and *P. schiedeana.*

Some species of *Persea* have dimorphic spinules. Because *Persea* shows various stages of reduction of the number of fertile stamens and/or anther cells (from the normal pattern of nine four-celled stamens to six four-celled and three two-celled or six four-celled stamens and three staminodia or nine two-celled stamens; Kopp, 1966), it would be worthwhile to investigate whether in species with dimorphic pollen grains each stamen has only one kind of pollen grain and inner and outer stamens have different pollen grains or whether each stamen possesses both kinds of pollen grains.

←

an electron-dense, structurally compact, fibrillar stratum inlaid with narrow, conical channels (arrow); the innermost layer denser than the other layers and likewise inlaid with channels (white arrow). TEM ×20,000.

TABLE 4. *Pollen-morphological data for Lauraceae. Five main pollen characters are compared: (1) diameter of pollen grains; (2) exine thickness; (3) intine thickness; (4) length of spinules; and (5) maximum and minimum number of spinules.*

	Diameter (µm)	Exine (µm)	Intine (µm)	Spinules (µm)	Maximum	Minimum	Remarks
Subfamily Lauroideae							
Tribe Perseeae							
Subtribe Perseineae							
Persea							
P. americana	30–36	0.5	4	< 0.5	1,174	815	spinules dimorphic, pointed and blunt, intermingled, 2 µm apart
P. caerulea	33–39	1	3	0.5	661	612	pollen grains dimorphic (a) with monomorphic spinules (b) with dimorphic spinules; spinules small, thick, blunt or small, thin and pointed, 3 µm apart
P. fulva	29–44	1	3	0.5	779	338	spinules in places dimorphic, 3 µm apart; in places crowded, 1 µm apart
P. mutisii	30–41	1	4	< 0.5	> 1,000	—	spinules dimorphic, pointed and blunt, intermingled, 1 µm apart
P. schiedeana	31–36	1.5	3	< 1	4,700	3,485	pollen grains dimorphic (a) spinules monomorphic (b) spinules dimorphic, pointed and blunt intermingled, 1 µm apart
P. veraguasensis	14–17	1	2	0.5	4,192	2,843	spinules 0.5 µm apart
Phoebe							
P. costaricana	22–26	< 1	< 2	< 1	650	425	spinules 2 µm apart
P. hammeliana	24–28	1	< 2	< 1	670	535	spinules 2 µm apart
P. helicterifolia	24–27	2	3	< 2	660	521	spinules 2 µm apart
P. mexicana	21–24	1	2	< 1	2,088	1,599	spinules 1 µm apart
P. porphyria	22–28	1	3	< 1	2,843	1,755	spinules 1 µm apart
P. smithii	30–33	1	3	< 1	631/987	521/815	spinules 2–2.5 µm apart, occasionally paired in places
Caryodaphnopsis							
C. fosteri	27–33	0.5	2	1.5	661	437	spinules 2–3 µm apart
Subtribe Beilschmiediineae							
Beilschmiedia							
B. miersii	28–38	2	2.5	1.5	710	580	spinules 2–3 µm apart
B. pendula	23–29	1	5	1	762	479	spinules 2 µm apart; in places 0.5 µm apart
Mezilaurus							
M. navalium	22–26	1	2	< 0.5	650	425	spinules 2 µm apart

TABLE 4. *Continued.*

	Diameter (μm)	Exine (μm)	Intine (μm)	Spinules (μm)	Maximum	Minimum	Remarks
Tribe Cinnamomeae							
Subtribe Cinnamomineae							
Ocotea							
O. calophylla	31–39	1	3	1	612	386	spinules 3 μm apart
O. cernua	17–19	1	2	< 0.5	1,309	1,047	spinules 1 μm apart
O. corymbosa	22–25	1	2	1	2,266	1,755	spinules 1 μm apart
O. cuprea	24–27	1	3	1	660	521	spinules 2 μm apart, frequently crowded on insulae
O. dendrodaphne	26–29	1.5	2.5	1	762	612	spinules 2 μm apart
O. ensifolia	26–28	1.5	2	1.5	928/412	612/271	spinules 2–3 μm apart
O. guianensis	20–26	1.5	2	1	2,451/612	1,450/362	spinules 1–2 μm apart
O. ira	23–28	1	3	< 0.5	2,843	1,918	spinules 1 μm apart, transparent, weak colpuslike or porelike areas seen in a few grains
O. kuhlmannii	24	1.5	2	1	612	521	spinules 2 μm apart
O. oblonga	20–24	1	2	< 0.5	521	362	spinules 2 μm apart
O. puberula	24–27	1.5	2.5	1	292	231	spinules 3 μm apart
O. pulchella	27–31	2	1.5	1	557	422	spinules 2.5 μm apart
O. skutchii	24–27	1	4	< 0.5	661	521	spinules 2 μm apart
O. spixiana	34–39	2	3	2	344	261	spinules 4 μm apart
O. tonduzii	25–27	1	2	1	2,643	2,266	spinules 1 μm apart
O. veraguensis	18–20	1	2	< 0.5	> 1,000	—	spinules 1 μm apart
O. villosa	27–29	2.5	5	2	762	666	spinules 2 μm apart
O. whitei	30–33	1	3	< 0.5	3,949	3,264	spinules 1 μm apart
Nectandra							
N. acutifolia	22–24	0.5	1.5	< 0.5	521	438	spinules 2 μm apart
N. ambigens	28–33	0.5	2	1.5	710	437	spinules 2–3 μm apart
N. baccans	24–29	1	2.5	< 1	762	521	spinules 2 μm apart
N. cissiflora	18–20	0.5	3	< 0.5	1,309	1,309	spinules 1 μm apart
N. coriacea	19–25	1	2	0.5	251	144	spinules 1.5–3 μm apart
N. cuspidata	26–29	1	2	< 0.5	762	612	spinules 2 μm apart
N. falcifolia	26–29	0.5	2.5	0.5	338/190	271/152	spinules 3–4 μm apart, in places crowded; dimorphic?
N. gardneri	28–33	1	3	1	986	710	spinules 2 μm apart
N. gentlei	22–27	1	4	0.5	2,643	1,755	spinules 1 μm apart

TABLE 4. *Continued.*

	Diameter (μm)	Exine (μm)	Intine (μm)	Spinules (μm)	Maximum	Minimum	Remarks
N. globosa	21–24	0.5	2.5	1	521	399	spinules 2 μm apart
N. grandiflora	25–27	1	3.5	1	293	251	spinules 3 μm apart
N. lanceolata	26–31	1.5	2.5	1	871	612	spinules 2 μm apart
N. loeseneri	19–23	1	2	0.5	1,918	1,309	spinules 1 μm apart
N. martinicensis	19–22	1	2	1	438	326	spinules 2 μm apart
N. membranacea	20–25	1	2	< 0.5	2,266	1,450	spinules 1 μm apart
N. perdubia	19–24	0.5	2	1	928	581	spinules 1.5 μm apart
N. purpurea	18–19	1	2	< 0.5	1,309	1,174	spinules 1 μm apart
N. reticulata	27–30	1	2	1	815	660	spinules 2 μm apart
N. salicifolia	22–27	1	2	1	660	438	spinules 2 μm apart
N. salicina	23–26	1	3	< 0.5	612	479	spinules 2 μm apart
Pleurothyrium							
P. densiflorum	21–24	0.5	1.5	< 0.5	2,088	1,599	spinules 1 μm apart
P. zulianense	22–24	0.5	1.5	< 0.5	2,088	1,755	spinules 1 μm apart
P. sp.	28–30	0.5	1.5	1	815	710	spinules 2 μm apart
Rhodostemonodaphne							
R. grandis	21–23	0.5	2.5	< 0.5	1,918	1,599	spinules 1 μm apart; ± vestigial
R. kunthiana	21–24	1	1	< 0.5	2,088/521	1,599/399	spinules 1–2 μm apart
Umbellularia							
U. californica	31–36	3.5	2.5	1	521	386	spinules 3 μm apart
Subtribe Anibineae							
Aiouea							
A. costaricensis	22–29	1	3	< 0.5	762/338	438/194	spinules 2–3 μm apart; porelike transparent areas devoid of spinules discernible
A. laevis	19–21	0.5	1.5	< 0.5	1,599	1,309	spinules 1 μm apart
A. trinervis	20–23	1	3	< 0.5	479	361	spinules 2 μm apart
Aniba							
A. burchellii	18–20	0.5	1.5	< 0.5	1,450	1,174	spinules 1 μm apart
A. canelilla	22–27	0.5	1.5	< 0.5	2,643	1,755	spinules 1 μm apart
A. firmula	20–23	0.5	1.5	< 0.5	1,918	1,450	spinules 1 μm apart; in a few pollen grains distinct 2–3 porelike or irregular openings seen
A. riparia × *kappleri*	16–19	0.5	2	< 0.5	5,237	3,714	spinules 0.5 μm apart

TABLE 4. *Continued.*

	Diameter (µm)	Exine (µm)	Intine (µm)	Spinules (µm)	Maximum	Minimum	Remarks
Endlicheria							
E. endlicheriopsis	17–21	0.5	2	< 0.5	1,599	1,047	spinules 1 µm apart
E. glomerata	15–19	0.5	2.5	0.5	1,309	815	spinules 1 µm apart
E. paniculata subsp. *poeppigii*	17–22	0.5	2	< 0.5	7,022	4,192	spinules 0.5 µm apart
E. sericea	24–27	1	2	1	660	521	spinules 2 µm apart
E. tessmannii	16–20	0.5	1.5	< 0.5	1,450	928	spinules 1 µm apart
E. verticillata	20–25	1	1	< 0.5	2,266	1,450	spinules 1 µm apart
Licaria							
L. armeniaca	27–33	1	3	< 0.5	3,949	2,643	spinules 1 µm apart
L. capitata	20–25	1	2.5	< 0.5	> 1,000	565	spinules 1–2 µm apart
L. peckii	23–25	0.5	3.5	< 0.5	2,266/1,754	566/479	spinules 1–2 µm apart
L. triandra	17–23	0.5	1.5	< 0.5	1,918	1,047	spinules 1 µm apart
Kubitzkia							
K. mezii	24–27	< 1	> 3	0.5	661	521	spinules 2 µm apart
Tribe Litseeae							
Subtribe Litseineae							
Litsea							
L. glaucescens	27–35	1	4	< 1	493	293	spinules 3 µm apart
Tribe Cryptocaryeae							
Subtribe Cryptocaryineae							
Cryptocarya							
C. aschersoniana	30–33	0.5	4	absent	—	—	exine smooth or wrinkled, its surface appearing interrupted
Subfamily Cassythoideae							
Cassytha							
C. filiformis	22–28	1	4	0.5	—	—	exine surface beset with densely spaced, minute excrescences

The exine ornamentation in all the taxa (except *Cryptocarya*) consists of solid, apparently simple spinules or as in *Nectandra reticulata, Ocotea cuprea, Persea americana, Phoebe porphyria,* and others, "wick-like" i.e., made up of twisted strands. They are pointed or blunt, uniformly spread over the surface or rarely, in some portions of a grain, in groups; the spinules are sometimes crowded as in *Nectandra ambigens* to give a rosettelike appearance, or they occur in pairs. Similar wicklike spinules have been reported in many groups, e.g., Euphorbiaceae (Thanikaimoni et al., 1984), Linaceae (Punt & den Breejen, 1981), Monimiaceae (Walker & Doyle, 1975) and Plumbaginaceae (Nowicke & Skvarla, 1977).

The density and morphology of spinules differs in different species. Thus the highest number of spinules per grain is met with in *Persea* and *Licaria,* and the lowest in *Beilschmiedia, Caryodaphnopsis,* and *Litsea.* Further, the size of the pollen grains does not seem related to the number of spinules. Spinules are usually monomorphic; however, dimorphic spinules have been found in *Nectandra falcifolia, Persea caerulea,* and *P. fulva.* Spinules are usually broad at base. Their common characteristic feature is the presence of a conspicuous, circular, cushion-like base which invariably protrudes proximally; its surface is either smooth or studded with granular to globular elements. In *Ocotea cuprea* these cushionlike structures are relatively big and compactly arranged, thereby giving a more or less rounded insulaelike appearance to the exine.

The stratification of the sporoderm presents interesting features that at times are difficult to interpret. A strikingly similar type of statified sporoderm has been reported in the Zingiberales and in certain monimiaceous genera. The fascinating aspect of the pollen wall is the extreme thinness of the exine and the thick, structurally complex intine.

The fine structure of the lauraceous genera investigated shows an electron-dense, extremely thin, coherent exine made up of granular, globular, or irregularly shaped elements and of spinules. Only in *Persea fulva* (Fig. 1C), *Endlicheria serica* (Fig. 11A), and *Cryptocarya aschersoniana* (Fig. 14D) is there a clear indication of parts of well-defined tectum supported by a well-defined bacular layer. In *Umbellularia californica* the exine surface and spinules are covered by a distinct, superficial coating referred to as "fuzzy surface coating" by Rowley & Skvarla (1986); traces of this material are also discernible in *Aiouea trinervis, Ocotea puberula, Persea fulva,* and *Phoebe helicterifolia.*

The coherent nature of the thin exine, which is emphasized in the present study, has often been compared with exines of some members of the Zingiberales (Kress et al., 1978; Stone et al., 1979) and reported as incoherent or "exine-less." The incoherent nature of any exine, however thin, or the conception of an "exine-less" pollen wall, both from a morphological and functional point of view, has been convincingly argued and rejected by Hesse & Waha (1983).

The dominant stratified layer of the sporoderm is the intine. This thick layer is completely destroyed by acetolysis and, in keeping with common wisdom, has to be interpreted as intine. In this layer an outer channeled zone can be easily recognized and has been designated variably: "lacunes" after Le Thomas, 1980; "tubules" according to Sedgley, 1979; "onciform zone" by Rowley & Vasanthy, 1980; "Zwischenkörper" in Kress & Stone, 1982; or simply outer intine or intine 1. These channels, which are long and narrow and of varying length, are predominantly radially aligned and partly or completely filled with osmiophilic material. Thin partition walls as encountered in *Strelitzia reginae* (Musaceae) (Hesse & Waha, 1983) are absent. It is postulated that these channels may act as deposits for material involved in pollen germinating or incompatibility processes (Stone et al., 1979; Hesse & Kubitzki, 1983).

It is remarkable that the characteristic sporoderm stratification encountered in lauraceous genera, namely extremely thin exine and a thick, stratified, channeled intine, is apparently limited to inaperturate pollen grains belonging to such disparate genera as *Canna*, *Heliconia*, *Hernandia*, and *Palmeria*.

Further, the massive channeled intinous zone mentioned above has been found also to resemble to a lesser extent that of the conifers (viz., *Larix europea*, Cupressineae, and Taxodineae) that Wodehouse (1932) noted and remarked as "one of the most remarkable examples of convergence I have yet encountered among pollen-grain forms."

The functional significance of the thickened intinous layers or onci frequently observed beneath apertures appears to be to act as storage areas for gametophytic incompatibility proteins (Heslop-Harrison, 1976).

TAXONOMY

There is uniformity of opinion among taxonomists that the family Lauraceae is rather old and probably derived from primitive members of the Monimiaceae of the *Hortonia*-type.

In Kostermans's (1957) classification, only a sequence of floral characters are adopted; not a chronological family tree, nor a paleontological succession, nor a phylogenetic trend has been envisaged, but similar genera are grouped.

Palynologically most of the relationships are justified, e.g., the genera *Persea* and *Phoebe* of the tribe Perseeae are satisfactorily included in the subtribe Perseineae, and thus separated from *Beilschmiedia* and *Mezilaurus* of the subtribe Beilschmiediineae. The pollen grains of *Persea* and *Phoebe* have the highest number of spinules per pollen grain, and their anthers are four-celled compared with *Beilschmiedia* and *Mezilaurus*, which have the lowest number of spinules and have two-celled anthers. The former two genera are easily separated from each other because the pollen grains of *Persea* are either dimorphic or if monomorphic, the spinules are dimorphic, whereas the pollen grains of *Phoebe* are wholly monomorphic. Among the Central American species of *Phoebe*, *P. mexicana* stands clearly apart due to its high number of spinules. This pollen feature supports the recognition of *P. costaricana* as distinct from *P. mexicana*.

The genera *Beilschmiedia* and *Mezilaurus* can be separated by the difference in size of spinules and in the surface of the basal cushions and exine. Pollen-morphologically, *Mezilaurus* does not seem to be close to *Licaria*.

Caryodaphnopsis, although similar to *Persea* in floral and fruit characters, has pollen grains quite unlike those of *Persea* and *Phoebe*. On the other hand, the pollen grains are comparable to those of *Beilschmiedia*, and recognition of *Caryodaphnopsis* is supported by pollen morphology. Its position in Richter's (1981) classification seems to be more appropriate than in those of Kostermans (1957) and Hutchinson (1964).

Kostermans (1957) divided *Ocotea*, of the tribe Cinnamomeae, subtribe Cinnamomineae, into three subgenera: *Ocotea*, *Nectandra* and *Pleurothyrium*. His contention that macromorphological differences, such as in the position of the anther cells, size and shape of the staminal glands, and cupule shape, are not big enough to maintain them as distinct genera does not improve the classification. Pollen-morphologically there are enough differences to recognize them as distinct genera. Pollen grains of *Ocotea* and *Pleurothyrium* are apparently very similar, including the organization of spinules, which suggest close relationship. However, the characters that distinguish them are pollen size and ultrastructural details of sporoderm. Pollen grains of *Nectandra* are quite distinct with respect to exine surface and to sporoderm details. There seems enough micro- and macromorphological characters to maintain these as three distinct genera. The transfer of the two species *Nectandra grandis* (Fig. 6D) and and *N. kunthiana* to the new genus *Rhodostemonodaphne* (Rohwer, 1986) seems justified, as the pollen grains are quite different from those of the other species investigated. The spinules in both species appear vestigial without the usual twisted strands easily discernible in other species.

The monotypic genus *Umbellularia* is considered to be related to *Litsea*. Pollen-morphologically such a relationship seems to exist as the pollen grains of the two genera are more or less of the same size, the number of spinules per pollen grain is more or less the same, and the ultrastructural details of the pollen wall are very similar.

Subtribe Anibineae of tribe Cinnamomeae is represented by seven genera, of which the pollen grains of five, *Aiouea*, *Aniba*, *Endlicheria*, *Licaria* and *Kubitzkia* (*Systemonodaphne* sensu Mez), have been investigated. These five genera are rather closely related, and taxonomic problems still remain unsolved in this group. *Aiouea*, recently revised by Renner (1982), appears to include species independently derived from four-celled ancestors. Some Central American *Aiouea* species are morphologically very similar to sympatric *Ocotea* species (van der Werff, 1987) and are much less similar to the Guyanan–Brazilian species group which includes the type species. The observation that *Ocotea ira* and *Aiouea costaricensis* both possess porelike, transparent areas devoid of spinules on the pollen wall (otherwise a very rare character in Lauraceae) strengthens the theory that *Aiouea costaricensis* is more closely related to sympatric *Ocotea* species of the *O. insularis* group (as defined by Rohwer, 1986) than to the S. American *Aiouea* species, and that *Aiouea* is a polyphyletic genus. Kubitzki (1982) considered *Aniba* and *Licaria* closely related but had no hesitation in maintaining them as separate genera, a point of view we share. MacBride's (1938) suggestion to treat *Licaria*, *Kubitzkia*, and *Endlicheria* (the only dioecious genus in this group) as subgenera of *Aniba* has never gained acceptance. *Kubitzkia* is probably closely related to *Licaria*, but is easily separated by the number of fertile stamens.

Pollen morphology also supports the interrelationship of the above genera, and at the same time distinguishes them from one another. All genera have pollen grains of more or less the same size and exhibit the highest number of spinules (excluding *Kubitzkia*) per pollen grain. The highest number of spinules is found in *Licaria*. There is a gradual decrease from *Endlicheria* to *Aniba* to *Aiouea*. *Kubitzkia*, with a much lower number of spinules per pollen grain (661/521), seems to be a misfit in this subtribe, and pollen morphology fails to support its taxonomic relationship with *Licaria*. Better placement would be in the vicinity of *Beilschmiedia* as classified by Hutchinson (1964).

In *Aiouea* the basal cushion of spinules is more or less smooth or in places surrounded by a ring of partially fused processes. In *Aniba* the basal cushions are not very pronounced, and the general surface of the exine is studded with granular processes. In *Endlicheria* densely spaced processes surround and hide the basal cushion of spinules. In *Licaria* the basal cushions are smooth and surrounded by a ring of densely spaced, partially fused processes of varying size and shape, and the general surface of exine is studded with densely spaced granular processes. In *Kubitzkia* the basal cushion of spinules is prominent and surrounded by a ring of densely spaced, partially fused processes of varying size and shape; the general surface of exine is studded with densely spaced, minute processes. Another group of pollen morphological features that distinguish these genera (except *Kubitzkia*, not investigated by TEM) are the ultrastructural details of the sporoderm.

In the classification proposed by Kostermans (1957), *Litsea* is included in subtribe Litseineae of tribe Litseeae. It is closely related to *Umbellularia*, and pollen morphology justifies this relationship. Pollen morphology would thus support the transfer of *Umbellularia* to subtribe Litseineae, corresponding with the classification of Hutchinson (1964) and Richter (1981).

Cryptocarya of tribe Cryptocaryeae, subtribe Cryptocaryineae, is considered isolated among the neotropical genera. Its isolated position is very well reflected in its pollen grains. Its pollen grains are quite different from those of the other genera investigated. The exine surface is devoid of spinules and spinuloid excrescences, instead it appears smooth and wrinkled. The inclusion of this genus by Richter (1981) is his Group I, along with *Beilschmiedia* and *Caryodaphnopsis*, is not supported pollen-morphologically.

Cassytha, of subfamily Cassythoideae, is a parasitic or partially autotrophic twiner. Because of its aberrant habit and ecology, it has often been treated as a separate family, Cassythaceae, but in floral characters it resembles Lauraceae and approaches *Cryptocarya*. The pollen grains of *Cassytha* are characteristic and unlike those of the other genera except *Cryptocarya*, which it resembles in the wrinkled exine surface but from which it differs by the presence of minute, scattered, irregular projections or low warts.

From the above account, pollen characters have been found useful in elucidating relationships of many genera but inadequate to clarify the positions of others. However, in the absence of any clear characters, it is important to assess critically each line of evidence and this we have attempted to do for the palynological data.

The treatment of Laurales in both classical and modern systems of classification is as a considerably old order. Hutchinson (1964) placed Laurales in his Lignoseae, this consisting of woody families. Engler (1936), however, did not consider the order as so primitive—in his view the amentiferous plants were the most ancient dicotyledons. Cronquist (1968) regarded the members of Laurales as rather primitive and placed them in the most primitive order Magnoliales. Takhtajan (1969), while formulating his system, took into account the importance of pollen morphology and considered the Magnoliales as the most primitive order; he accepted Laurales as near Magnoliales but slightly more advanced.

The inaperturate type of pollen grains of Lauraceae are also encountered in some families of Laurales, such as Amborellaceae, Gomortegaceae, Gyrocarpaceae, and Hernandiaceae and in *Sarcandra* (Chloranthaceae), *Hortonia*, *Levieria*, *Peumus*, and *Tambourissa* (Monimiaceae). The rest of lauralean families exhibit apertures that are monosulcate or disulculate or diporate. It is believed that the inaperturate condition is palynologically more advanced than a monosulcate condition from which the former has been derived; Doyle (1969) postulated such derivation on the basis of the Cretaceous pollen record.

Kostermans (1957) postulated a development within the Lauraceae from genera with a very shallow floral tube, where the fruit is not subtended by a cupule (tribe Perseeae), through genera with a deeper floral tube, where the fruit at maturity is subtended by a cupule up to one-third the size of the fruit (tribe Cinnamomeae) and genera with a deep floral tube that fully encloses the fruit (tribe Cryptocaryeae). If the pollen-morphological data are interpreted in relation to this view, *Persea* could be regarded as the most primitive genus because of the large number of spinules; and if the reduction of the number of spinules is interpreted as an advanced trait, *Cryptocarya*, because of the total absence of spinules, would stand out as advanced. Thus these two genera would represent the two extremes, and the remaining genera, because of the intergrading characteristics (size of pollen grains and number of spinules), would fall in between but not necessarily in a phylogenetic sequence. *Cassytha* is the only herbaceous genus that is distinct from the rest of the genera because of its habit. The pollen grains exhibit spinules reduced into minute excrescences, and this suggests a major evolutionary trend. Pollen morphology might provide additional evidence to support separating *Cassytha* into a subfamily of its own.

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LIST OF SPECIES INVESTIGATED

Aiouea Aubl.
  A. costaricensis (Mez) Kosterm.—Costa Rica, *Hartshorn 1121.*
  A. laevis (Mart.) Kosterm.—Venezuela, *Bernardi 7937.*
  A. trinervis Meissn.—Brazil, *Mori 16711.*
Aniba Aubl.
  A. burchellii Kosterm.—Brazil, *Heringer & Eiten 15154.*
  A. canelilla (Kunth) Mez—Brazil, *Heringer et al. 16021.*
  A. firmula (Nees & Mart.) Mez—Brazil, Cult. Bot. Gardn. Rio de Janeiro 110302.
  A. riparia × *A. kappleri*—Venezuela, *L. Marcano Berti 334.*
Beilschmiedia Nees
  B. miersii (Gay) Kosterm.—Chile, *Zöllner 11607.*
  B. pendula (Sw.) Benth.—Panama, *Croat 12928.*
Caryodaphnopsis Airy Shaw
  C. fosteri v. d. Werff—Peru, *Foster 9585.*
Cassytha L.
  C. filiformis L.—Venezuela, *Liesner & Gonzalez 5783.*
Cryptocarya R. Br.
  C. aschersoniana Mez—Brazil, *Hoehne s.n.*
Endlicheria Nees
  E. endlicheriopsis (Mez) Kosterm.—*Maguire 24898a.*
  E. glomerata Mez—Brazil, *Heringer & Eiten 15154.*
  E. paniculata (Spreng.) MacBr. subsp. *poeppigii* (Kosterm.) Koch, ined.—Peru, *Schunke 2924.*
  E. sericea Nees—Brazil, *Ratter et al. 1278.*
  E. tessmannii O. C. Schmidt—Peru, *Croat 20771.*
  E. verticillata Mez—Peru, *Woytkowski 6304.*
Kubitzkia v. d. Werff
  K. mezii (Kosterm.) v. d. Werff—Brazil, *Pires et al. 50919* (NY); Surinam, *Irwin 55719.*
Licaria Aubl.
  L. armeniaca (Nees) Kosterm.—Peru, *Revilla et al. 2571.*
  L. capitata (Schlecht. & Cham.) Kosterm.—Guatemala, *Lundell 15769.*
  L. peckii (I. M. Johnston) Kosterm.—Belize, *Proctor 36035.*
  L. triandra (Sw.) Kosterm.—Venezuela, *Steyermark et al. 122775.*
Litsea Lam.
  L. glaucescens Kunth—Mexico, *Breedlove 33 753.*
Mezilaurus Taubert
  M. navalium (Allemao) Taubert—Brazil, *Glaziou 1212.*
Nectandra Roland. ex Rottb.
  N. acutifolia (Ruiz & Pavon) Mez—Ecuador, *Mexia 8465.*
  N. ambigens (Blake) Allen—Mexico, *Wendt et al. 3190.*
  N. baccans (Meissn.) Mez—Venezuela, *Aristeguieta 7281.*
  N.? cissiflora Nees—Bolivia, *Krukoff 10890.*
  N. coriacea (Sw.) Griseb.—Mexico, *Breedlove 24564.*
  N. cuspidata Nees—Brazil, *Irwin et al. 21038.*
  N. falcifolia (Nees) Castigl.—Argentina, *Krapovickas & Irigoyen 18390.*
  N. gardneri Meissn.—Brazil, *Irwin et al. 16647.*
  N. gentlei Lundell—Panama, *Mori & Kallunki 2996.*
  N. globosa (Aubl.) Mez—Panama, *Croat 7343.*
  N. grandiflora Nees—Brazil, *Hatschbach 32569.*
  N. lanceolata Nees—Argentina, *Schwarz 5103.*
  N. loeseneri Mez—Mexico, *Brigada Vazquez 1575.*
  N. martinicensis Mez—Costa Rica, *Hartshorn 1226*; Venezuela, *Liesner et al. 7927.*
  N. membranacea (Sw.) Griseb.—Costa Rica, *Hartshorn 1753.*
  N. perdubia Lundell—Mexico, *Hinton 13918.*
  N. purpurea (Ruiz & Pavon) Mez—Panama, *Croat 7834.*
  N. reticulata (Ruiz & Pavon) Mez—Mexico, *Dorantes 4176.*
  N. salicifolia (Kunth) Nees—Guatemala, *R. Tun Ortiz 821.*
  N. salicina Allen—Costa Rica, *Koptur SK-103.*
Ocotea Aubl.
  O. calophylla Mez—Colombia, *García-Barriga 20740.*
  O. cernua (Nees) Mez—Belize, *Proctor 36013.*
  O. corymbosa (Meissn.) Mez—Brazil, *Smith et al. 14596.*
  O. cuprea Mez—Peru, *Rimachi 4499.*
  O. dendrodaphne Mez—Costa Rica, *Burch 4589.*
  O. ensifolia Mez—Brazil, *Eiten 10923.*
  O. guianensis Aubl.—Venezuela, *Steyermark 117621.*
  O. ira Mez & Pitt.—Panama, *Lao & Gentry 548.*
  O. kuhlmannii Vattimo—Brazil, *Handro s.n.*
  O. oblonga (Meissn.) Mez—Panama, *Croat 16515.*
  O. puberula Nees—Panama, *Nee & Gentry 8683.*
  O. pulchella Mart.—Brazil, *Hatschbach 20405.*
  O. skutchii Allen—Panama, *Croat 9780.*
  O. spixiana (Nees) Mez—Brazil, *Chagas 332.*
  O. tonduzii Standl.—Costa Rica, *Haber 191.*
  O. veraguensis (Meissn.) Mez—Mexico, *Brigada Dorantes 2881.*
  O. villosa Kosterm.—Brazil, *Ramalho 1863*-RB208640.
  O. whitei Woodson—Panama, *Mori & Kallunki 5625.*
Persea Mill.
  P. americana Miller—Mexico, *Q. Valdivia 176.*
  P. caerulea (Ruiz & Pavon) Mez—Venezuela, *Steyermark 104771.*
  P. fulva Kopp—Brazil, *Irwin et al. 30301.*
  P. mutisii Kunth—Venezuela, *Luteyn & Lebrón-Luteyn 6051.*

- *P. schiedeana* Nees—Panama, *Hammel et al. 6966.*
- *P. veraguasensis* Seem.—Panama, *Tyson 6689.*

Phoebe Nees
- *P. costaricana* Mez & Pittier—Panama, *v. d. Werff 7315.*
- *P. hammeliana* Burger, ined.—Costa Rica, *Hammel 14091.*
- *P. helicterifolia* (Meissn.) Mez—Mexico, *Breedlove 34800.*
- *P. mexicana* Meissn.—Panama, *Croat 14674.*
- *P. porphyria* (Griseb.) Mez—Argentina, *Venturi 7554.*
- *P. smithii* Allen—Costa Rica, *Hartshorn 2130.*

Rhodostemonodaphne Rohwer & Kubitzki
- *R. grandis* (Mez) Rohwer—Venezuela, *Blanci 278.*
- *R. kunthiana* (Nees) Rohwer—Peru, *Croat 19790.*

Pleurothyrium Nees
- *P. densiflorum* A. C. Smith—Peru, *Gentry & Revilla 16627.*
- *P. zulianense* Lasser—Venezuela, *de Bruyn 1422.*
- *P.* sp.—Peru, *Kayap 145.*

Umbellularia Nutt.
- *U. californica* (Hook. & Arn.) Nutt.—U.S.A., Cult. California, Berkeley, *Axelrod s.n.*

THE TAXONOMIC SIGNIFICANCE OF POLLEN MORPHOLOGY IN THE *COLUMNEA* ALLIANCE (GESNERIACEAE: GESNERIOIDEAE)[1]

Karen J. Fritze[2] *and Norris H. Williams*[3,4]

ABSTRACT

Pollen of 67 species of the five genera of the Columnea *alliance (Gesneriaceae: Gesnerioideae) was examined to assess its value in generic classifications. Several distinct groups of pollen can be recognized by pollen shape, pattern of exine sculpturing, and shape and size of the colpus.* Columnea *sensu stricto has a peculiar pollen type supporting its treatment as distinct from the other four genera of the alliance.* Bucinellina *is also distinct from the other genera, and its status as a genus is likewise supported. Pollen structure does not confirm the distinctiveness of* Trichantha, Pentadenia, *and* Dalbergaria *and may be used better at the sectional rather than the generic level.*

The mainly tropical family Gesneriaceae contains over 2,800 species. A large influx of collections of newly discovered species from the American tropics has cast doubts on some traditional generic limits in the exclusively neotropical subfamily Gesnerioideae. Parallel adaptations to certain classes of pollinators have become apparent and complicate the efforts of taxonomists. Taking this into consideration, Wiehler (1983) proposed new generic and tribal limits for the Gesnerioideae and a new subfamily (Coronantheroideae). His work parallels Burtt's (1963) for subfamily Cyrtandroideae, and it is in the context of Wiehler's classification that this study was done.

The *Columnea* alliance (tribe Episcieae) is a natural group of closely related genera that share ornithophily as the pollinator syndrome. The alliance comprises over 240 species in five genera: *Pentadenia* Hanst. (ca. 30 species), *Dalbergaria* Tussac (ca. 90 species), *Trichantha* Hook. (ca. 70 species), *Bucinellina* Wiehler (2 species), and *Columnea* L. (ca. 75 species, Wiehler, 1983). One of the main taxonomic problems in the Episcieae is the disposition of these taxa. Should species distributed variously in several groups formerly regarded as sections of *Columnea* in the broad sense be given generic status, or should they be treated as subgeneric groups of *Columnea*? Morley (1976), who based his conclusions mainly on cytological and hybridization results of Sherk & Lee (1967) and Moore & Lee (1967), disputed treating them as distinct genera. Morton, who worked with *Trichantha* and *Columnea* for a number of years, first lent support to the concept of the

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genus *Trichantha* (Morton, 1963) but later reversed his opinion (Morton, 1971). He found that the appendages in the sinuses between corolla lobes that distinguished his concept of *Trichantha* from other taxa were rudimentary throughout the complex. However, Wiehler (1983) maintained that on the basis of several important characters, *Trichantha* and the other four genera are as distinct from one another as from any other genera in the tribe and therefore should be given generic status.

Among the characters Wiehler (1973) considered most important in arriving at generic limits within the *Columnea* alliance and in other Episcieae are fruit type, number of nectary glands present and their degree of dorsal connation, plant habit, and corolla shape. The importance of corolla shape is a source of debate in the classification of the *Columnea* alliance. Within this group, generic limits based on corolla morphology are vague. Although he used it as a convenient means for separating certain genera, Wiehler de-emphasized corolla shape in his overall classification of the subfamily, since it appears to be an adaptation to a pollinator class and is not necessarily indicative of close relationships among taxa. In other words, it is of taxonomic use in separating species but contributes little to an evaluation of systematic relationships. Morley (1973, 1974, 1976), however, believed that degree of corolla zygomorphy is correlated with degree of crossability and is therefore important to classification in the *Columnea* alliance.

Five separate nectary glands distinguish *Pentadenia* from the rest of the Episcieae. All other genera in the Episcieae possess glands which vary in degree of reduction and dorsal connation even within species (Wilson, 1974). In the *Columnea* alliance (except *Pentadenia*) the nectary consists solely of a large double dorsal gland.

The "fern-frond" habit (or extreme anisophylly) makes *Dalbergaria* distinct in the alliance (Wiehler, 1971). Plant habit varies within other genera of the *Columnea* alliance.

Fruit type in the Episcieae is a valuable suprageneric character. It separates the *Drymonia* complex from the *Episcia* complex, the two having different types of capsules, and separates both from the *Columnea* alliance, which has a berry. Within the *Columnea* alliance genera differ with respect to fruit shape and color. Subtle differences in shape create some skepticism regarding its reliability (Morley, 1976).

Published studies of gesneriaceous pollen are mainly morphological and make little mention of the taxonomic implications. Woods (1964) studied 180 species in over 50 genera and made a distinction between Burtt's subfamilies based on pollen-wall sculpturing and grain size. Uniform or homobrochate exines are more prevalent in the Cyrtandroideae; heterobrochate exines are more prevalent in the Gesnerioideae. Grains tend to be larger in the Gesnerioideae than in the Cyrtandroideae.

Erdtman (1966) surveyed 20 species from 17 genera of the Gesneriaceae with the light microscope and supplied a diagram of *Columnea microphylla* pollen. Melhem & Mauro (1973) obtained data on eight local species from three genera in São Paulo, Brazil. Based on their observations and those of Erdtman, they concluded that there was great variation of pollen types in the family. They remarked only on morphological distinctions among pollen of these species and included no taxonomic interpretations.

Skog (1976), in his taxonomic treatment of the tribe Gesnerieae, presented a brief discussion of his observations on the grains of 27 examples. He made use of the scanning electron microscope, but little information could be obtained from his micrographs other than sculpturing patterns, since the pollen grains were collapsed.

The absence of pollen data from Wiehler's (1973) study prompted a preliminary SEM survey by Williams (1978) of 30 species representing 19 genera to ascertain whether or not pollen might be of use in further clarifying systematic relationships in the Gesnerioideae. Williams (1978) found a wide variety of forms in the Gesneriaceae, particularly in tribe Epi-

TABLE 1. *Species examined.*

Species	Greenhouse Accession Number	Origin
Columnea arguta C. Morton	G-979 SEL	Panama
C. bilabiata Seemann	W-2233 SEL	Colombia
C. billbergiana Beurling	W-1166 SEL	Panama
C. cobana F. D. Smith	W-2056 SEL	Guatemala
C. dodsonii Wiehler	W-1500 SEL	Ecuador
C. dressleri Wiehler	W-2176 SEL	Panama
C. erythrophaea Decne.	G-1057 SEL	Mexico
C. flaccida Seemann	G-327 SEL	Panama
C. gallicauda Wiehler	W-2179 SEL	Panama
C. gloriosa Sprague	W-2131 SEL	Panama
C. guatemalensis Sprague	W-2055 SEL	Guatemala
C. hirsutissima C. Morton	W-2132 SEL	Panama
C. kienastiana Regel	W-1694 SEL	Colombia
C. kucyniakii Raym.	W-2020 SEL	Ecuador
C. linearis Oersted	G-325 SEL	Costa Rica
C. maculata C. Morton	W-2262 SEL	Panama
C. nicaraguensis Oersted	W-2641 SEL	Panama
C. oerstediana Klotzsch ex Oersted	W-2270 SEL	Panama
C. purpusii Standley	G-1209 SEL	Mexico
C. querceti Oersted	W-2641 SEL	Costa Rica
C. repens (Hook.) Hanst.	G-920 SEL	Jamaica
C. rubra C. Morton	W-2236 SEL	Panama
C. rubricaulis Standley	W-2328 SEL	Nicaragua
C. rutilans Sw.	G-843 SEL	Jamaica
C. schiedeana Schldl.	G-725 SEL	Mexico
C. verecunda C. Morton	G-87 SEL	Costa Rica
C. zebranella Wiehler	W-1595 SEL	Panama
Dalbergaria asteroloma Wiehler	W-2247 SEL	Ecuador
D. aureonitens (Hook.) Wiehler	W-1818 SEL	Venezuela
D. cruenta (Morley) Wiehler	W-1146 SEL	Panama
D. eburnea Wiehler	W-1704 SEL	Colombia
D. ericae (Mansf.) Wiehler	W-1630 SEL	Ecuador
D. florida (C. Morton) Wiehler	W-1622 SEL	Panama
D. inaequilatera (Poeppig) Wiehler	W-2036 SEL	Ecuador
D. kahlbreyeriana (Masters) Wiehler	W-1590 SEL	Colombia
D. perpulchra (C. Morton) Wiehler	W-1572 SEL	Panama
D. picta (Karsten) Wiehler	W-1794 SEL	Colombia
D. polyantha Wiehler	W-1152 SEL	Panama
D. puyana Wiehler	W-2040 SEL	Ecuador
D. sanguinea (Pers.) Steudel	W-1709 SEL	Panama
D. sanguinea (Pers.) Steudel	G-85 SEL	Hispaniola
D. sanguinea (Pers.) Steudel	W-1628 SEL	Panama
D. silvarum (C. Morton) Wiehler	W-2450 SEL	Panama
D. vittata Wiehler	W-2265 SEL	Panama
Pentadena augustata Wiehler	W-2185 SEL	Costa Rica
P. byrsina Wiehler	W-2138 SEL	Ecuador
P. ecuadorana Wiehler	W-1894 SEL	Ecuador
P. microsepala (C. Morton) Wiehler	W-1837 SEL	Venezuela
P. nervosa Kl. ex Oersted	W-1948 SEL	Panama
P. orientandina Wiehler	W-2273 SEL	Ecuador
P. spathulata (Mansf.) Wiehler	W-1955 SEL	Ecuador
P. strigosa (Benth.) Hanst.	W-4128 SEL	Colombia
P. zapotaliana Wiehler	W-2167 SEL	Ecuador
Trichantha ambigua (Urban) Wiehler	G-804 SEL	Puerto Rico

TABLE 1. *Continued.*

Species	Greenhouse Accession Number	Origin
T. brenneri Wiehler	W-2275 SEL	Ecuador
T. calotrica (F. D. Smith) Wiehler	W-2181 SEL	Panama
T. citrina Wiehler	W-2451 SEL	Panama
T. dissimilis (C. Morton) Wiehler	W-1177 SEL	Panama
T. filifera Wiehler	W-1631 SEL	Colombia
T. herthae (Mansf.) Wiehler	W-1573 SEL	Ecuador
T. minor Hook.	W-1685 SEL	Colombia
T. mira (Morley) Wiehler	W-1586 SEL	Panama
T. moorei (C. Morton) C. Morton	W-2193 SEL	Panama
T. parviflora (C. Morton) Wiehler	W-1993 SEL	Panama
T. pulchra Wiehler	W-2368 SEL	Panama
T. purpureovittata Wiehler	W-1721 SEL	Peru
T. tenensis Wiehler	W-1585 SEL	Ecuador
Bucinellina nariniana (Wiehler) Wiehler	W-1642 SEL	Colombia
B. paramicola (Wiehler) Wiehler	W-1634 SEL	Colombia

scieae. Fritze (1979) found the diversity of pollen to be of potential taxonomic use in the *Columnea* alliance, and Williams (1978) introduced a successful technique for preparing gesneriaceous pollen that shows expanded, clean grains and allows full observation of all external features.

MATERIALS AND METHODS

Pollen was collected from mature anthers of living plants grown in the greenhouses at the Marie Selby Botanical Gardens, Sarasota, Florida (Table 1). The pollen was acetolyzed following a modified method of Erdtman (1966) and was stored in 70% ethyl alcohol (EtOH). Slides for vouchers were made from which sizes and shapes of pollen grains could be determined. Measurements of the lengths of the polar and equatorial axes of 50 grains per species of representative species were made at 400× using an ocular micrometer. Pollen for the scanning electron microscope (SEM) was dehydrated through an alcohol series followed by an amyl acetate/EtOH series (1 : 3, 1 : 1, 3 : 1, 100% amyl acetate). A drop of suspended pollen was then placed on a round glass coverslip and attached to an SEM stub with double-sided tape. The pollen was air dried under a cover to prevent contamination. Dried pollen was coated with 5 nm of gold palladium and scanned with a Cambridge Stereoscan model S4-10 instrument at 5, 10, or 20 kV. Fractured pollen was also viewed with the SEM. Pollen was transferred from the original SEM stub to a second stub fitted with a piece of double-sided tape covering the entire surface. Transfer was accomplished by touching the two stubs together until the pollen adhered to the tape. The process was repeated using a third stub with double-sided tape on it, which was pressed against the second stub. The adhesion of the pollen grains to both stubs pulled the grains apart. This procedure requires no elaborate microtomy and yields replicates with no loss of material. The fractured grains were recoated and scanned. Photographs were taken using Type 665 Positive/Negative Land film with a Polaroid camera mounted on the microscope, and negatives were later contact printed.

NOTE ON TERMINOLOGY

Terminology used for the apertures, shape, and areas of the surface of the pollen grain follows Erdtman (1966). Since Erdtman's terms do not extend to the detail of exine sculpturing revealed by the SEM, it is necessary to make a precise distinction between the punctate and reticulate patterns found in the *Columnea* alliance. An exine is punctate if the tectum is perforate and the majority of the perforations are much smaller in diameter than the width of the muri (remnants of the tectum). The exine is reticulate if the punctae are enlarged (lumina) and at least as wide as the muri. A long aperture extends beyond half the distance from the equatorial margin of the grain to the polar axis when seen in polar view (Fig. 2E). An aperture of intermediate length reaches about one-half this distance (Fig. 8C), and a short aperture extends less than half this distance (Fig. 12G, H). Terms describing exine structure follow Walker (1974a)

RESULTS AND OBSERVATIONS

Several pollen types appeared with some overlap among genera. Types are distinguished mainly by shape, exine pattern, and aperture length and shape. All grains are monads, isopolar, and tricolp(or)ate, and either punctate or reticulate. Their sizes, based on the length of the longest axis, range from approximately 28 to 51 μm. The features are summarized for each species in Table 2.

By far the greatest homogeneity turned up in *Columnea*, in which 26 species were examined (Figs. 1, 2, 3, 4, 5A–C). With the exception of three species, all have subprolate to spheroidal grains (see P/E, Table 2) with uniformly punctate exine, long, elliptic apertures, and circular ambs. There are slight differences in size and shape of punctae and apertures between species. *Columnea repens* and *C. rutilans* (Fig. 5B, C) stand apart by having suboblate or oblate grains, exine reticulate grading to punctate adjacent to the colpi and at the polar regions, tapered apertures, and triangular ambs. *Columnea kucyniakii* has suboblate grains, exine reticulate grading to punctate adjacent to the colpi and poles, long, sharply tapered apertures, and triangular ambs.

The majority of the 15 *Dalbergaria* species examined (Figs. 5D–H, 6, 7, 8) have grains distinct from those of *Columnea*. Those of the former are suboblate and have the exine reticulate grading to punctate adjacent to the colpi and at the poles, long, sharply tapered apertures, and angularaperturate, circular or triangular ambs. *Dalbergaria aureonitens*, *D. sanguinea*, and *D. florida* (Fig. 8) do not fit the general pattern; they have pollen suboblate to spheroidal, reticulate (as above, but

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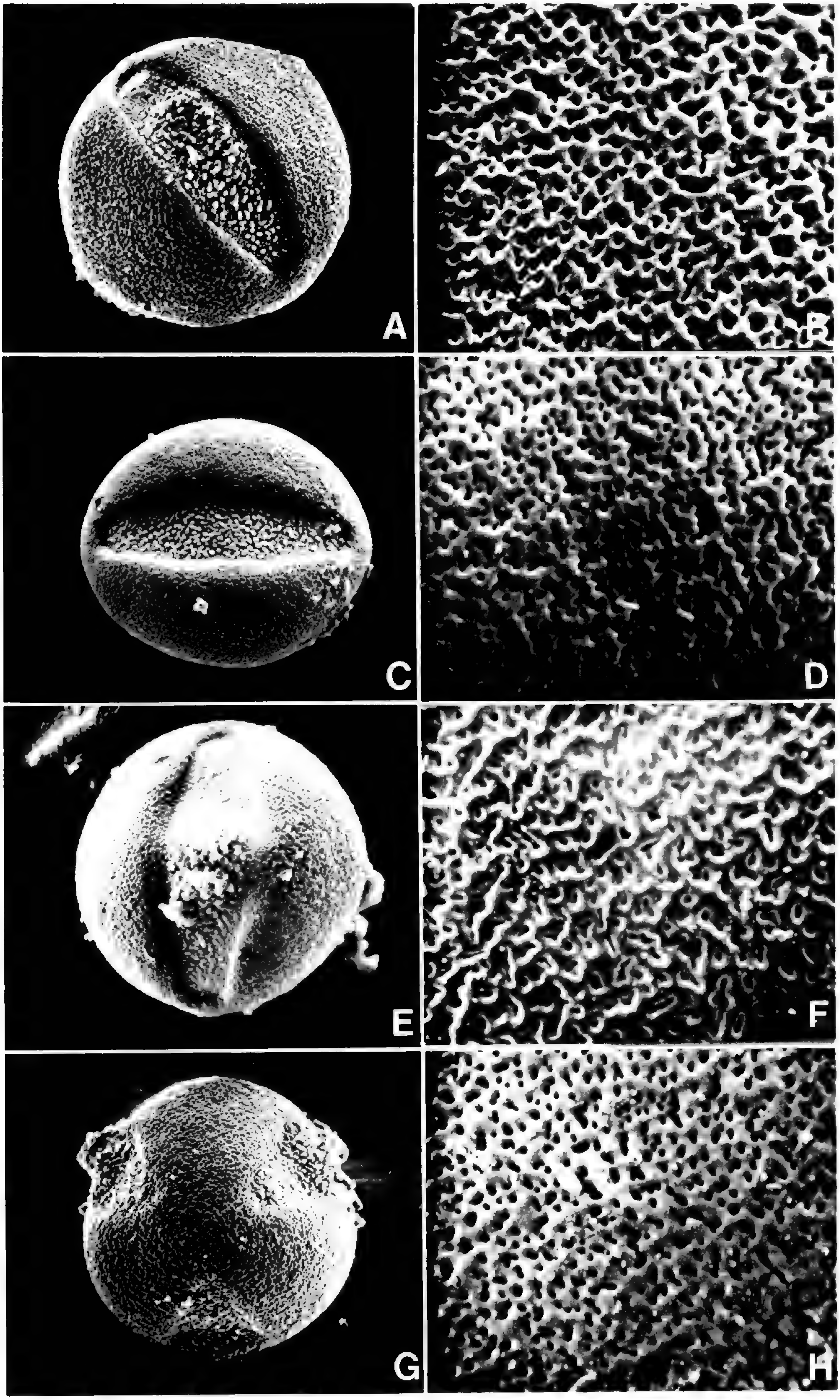
FIGURE 1.—*A.* Columnea schiedeana, *equatorial view; ×1,550.*—*B.* C. schiedeana, *mesocolpial region; ×7,333.*—*C.* C. verecunda, *equatorial view; ×1,550.*—*D.* C. verecunda, *mesocolpial region; ×7,333.*—*E.* C. querceti, *equatorial view; ×1,387.*—*F.* C. querceti, *mesocolpial region; ×7,333.*—*G.* C. purpusii, *polar view; ×1,500.*—*H.* C. purpusii, *mesocolpial region; ×7,333.*

FIGURE 2.—*A.* Columnea arguta, *equatorial view; ×1,300.*—*B.* C. arguta, *at end of colpus; ×5,717.*—*C.* C. guatemalensis, *equatorial view; ×1,333.*—*D.* C. guatemalensis, *mesocolpial region; ×6,833.*—*E.* C. cobana, *polar view; ×1,383.*—*F.* C. cobana, *mesocolpial region; ×7,000.*—*G.* C. kienastiana, *polar view; ×1,500.*—*H.* C. kienastiana, *mesocolpial region; ×8,000.*

FIGURE 3.—*A.* Columnea linearis, *equatorial view; ×1,567.*—*B.* C. linearis, *mesocolpial region; ×7,333.*—*C.* C. hirsutissima, *polar view; ×1,433.*—*D.* C. hirsutissima, *mesocolpial region; ×6,867.*—*E.* C. dressleri, *equatorial region; ×1,333.*—*F.* C. dressleri, *mesocolpial region; ×6,667.*—*G.* C. dodsonii, *equatorial view; ×7,833.*—*H.* C. dressleri, *exine fracture through mesocolpial region; ×10,000.*

FIGURE 4.—*A.* Columnea gallicauda, *equatorial view; ×1,383.*—*B.* C. zebranella, *polar view; ×1,687.*—*C.* C. flaccida, *equatorial view; ×1,483.*—*D.* C. rubricaulis, *equatorial view; ×1,383.*—*E.* C. oerstediana, *equatorial view; ×1,307.*—*F.* C. bilabiata, *polar view; ×1,467.*—*G.* C. rubra, *polar view; ×1,433.*—*H.* C. erythrophaea, *polar view; ×1,500.*

FIGURE 5.—*A.* Columnea billbergiana, *equatorial view; ×1,316.*—*B.* C. repens, *polar view; ×1,233.*—*C.* C. rutilans, *polar view; ×1,300.*—*D.* Dalbergaria silvarum, *polar view; ×1,493.*—*E.* D. puyana, *polar view; ×1,733.*—*F.* D. polyantha, *polar view; ×1,450.*—*G.* D. asteroloma, *polar view; ×1,350.*—*H.* D. ericae, *exine fracture through colpus; ×8,000.*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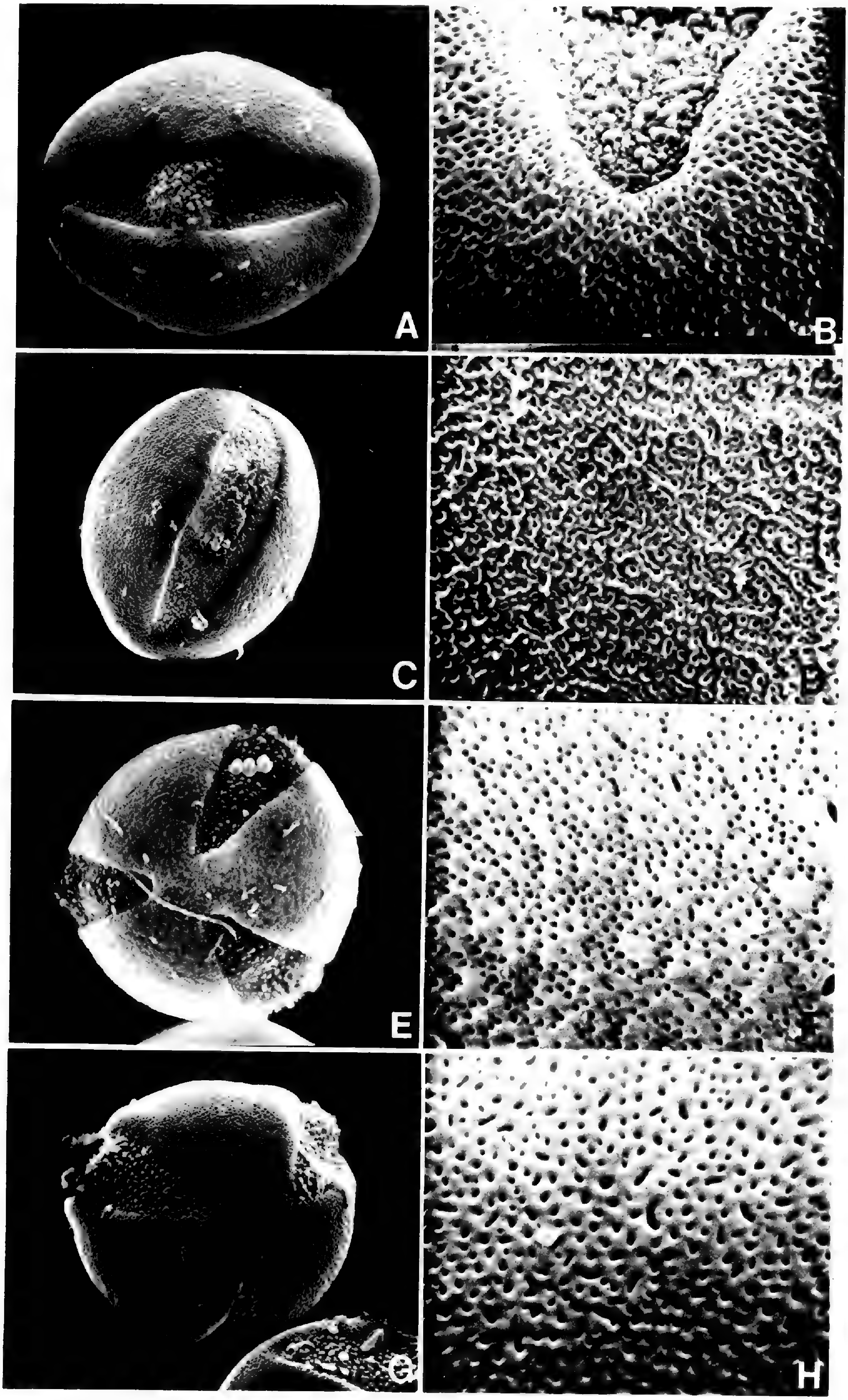
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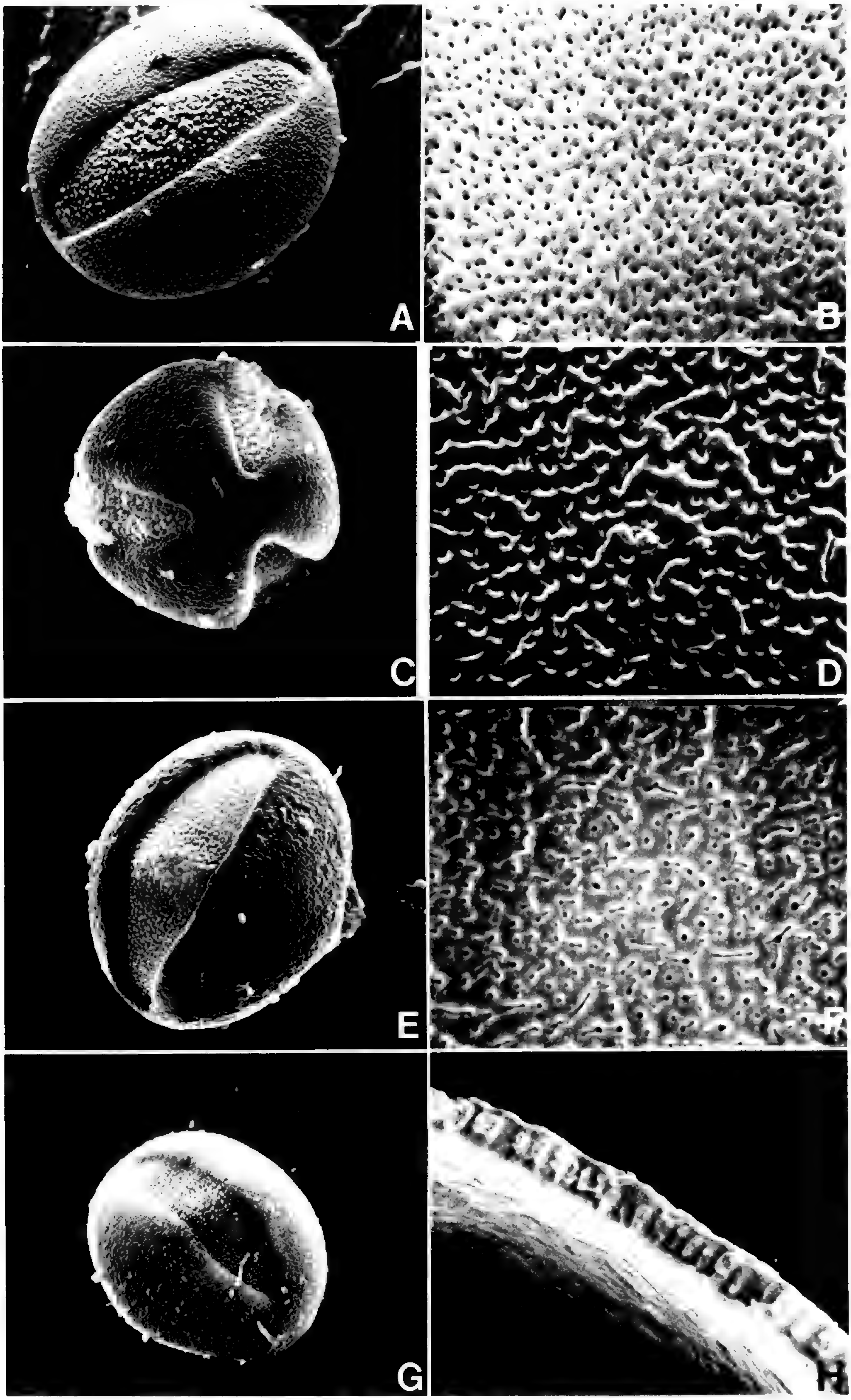
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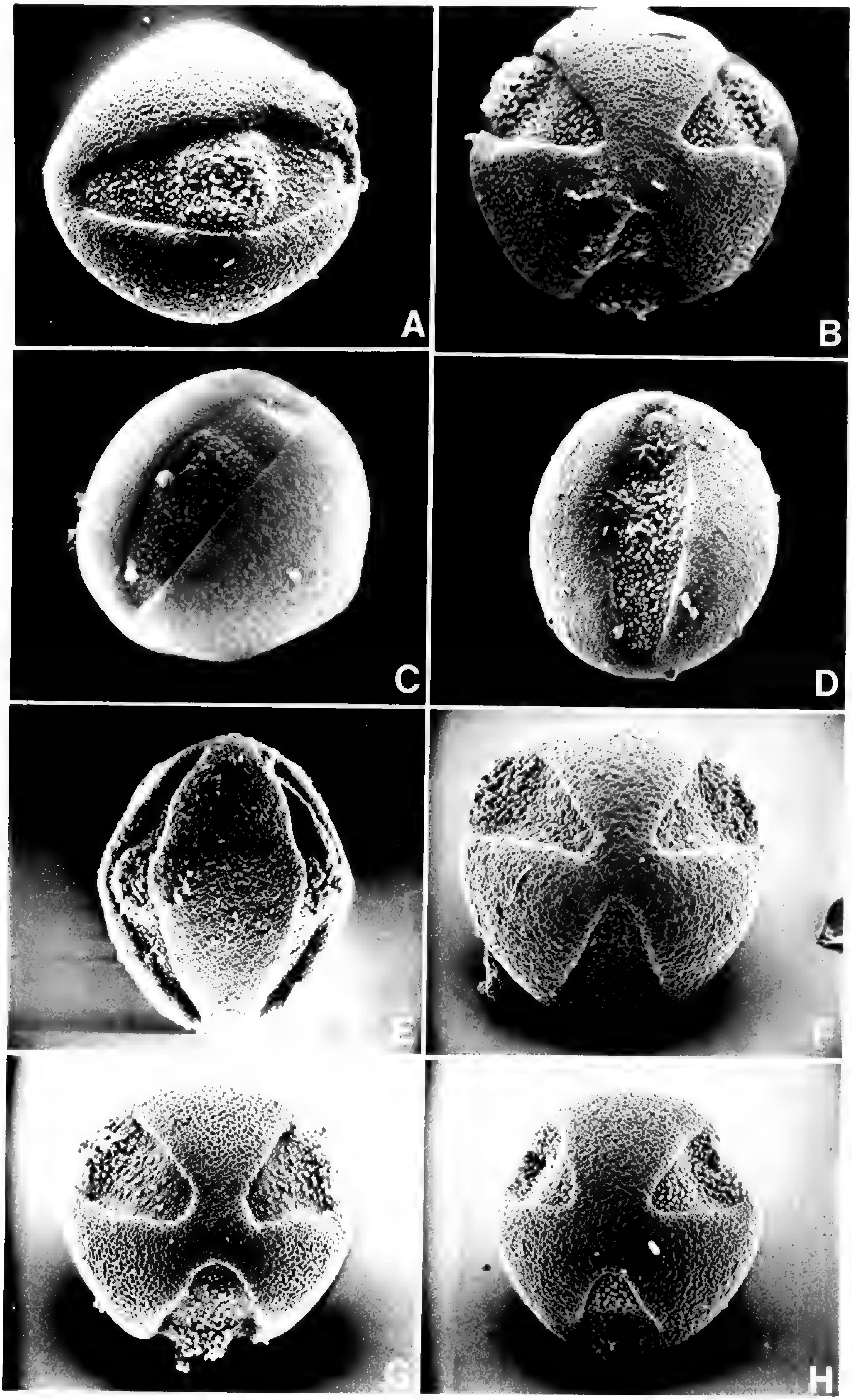
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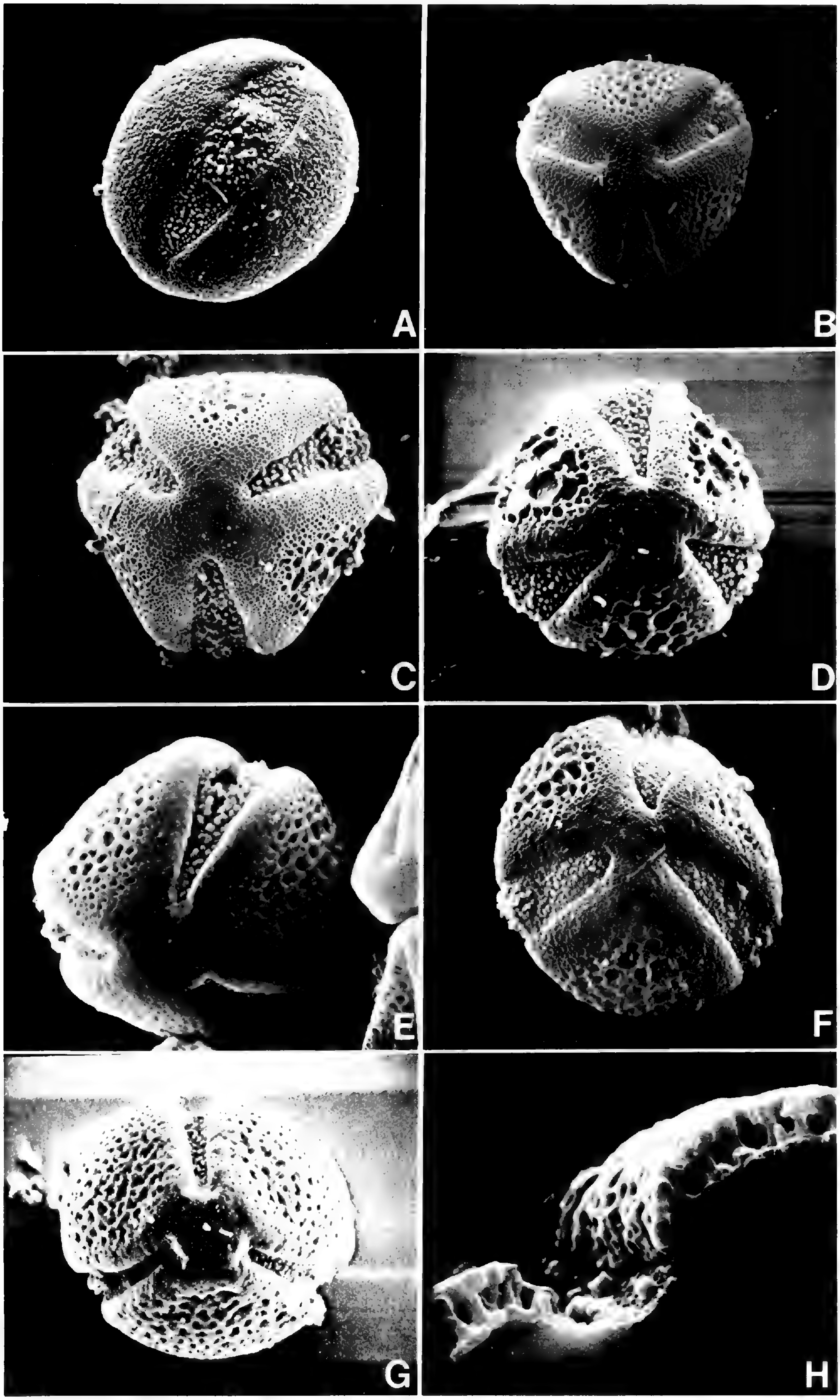
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the reticulation not reduced to punctae at the poles), and with the colpi more elliptic, these of intermediate length. *Dalbergaria eburnea* (Fig. 7E, F) and *D. asteroloma* (Fig. 5G) grains are suboblate to spheroidal with the tectum nearly punctate, tectal perforations near the colpi and at the poles reduced in size or absent, and the apertures narrow.

Three distinct types of pollen are found within *Trichantha* (15 species examined). One type (Figs. 9A–G, 10E) is suboblate with a reticulate exine becoming punctate adjacent to the colpi and at the poles and has long apertures widest at the equator and a triangular amb. These grains resemble pollen of *Dalbergaria* and *Pentadenia orientandina. Tricantha ambigua*, a tetraploid, has pollen of this type but with four apertures (Fig. 10C). A second type of pollen with short colpi (Fig. 10A, B, G, H) is oblate to spheroidal, reticulate, and punctate around the colpi with intermediate elliptic apertures; this type has a somewhat triangular amb. The third type (Fig. 11A–D) is suboblate and punctate, and has very short oval apertures (almost like pores); its amb is circular to slightly triangular.

Most species of *Pentadenia* (9 species examined) possess suboblate to oblate grains that are reticulate, becoming punctate adjacent to the colpi but remain reticulate at the poles; they have either short or intermediate apertures and somewhat triangular ambs (Figs. 12A–H, 13C, D). *Pentadenia ecuadorana* (Fig. 12C, D), *P. microsepala* (Fig. 12E, F), and *P. angustata* (Fig. 13C) grains have narrow apertures of intermediate length, but the apertures are widest at the equator. Grains of *Pentadenia spathulata* (Fig. 12G) and *P. zapotalana* (Fig. 12H) have short elliptic apertures. *Pentadenia orientandina* pollen (Fig. 13A, B) is suboblate and reticulate, grading to punctate at the poles and adjacent to the colpi; it has long luminal baculae, long apertures tapered at the poles, and circular ambs. It stands apart from other pentadenias and resembles some *Trichantha* pollen types (e.g., Fig. 9). *Pentadenia strigosa* (Fig. 13E, F) pollen shows a combination of features found nowhere else in the *Columnea* alliance. The pollen is suboblate and reticulate with long luminal baculae, and the reticulum is neither reduced at the poles nor around the colpi. It has long, elliptic, slightly tapered apertures and a circular amb.

Bucinellina, with only two species (Fig.

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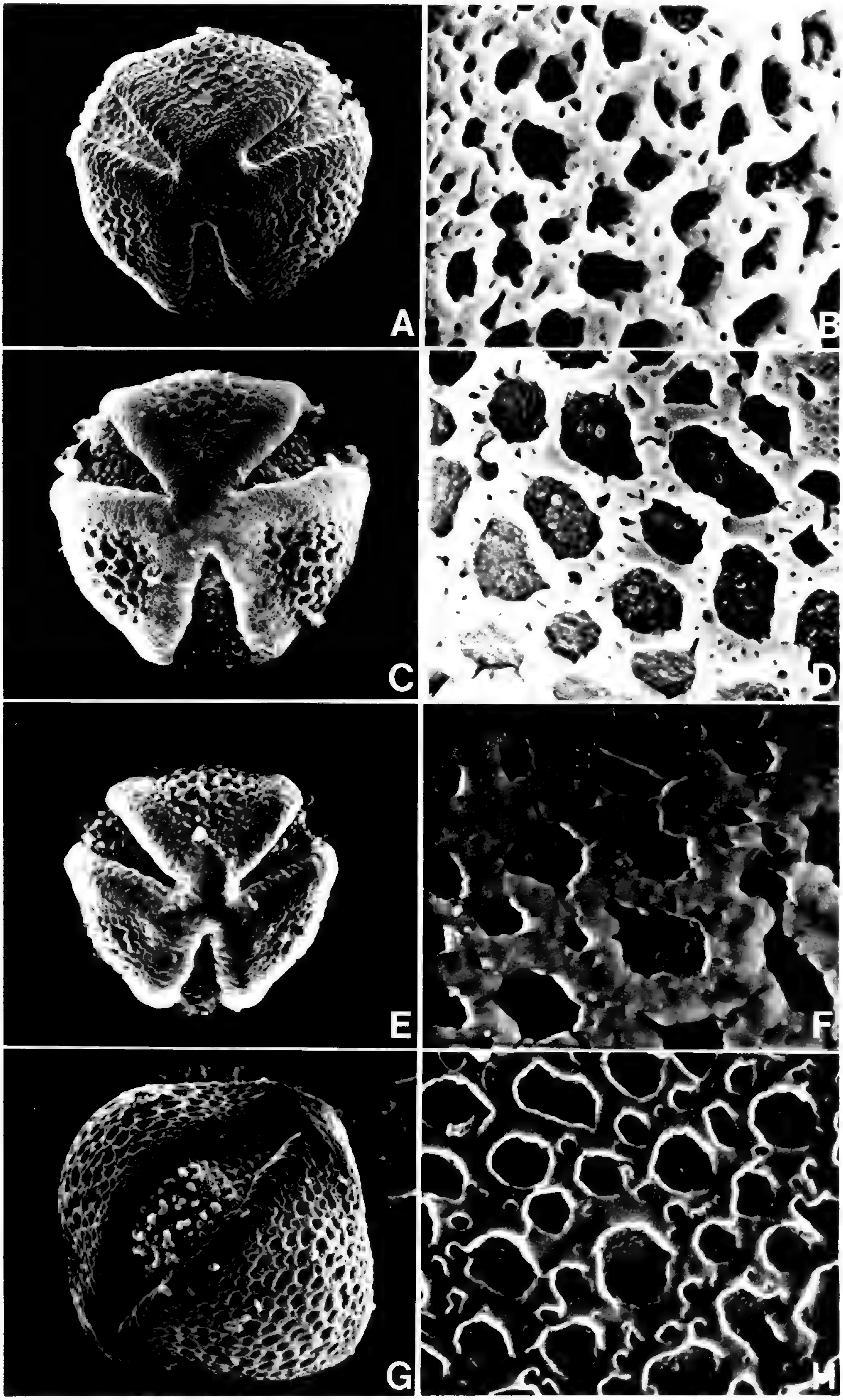
FIGURE 6.—*A*. Dalbergaria cruenta, *polar view;* ×*1,516*.—*B*. D. cruenta, *mesocolpial region;* ×*7,333*.—*C*. D. kahlbreyeriana, *polar view;* ×*1,383*.—*D*. D. kahlbreyeriana, *mesocolpial region;* ×*6,667*.—*E*. D. perpulchra, *polar view;* ×*1,500*.—*F*. D. perpulchra, *mesocolpial region;* ×*7,500*.—*G*. D. inaequilatera, *equatorial view;* ×*1,833*.—*H*. D. inaequilatera, mesocolpial region; ×6,000.

FIGURE 7.—*A*. Dalbergaria vittata, *polar view;* ×*1,500*.—*B*. D. vittata, *mesocolpial region;* ×*7,333*.—*C*. D. ericae, *equatorial view;* ×*1,400*.—*D*. D. ericae, *mesocolpial region;* ×*7,000*.—*E*. D. eburnea, *equatorial view;* ×*1,500*.—*F*. D. eburnea, *mesocolpial region;* ×*7,500*.—*G*. D. picta, *polar view;* ×*1,367*.—*H*. D. picta, *adjacent to aperture;* ×*6,833*.

FIGURE 8.—*A*. Dalbergaria florida, *polar view;* ×*1,367*.—*B*. D. florida, *mesocolpial region;* ×*6,833*.—*C*. D. sanguinea, *(W-1628) polar view;* ×*1,833*.—*D*. D. sanguinea, *(W-1628) mesocolpial region;* ×*7,500*.—*E*. D. sanguinea, *(G-85) polar view;* ×*1,517*.—*F*. D. sanguinea, *(W-1709) polar view;* ×*1,443*.—*G*. D. aureonitens, *polar view;* ×*1,510*.—*H*. D. aureonitens, *exine fracture through mesocolpial region;* ×*5,000*.

FIGURE 9.—*A*. Trichantha tenensis, *polar view;* ×*1,333*.—*B*. T. brenneri, *polar view;* ×*1,250*.—*C*. T. purpureovittata, *polar view;* ×*1,233*.—*D*. T. citrina, *equatorial view;* ×*1,383*.—*E*. T. mira, *polar view;* ×*1,383*.—*F*. T. moorei, *equatorial view;* ×*1,283*.—*G*. T. minor, *polar view;* ×*1,200*.—*H*. T. calotricha, *exine fracture through mesocolpial region;* ×*4,833*.

FIGURE 10.—*A*. Trichantha filifera, *polar view;* ×*1,117*.—*B*. T. dissimilis, *polar view;* ×*1,100*.—*C*. T. ambigua, *polar/equatorial view;* ×*1,200*.—*D*. T. ambigua, *mesocolpial region;* ×*6,000*.—*E*. C. kucyniakii, *polar view;* ×*1,483*.—*F*. C. kucyniakii, *mesocolpial region;* ×*7,333*.—*G*. T. calotricha, *polar view;* ×*1,150*.—*H*. T. calotricha, *mesocolpial region;* ×*6,000*.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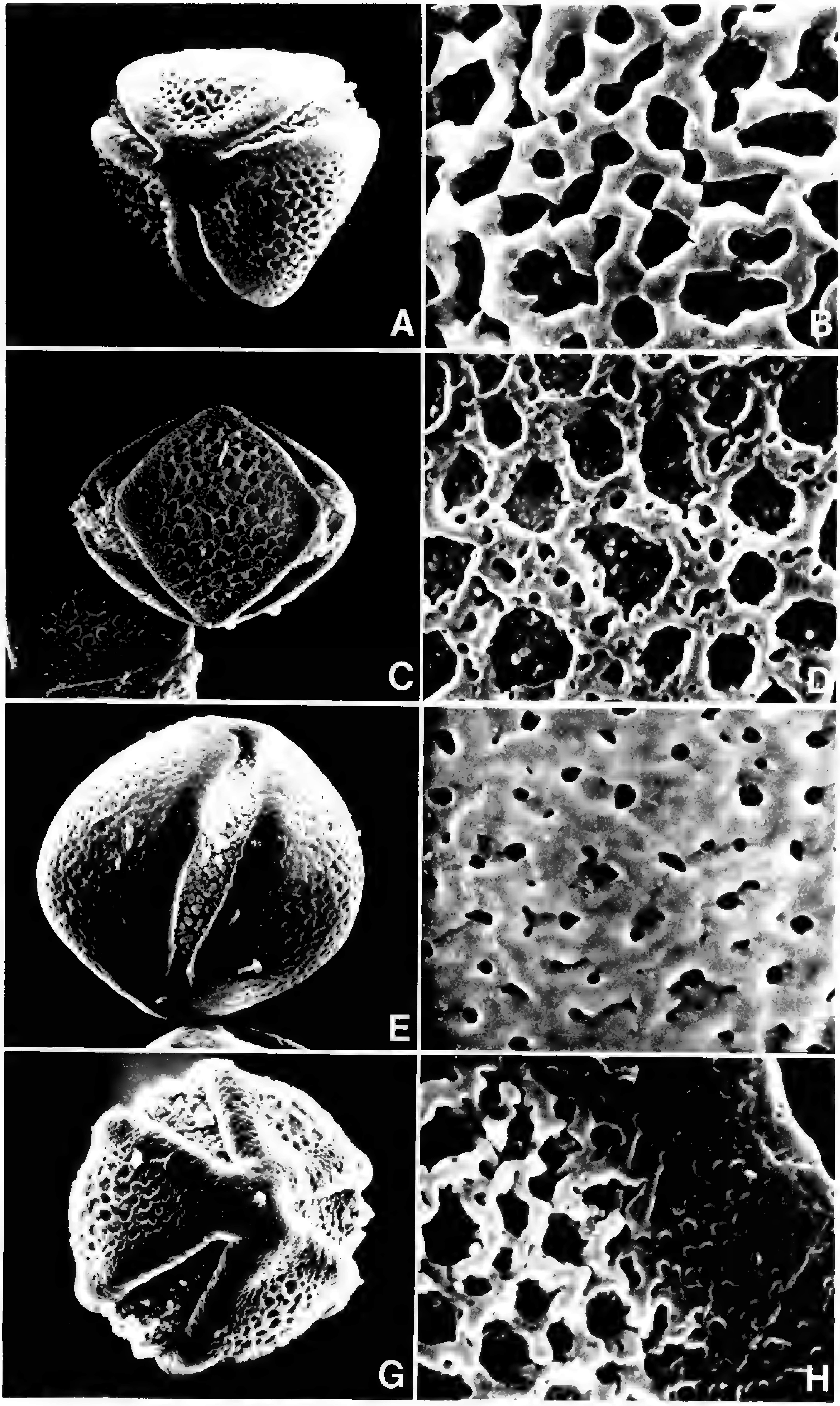
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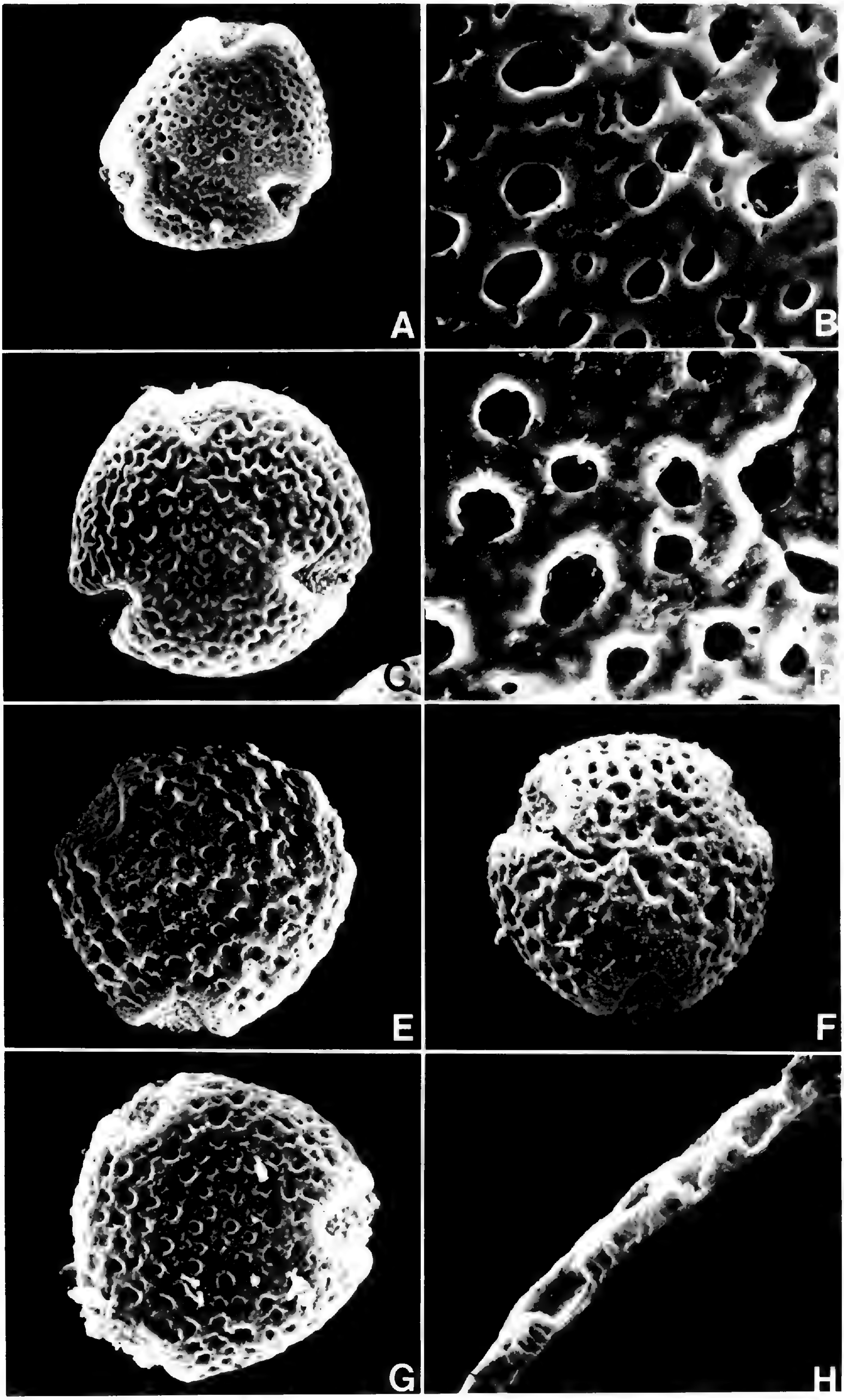
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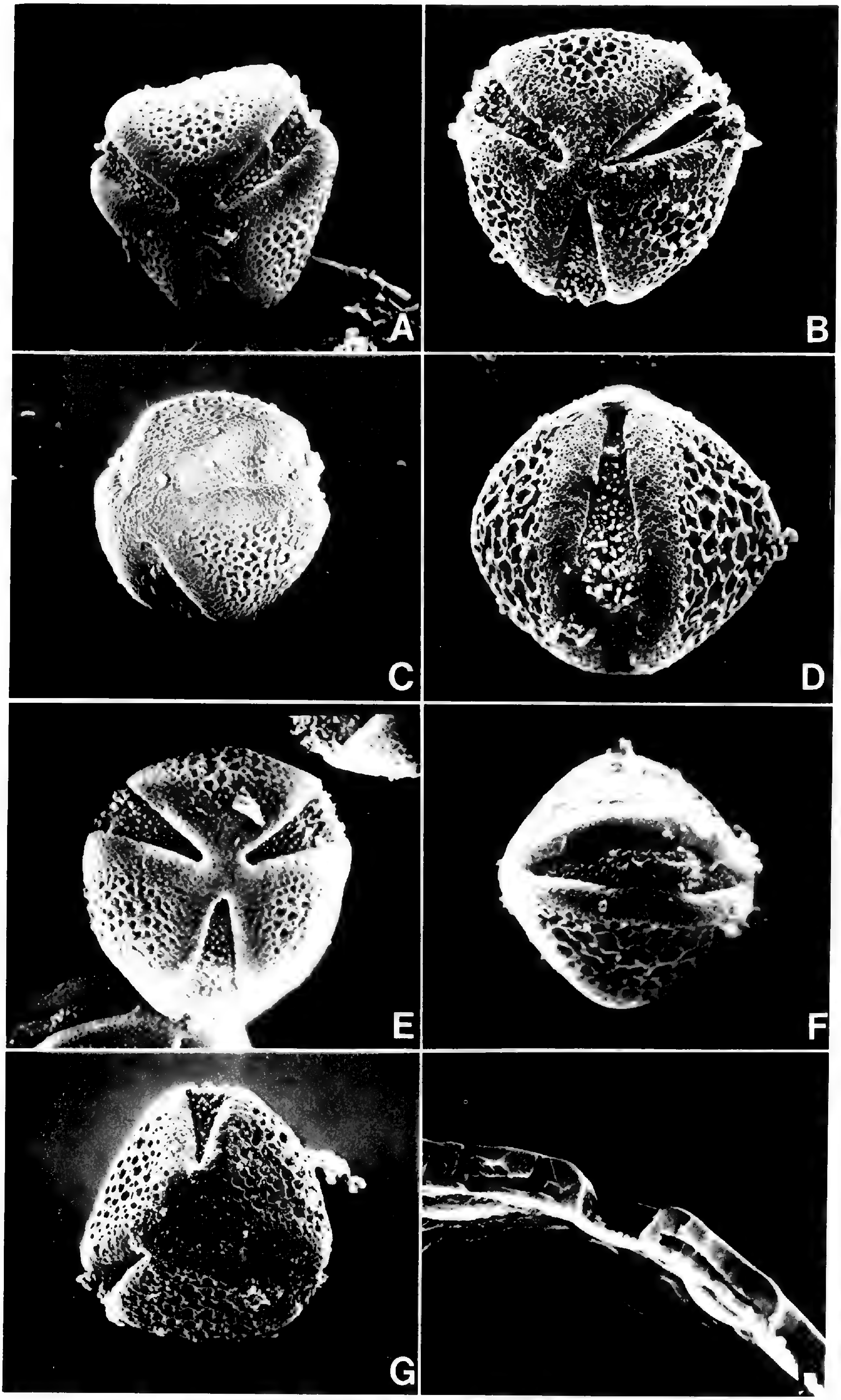
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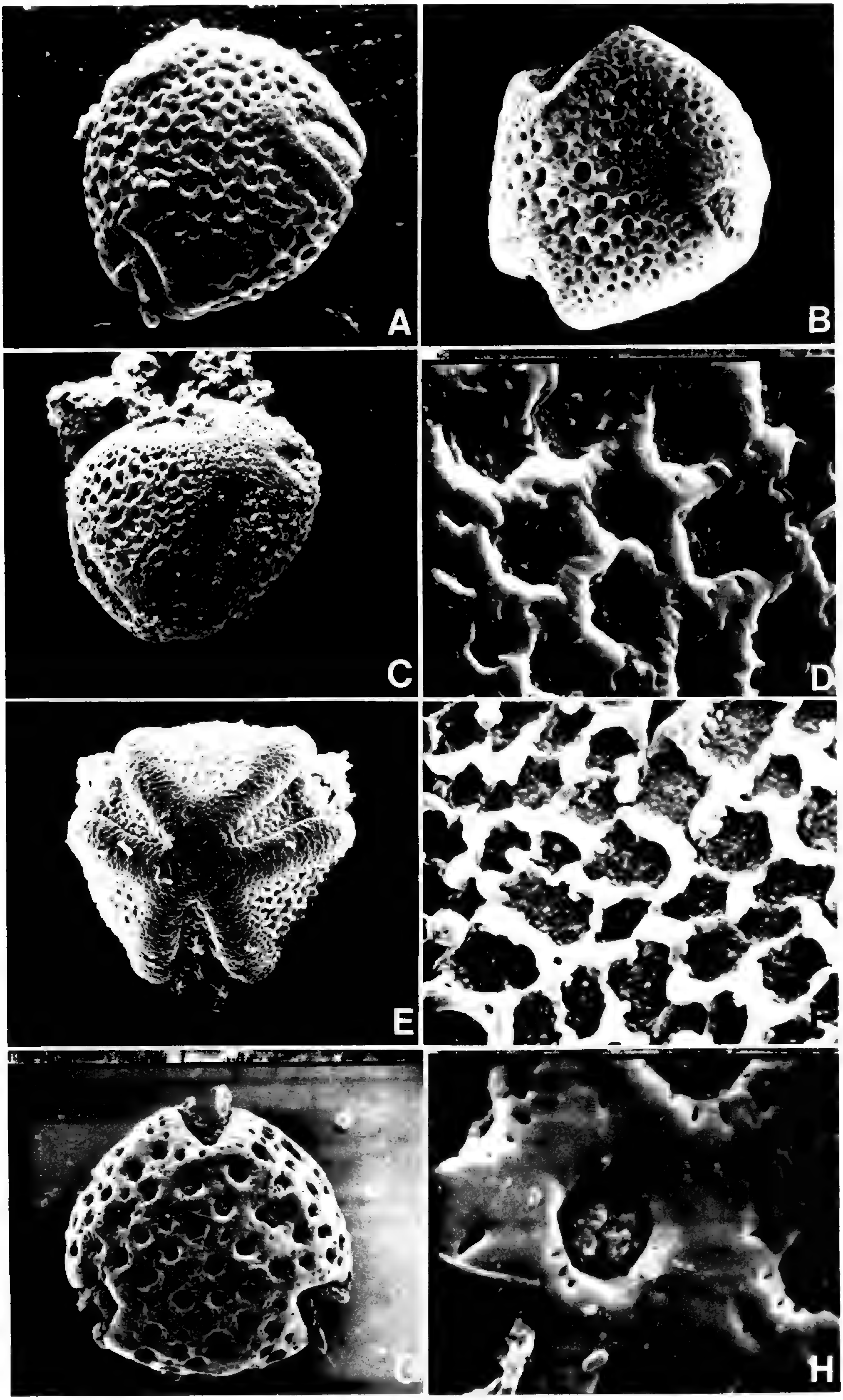
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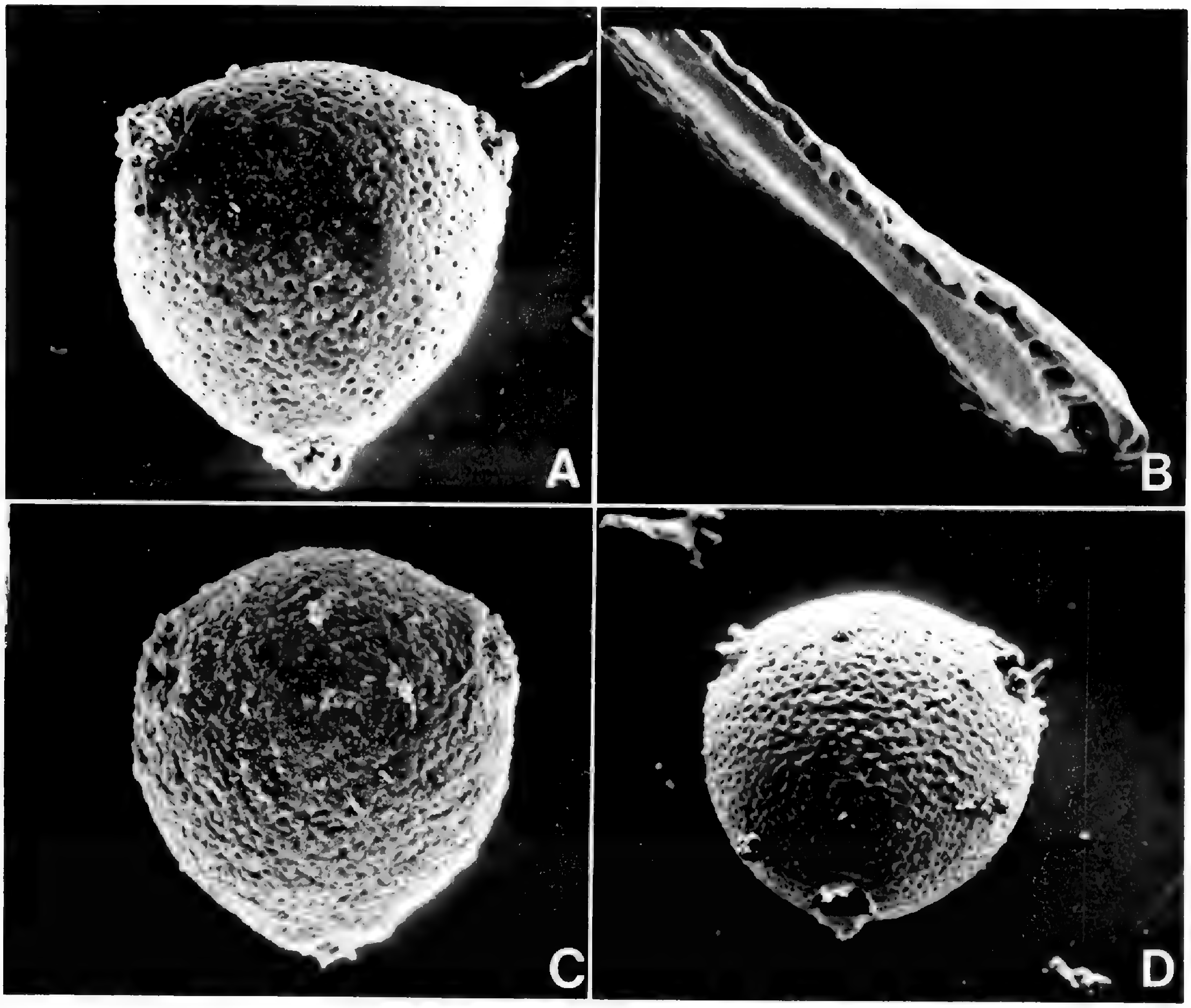

FIGURE 11.—*A*. Trichantha pulchra, *polar view;* ×*1,100.*—*B*. T. pulchra, *exine fracture adjacent to colpus;* ×*5,267.*—*C*. T. parviflora, *polar view;* ×*1,423.*—*D*. T. herthae, *polar view;* ×*1,133.*

13G, H), has pollen that is readily recognizable by its extreme oblate shape, short oval apertures, and triangular ambs. The two species, however, show a sharp difference in exine patterns: *Bucinellina nariniana* has reticulate sculpturing (Fig. 13G) with wide muri, and *B. paramicola* (Fig. 13H) is nearly tectate-imperforate.

One fracture was made of each type of grain in the *Columnea* alliance. Although they do not reveal layers visible with TEM, fractures provide useful data. One can see a diversity of exines, each with a different nexine-to-sexine ratio and nexine-to-tectum and columellae ratios. The exine of *Columnea dressleri* pollen (Fig. 3H) is very uniform with closely packed columellae and a nexine-to-sexine ratio of approximately 1 : 6. The tectum and nexine are of equal thickness. *Dalbergaria ericae* pollen (Fig. 5H) by contrast, has a nexine-to-tectum ratio of about 1 : 3. The nexine-to-sexine ratio approximates 1 : 8. The nexine becomes thick next to the colpus, and the columellae are evenly spaced but

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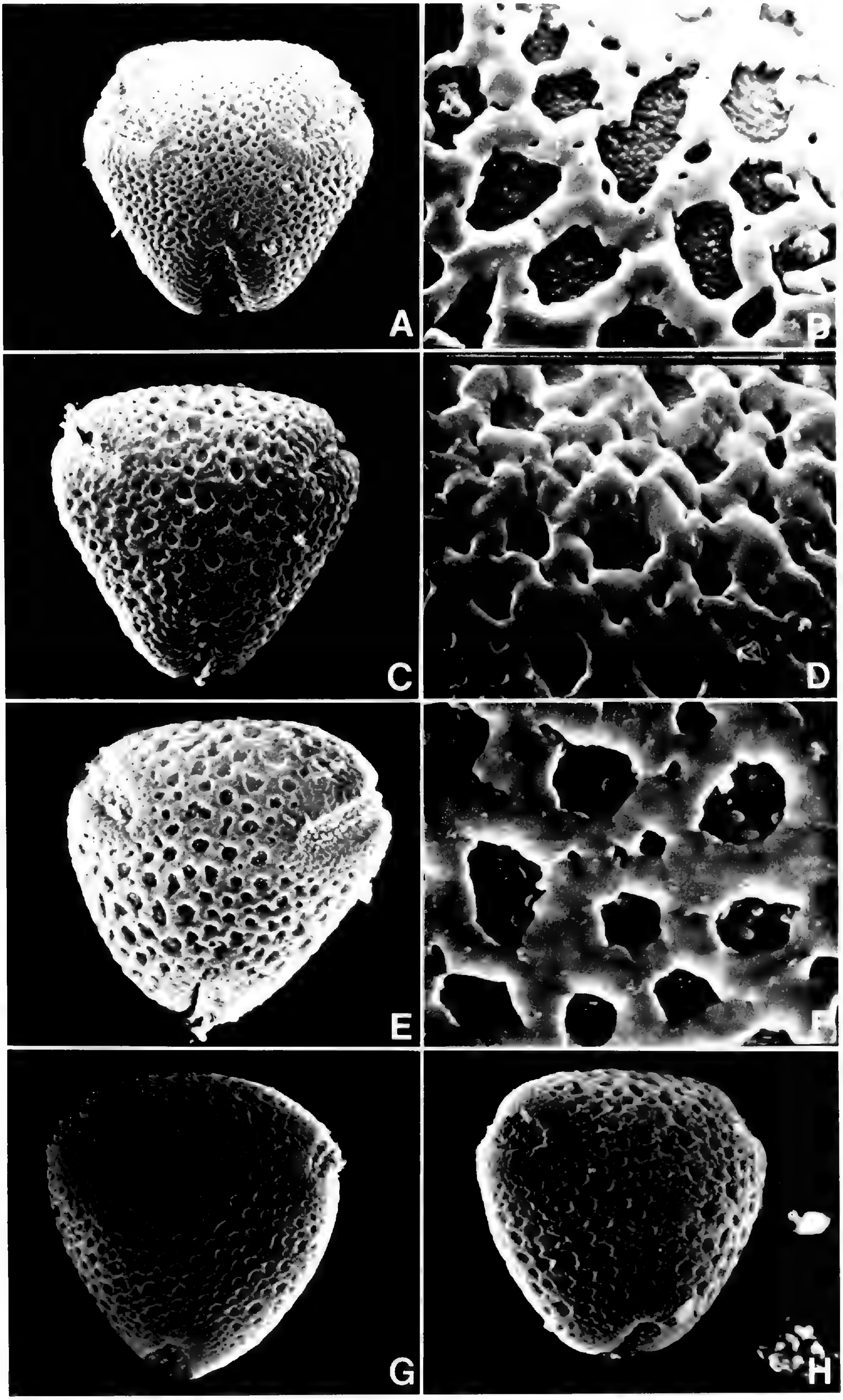
FIGURE 12.—*A*. Pentadenia nervosa, *polar view;* ×*1,200.*—*B*. P. nervosa, *mesocolpial region;* ×*7,500.*—*C*. P. ecuadorana, *polar view;* ×*1,300.*—*D*. P. ecuadorana, *mesocolpial region;* ×*6,000.*—*E*. P. microsepala, *polar view;* ×*1,533.*—*F*. P. microsepala, *mesocolpial region;* ×*7,667.*—*G*. P. spathulata, *polar view;* ×*1,353.*—*H*. P. zapotalana, *polar view;* ×*1,333.*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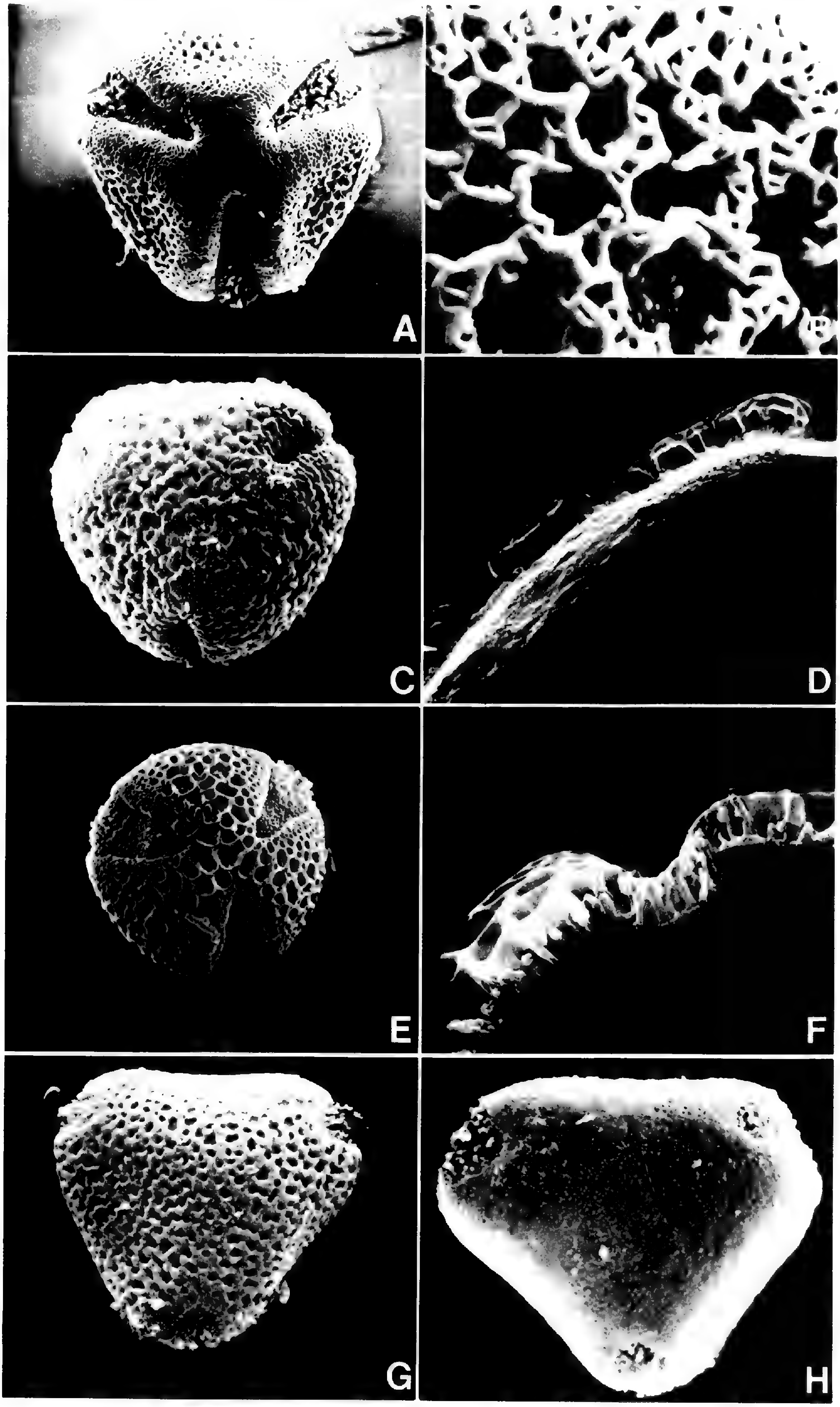
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absent in the lumina. *Dalbergaria aureonitens* (Fig. 8H) has a similar exine, but the columellae are much more irregularly spaced, since they do not occur in the lumina where there is no tectum.

Trichantha calotricha pollen (Fig. 9H) has a tectum over three times thicker than the nexine. The columellae are short and vary in girth. *Trichantha pulchra* pollen (Fig. 11B) is at variance with all others examined in that its nexine is about five times thicker than the tectum and increases in thickness at the colpus. The columellae are unequally spaced and relatively short.

The nexine and tectum of *Pentadenia spathulata* (Fig. 13D) are of equal thickness, and the columellae are well spaced but absent where there is no tectum. *Pentadenia strigosa* (Fig. 13F) shows a thick tectum relative to the nexine, and baculae fill the lumina.

Discussion

Pollen characters are constant, at least within certain genera and subgeneric groups, and appear to be of taxonomic use. The characters found to be most useful are overall shape, sculpturing, and aperture length. Size did not appear significant, although pollen of *Tricantha* tends to be slightly larger compared with other genera.

Some pollen forms are associated with corolla form and sometimes with general morphology of the parent plant. The more variation there is in corolla form in a genus, the more variation there is in pollen form. The cohesiveness of macromorphological characters in *Columnea* is supported by remarkable pollen uniformity; the uniformly punctate exine is characteristic of the genus. All species with this pollen type possess the characteristic galea of the flower. However, species outside the genus *Columnea* that exhibit a similar "columneoid" corolla do not have the pollen characteristics of *Columnea* (*Dalbergaria picta*, *D. ericae*, *D. kalbreyeriana*).

Pollen of *Columnea repens* and *C. rutilans*, the only two columneas examined that occur outside the mainland of Central and South America, is different from that of mainland species (Figs. 5B, C). These two species are endemic to Jamaica, and different selection pressures there could be a factor in their divergence from the general pattern. *Columnea kucyniakii* does not fit very well with the remainder of the genus *Columnea*. Its pollen is more similar to the pollen of *Dalbergaria* or *Trichantha*, but the species does not easily fit into the concept of either of the genera in terms of floral features and general habit (Wiehler, pers. comm.).

The two species of *Bucinellina* share the same grain shape and aperture size, but they have different exine patterns and a slight difference in grain size. They are from the same general locality, and their flowers and habit are fairly similar; the reason for the pollen difference is not evident.

Trichantha purpureovittata, *T. tenensis*, and *T. brenneri* are closely related and have similar corollas as well as similar general plant habit (Wiehler, 1975). The similarity of their pollen correlates well with these characters. *Trichantha pulchra*, *T. herthae*, and *T. parviflora* make up another group of morphologically similar species (Wiehler, 1977, pers. comm.). They have small yellow corollas with tough, incurved lobes and similar pollen. *Trichantha calotricha* has a corolla similar to those of the rest of this group, but its pollen is very different. *Trichantha citrina* and *T. mira* are also closely related to each other (Wiehler, 1978), and their pollen reflects this relationship.

Dalbergaria species have similar pollen and a moderate degree of uniformity in their

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FIGURE 13.—*A*. Pentadenia orientandina, *polar view;* ×*1,400*.—*B*. P. orientandina, *mesocolpial region;* ×*7,333*.—*C*. P. angustata, *polar view;* ×*1,467*.—*D*. P. spathulata, *exine fracture near colpus (far right);* ×*7,083*.—*E*. P. strigosa *polar view;* ×*1,467*.—*F*. P. strigosa, *exine fracture at polar end of colpus;* ×*5,067*.—*G*. Bucinellina nariniana, *polar view;* ×*1,467*.—*H*. B. paramicola, *polar view;* ×*1,633*.

TABLE 2. *Summary of pollen characters in the* Columnea *alliance. p = punctate, r = reticulate, s = short, l = long, i = intermediate, c = circular, a = angular, e = elliptic, o = oval, n = narrow, t = tapered at poles; P/E = ratio of polar axis length to equatorial axis length.*

		Sculpture			Colpus		
Species	P/E	Apocolpium	Mesocolpium	Colpus Border	Length	Shape	Amb
Columnea arguta	1.20	p	p	p	l	e	c
C. bilabiata	—	p	p	p	l	et	c
C. billbergiana	—	p	p	p	l	e	c
C. cobana	0.92	p	p	p	l	et	c
C. dodsonii	—	p	p	p	l	e	c
C. dressleri	1.12	p	p	p	l	e	c
C. erythrophaea	—	p	p	p	l	e	c
C. flaccida	—	p	p	p	l	e	c
C. gallicauda	—	p	p	p	l	e	c
C. gloriosa	—	p	p	p	l	e	c
C. guatemalensis	1.10	p	p	p	l	e	c
C. hirsutissima	1.04	p	p	p	l	e	c
C. kienastiana	1.02	p	p	p	l	et	c
C. kucyniakii	—	p	r	p	l	t	a
C. linearis	1.09	p	p	p	l	e	c
C. maculata	1.16	p	p	p	l	e	c
C. nicaraguensis	—	p	p	p	l	e	c
C. oerstediana	—	p	p	p	l	e	c
C. purpusii	0.99	p	p	p	l	e	c
C. querceti	0.99	p	p	p	l	e	c
C. repens	0.72	p	r	p	l	t	a
C. rubra	—	p	p	p	l	e	c
C. rubricaulis	—	p	p	p	l	e	c
C. rutilans	0.89	p	r	p	l	t	a
C. schiedeana	0.94	p	p	p	l	e	c
C. verecunda	0.90	p	p	p	l	e	c
C. zebranella	1.10	p	p	p	l	et	c
Dalbergaria asteroloma	—	p	r	p	l	n	c
D. aureonitens	0.89	r	r	p	i	e	c
D. cruenta	0.78	p	r	p	l	t	a
D. eburnea	0.89	p	p	p	l	nt	a
D. ericae	0.76	p	r	p	l	t	a
D. florida	0.84	r	r	p	i	e	a
D. inaequilatera	0.78	p	r	p	l	t	a
D. kahlbreyeriana	—	p	r	p	l	t	a
D. perpulchra	0.78	p	r	p	l	t	a
D. picta	0.85	p	r	p	l	t	a
D. polyantha	0.76	p	r	p	l	t	c
D. puyana	0.86	p	r	p	l	t	a
D. sanguinea[1]	—	r	r	p	i	e	c
D. sanguinea[2]	—	r	r	p	i	e	c
D. sanguinea[3]	0.91	r	r	p	i	et	c
D. silvarum	0.70	p	r	p	l	t	c
D. vittata	0.80	p	r	p	l	t	a
Pentadenia angustata	—	r	r	p	i	n	a
P. byrsina	—	r	r	p	i	t	a
P. ecuadorana	0.75	r	r	p	i	n	a
P. microsepala	—	r	r	p	i	n	a
P. nervosa	—	r	r	p	i	t	a
P. orientandina	—	p	r	p	l	t	a

TABLE 2. *Continued.*

		Sculpture			Colpus		
Species	P/E	Apocolpium	Mesocolpium	Colpus Border	Length	Shape	Amb
P. spathulata	—	r	r	p	s	e	a
P. strigosa	0.82	r	r	r	l	t	c
P. zapotalana	—	p	r	p	s	e	a
Trichantha ambigua	—	p	r	p	i	n	a
T. brenneri	—	p	r	p	l	t	a
T. calotricha	0.79	r	r	p	i	e	a
T. citrina	0.80	p	r	p	l	t	a
T. dissimilis	0.66	r	r	p	i	e	a
T. filifera	—	r	r	p	i	e	a
T. herthae	0.86	p	p	p	s	o	c
T. minor	0.86	p	r	p	l	t	a
T. mira	0.75	p	r	p	l	t	c
T. moorei	0.85	p	r	p	l	t	a
T. parviflora	—	p	p	p	s	o	c
T. pulchra	—	p	p	p	s	o	c
T. purpureovittata	0.94	p	r	p	l	t	a
T. tenensis	0.79	p	r	p	l	t	a
Bucinellina paramicola	—	p	p	p	s	o	a
B. nariniana	—	r	r	p	s	o	a

[1] Accession number W-1709.
[2] Accession number G-85.
[3] Accession number W-1628.

corollas. Most pollen grains show slight variations on a theme, e.g., long apertures and a tectum punctate around the colpi and at the poles. Pollen of *Dalbergaria sanguinea*, a tetraploid, is no larger than that of the rest of the genus but is distinct by showing no reduction of the reticulum at the poles and by having apertures of intermediate length. *Dalbergaria aureonitens* is closely related to *D. sanguinea* (Wiehler, 1973), which is reflected by pollen similarities between them. *Dalbergaria florida* is somewhat atypical in the genus although its pollen exhibits features that closely resemble *Dalbergaria sanguinea* and *D. aureonitens*.

In *Pentadenia* there is a relatively high degree of uniformity in corolla forms (Wiehler, pers. comm.) and in the pollen. Most corollas are tubular, small, and generally nondescript. *Pentadenia strigosa*, however, is strikingly different from the rest of the species in the alliance in its much larger corolla and peculiar pollen characteristics, probable adaptations to pollination by bats.

The Gesneriaceae are placed in the relatively advanced order Scrophulariales, and the reticulate, tricolpate pollen of Gesneriaceae is advanced among dicotyledons (Walker & Doyle, 1975). This family has a specialized shape in that it departs from the spherical. The exine pattern is specialized as it differs from the primitive tectate grain. A reduction in aperture size can be seen, particularly in the Episcieae.

Some similarities to pollen of other families in the order Scrophulariales can be seen in pollen of the Gesneriaceae. In the Scrophulariaceae and Myoporaceae one finds tricolpate pollen (Niezgoda & Tomb, 1975) and finely reticulate exines reminiscent of *Columnea*. The colpi are long, but the apertures are diorate, a rare type not found in the Gesneriaceae. Erdtman (1966) found tri-colp(or)ate, oblate-spheroidal, subprolate, or prolate-spheroidal pollen in the Scrophulariaceae. These attributes are within the range of pollen features of the Gesneriaceae.

Boj (1961) made an extensive survey of

the Acanthaceae and found few features that can be compared to the Gesneriaceae other than the reticulate exine. Erdtman (1966) examined 55 species in 35 genera of Acanthaceae and found it to have uniform pollen. One tricolporoid type is subprolate to prolate and has fine reticulation in which the brochi decrease in size toward the colpi. The grains are also within the size range found in the Gesneriaceae.

Buurman (1977) found a number of features in Bignoniaceae similar to those of gesneriaceous pollen. The number of apertures varies, but the tricolpate type exhibits a prolate shape and a uniformly punctate tectum, the lumina of which decrease (almost imperceptibly) in size adjacent to the colpi. These features are predominant in Gesneriaceae tribe Gloxineae (see Williams, 1978). Buurman (1977) outlined within the tricolpate group some evolutionary trends that may have some application to the Gesneriaceae (see below). Erdtman (1966) examined pollen of 25 species in 20 bignoniaceous genera and found a size range that exceeds that of the Gesneriaceae.

This study has answered several questions regarding pollen use in taxonomic considerations of the *Columnea* alliance. Pollen characters separate *Columnea* and *Bucinellina* from the rest of the alliance, but there is much variation within the other genera. Pollen appears to be useful, however, in several ways. Subgeneric groups that exhibit similar pollen could be classified as sections, since they are found to be closely related by other criteria. Differences between species in some pollen features are more apparent than differences between genera, so pollen characters seem to be good species indicators. Pollen does appear to be useful for separating the *Columnea* alliance from other alliances and other alliances from each other.

Evolutionary trends based on the pollen information gathered here can be related to Buurman's (1977) scheme. Tectal features in the *Columnea* alliance exhibit a trend from perforate to uniformly reticulate to punctate near colpi and at poles. Caution must be exercised when this scheme is applied to the *Columnea* alliance, however, since next to *Bucinellina*, *Columnea* is considered most advanced, but it has a uniformly punctate tectum. The shape and size of the grains in the *Columnea* alliance exhibit a trend from spherical and small to oblate or prolate and large. We postulate that the ancestral pollen was tricolpate, spherical, and uniformly reticulate with small lumina, much like pollen that occurs in the tribe Gloxineae (Williams, 1978).

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OBSERVATIONS ON THE CHROMOSOME CYTOLOGY OF VELLOZIACEAE

Peter Goldblatt[1] *and Muriel E. Poston*[2]

ABSTRACT

Chromosome numbers of 15 species in four of the six genera of Velloziaceae were counted from root tip squashes. The family was previously known cytologically from a single count, although our preliminary findings have been reported elsewhere. The American Barbacenia *has* n = *17, while* Vellozia *has species with* n = *8 and 7. The African* Xerophyta *has* n = *24 in two species examined, and the monotypic* Talbotiopsis *has* n = *24, a count substantiating an earlier record of* n = *24–26. A base number of* x = *9 is proposed for Velloziaceae.* Barbacenia *appears to be a paleotetraploid genus,* Vellozia *a hypodiploid, and* Xerophyta *and* Talbotiopsis *are possibly paleohexaploids on the derived base of* n = *8.*

Velloziaceae are a small family of petaloid monocots comprising six genera, *Barbacenia* (102), *Barbaceniopsis* (3), *Nanuza* (1), and *Vellozia* (122) in South America, and *Xerophyta* (50) and *Talbotiopsis* (1) in sub-Saharan Africa, south Arabia, and Madagascar. Until recently, Velloziaceae were barely known cytologically, the only chromosome record being $n = 24$–26 for *Talbotiopsis elegans* (Stenar, 1925, as *Vellozia*). Attention was first drawn to the lack of cytological information for Velloziaceae by Ayensu (1973) in his extensive study of the family. In a review of cytological evolution in the angiosperms, Raven (1975) again focused attention on the scant cytological data for the family, stimulating this investigation. Preliminary findings, unfortunately inexact, were included in Raven's review. These and additional counts are presented here with corrections where necessary.

MATERIALS AND METHODS

Plants for study were obtained from a live collection maintained at the Smithsonian Institution by Drs. L. B. Smith and E. S. Ayensu for their anatomical and taxonomic studies of the family. The material of *Xerophyta retinervis* was gathered in the wild by Goldblatt specifically for cytological study. Species examined are listed in Table 1 with collection data and chromosome numbers.

All counts were made from root tip mitoses. Roots were harvested from actively growing plants and pretreated in 0.003 M hydroxyquinoline for six hours at refrigerator temperatures. They were then fixed in 3 : 1 ethanol–acetic acid, hydrolyzed in 10% HCl for six minutes, and then squashed in lacto-propionic orcein.

OBSERVATIONS

Barbacenia

A diploid number of $2n = 34$ was found in each of four species of *Barbacenia* examined (Table 1). A preliminary count for this genus, $n = 16$ (Goldblatt in Raven, 1975), is incorrect. Chromosomes are all of similar size, 1–2.5 μm long, and are metacentric to submetacentric.

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TABLE 1. *Chromosome numbers in Velloziaceae. All counts are original except one for* Talbotiopsis, *for which a reference is given.*

Species	Haploid No. *n*	Collection Data
Barbacenia		
B. aff. *albiflora* L. B. Smith	17	Brazil. Minas Gerais: Biri-Biri, Mun. Diamantina, *Hatschbach 30183* (US).
B. coronata P. Ravenna	17	Brazil. Minas Gerais: Pico Itambe, *Hatschbach 30095* (US).
B. globata Goethart & Henrard	17	Brazil. Minas Gerais: Cons. Mata, *Hatschbach 30212* (US).
B. paranaensis L. B. Smith	17	Brazil. Parana: Fda. Morungaia, rio do Furil Mun. Senges, *Hatschbach 29212* (US).
Vellozia		
sect. *Radia*		
V. hirsuta Goethart & Henrard	7	Brazil. Minas Gerais: Diamantina, Serra do Espinhaco, *Smith & Ayensu 15999* (US).
V. riedeliana Goethart & Henrard	7	Brazil. Minas Gerais: 27 km W of Serro, *Smith & Ayensu 15983* (NY).
V. tubiflora (A. Rich.) Kunth	7	Brazil. Minas Gerais: Rio Itacambirucu, Grão-Mogol, *Hatschbach 41274* (US).
sect. *Vellozia*		
V. alata L. B. Smith	7	Brazil. Minas Gerais: 3 km N of Chapeado Sol. Serra do Ciop, *Smith & Ayensu 15951* (US).
V. bahiana L. B. Smith & Ayensu	8	Brazil. Bahia: exact locality unknown, *Maia s.n.* (US).
V. caruncularis Mart. ex Seubert	7	Brazil. Minas Gerais: 9 km W of Serro Cerrado, *Smith & Ayensu 15977* (US).
V. compacta Mart. ex Schultes f.	8	Brazil. Minas Gerais: 27 km W of Serro, *Smith & Ayensu 15986* (US).
V. pterocarpa L. B. Smith & Ayensu	8	Brazil. Minas Gerais: Diamantina, *Hatschbach & Ahumada 31705* (US).
Xerophyta		
X. humilis (Baker) Dur. & Schinz	24	South Africa, without precise locality, *Gaff s.n.*, no voucher.
X. retinervis Baker	24	South Africa: Pretoria, hills at Bot. Res. Inst., *Goldblatt s.n.*, no voucher.
Talbotiopsis		
T. elegans (Hook. f.) L. B. Smith	24 24–26	South Africa: exact locality unknown, *Meyer s.n.* (NA). Stenar, 1925.

Vellozia

The preliminary count (Goldblatt in Raven, 1975) for the genus, $n = 9$, was not confirmed by further examination. Species of *Vellozia* sect. *Radia* have $2n = 14$, while $2n = 16$ and 14 were found in species of sect. *Vellozia*. A third section, *Xerophytoides*, is so far uncounted. The chromosomes are comparable in size and appearance to those of *Barbacenia*. In some preparations two diffuse, lightly staining areas stand out. The significance of these shadowy chromatic bodies is unclear, but they do not seem to be chromosomes.

Xerophyta

A diploid number of $2n = 48$ was found in the two species of this Afro-Madagascan genus counted, *Xerophyta humilis* and *X. retinervis*. Chromosomes are generally similar in size and appearance to those of *Barbacenia*, and 1–2 μm long.

Talbotiopsis

One collection of this monotypic genus, renamed *Talbotiopsis* (= *Talbotia*) by Smith (1985), was examined. Our count, $2n = 48$, substantiates Stenar's (1925) report of $n = 24–26$ for *T. elegans* (published under the synonym *Vellozia elegans*). Chromosomes of *Talbotiopsis* are similar to those of *Xerophyta.*

DISCUSSION

The chromosome data presented can only be regarded as preliminary for Velloziaceae, given that we now have counts for just 15 species in four genera out of a total of 250 species in six genera. Nevertheless, the available counts are fairly consistent within genera and so suggest that they comprise a representative sample of the chromosome variation in Velloziaceae.

The counts suggest the following hypothesis of cytological evolution. First, base number may be $x = 9$ for Velloziaceae. It follows that the number $n = 17$ in *Barbacenia* would represent aneuploid reduction from a paleotetraploid base of $n = 18$. The numbers $n = 8$ and 7 in *Vellozia* are then interpreted as aneuploid on the family base of $n = 9$. *Xerophyta* and *Talbotiopis* appear to be paleohexaploids derived from the secondary base of $x = 8$. The shared number in *Xerophyta* and *Talbotiopsis* supports the current belief (Ayensu, 1973) that these two African genera are more closely allied to one another than to the other genera of the family, all South American. Other scenarios can be constructed, but the one outlined seems to us the most parsimonious, and thus recommended at least in the light of current knowledge of Velloziaceae and the patterns of numerical chromosome change that occur in plants (Raven, 1975; Goldblatt, 1980). A base number of $x = 8$ for Velloziaceae appears at first to be a more parsimonious interpretation, with polyploid doubling (to $n = 16$) and subsequent aneuploid increase to achieve $n = 17$ in *Barbacenia.* However, given that ascending aneuploidy is at least four times less common in the flowering plants than descending aneuploidy, we think the latter possibility is less likely, although not implausible.

The chromosome numbers in Velloziaceae tell us little about possible relationships of the family. The most critical current phylogenetic opinion (Dahlgren et al., 1985) treats Velloziaceae as the sole family of Velloziales, one of six single family orders comprising Bromeliiflorae. The reasons for removing Velloziaceae from Liliiflorae and Liliales, to which the family is traditionally assigned, include the *Strelitzia*-like epicuticular waxes, copious starchy endosperm, and stomata with subsidiary cells (Dahlgren et al., 1985). All of these apparently fundamental features correspond with other families of Bromeliiflorae and conflict with Liliiflorae.

Base number in the Bromeliaceae, the family and order possibly closest to Velloziaceae, is $x = 25$ (Raven, 1975), which contrasts sharply with the suggested $x = 9$ in Velloziaceae. Cytology thus appears to contribute little to our understanding of relationships of the families of Bromeliiflorae. However, there seems reason to suppose that if Bromeliiflorae sensu Dahlgren et al. do constitute a natural alliance, then $x = 9$ or 8 are important base numbers. Other orders of Bromeliiflorae include Philydrales (Philydraceae, $x = 9$ or 8), Haemodorales (Haemodoraceae, possibly $x = 8$), and Pontederiales (Pontederiaceae, $x = 8$) (base numbers from Goldblatt, 1980). The last order included in Bromeliiflorae by Dahlgren et al., Typhales, with $x = 15$, is very different and may even be misplaced here.

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CHROMOSOME COUNTS AND KARYOMORPHOLOGY OF SOME WEST TROPICAL AFRICAN SCILLEAE (LILIACEAE)

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ABSTRACT

Karyomorphological analyses of Urginea ensifolia, U. pauciflora, Drimiopsis barteri, Dipcadi tacazzeanum, *and* D. longifolium *are presented. All the materials investigated were obtained from the wild in Nigeria. The karyotypes and chromosome counts are new records for the five species. Both* Urginea *species are* 2n = *20,* Drimiopsis barteri *is* 2n = *24,* Dipcadi tacazzeanum and D. longifolium *are* 2n = *12 and* 2n = *24, respectively. Other members of* Urginea *and all the known species of* Albuca, *which have previously been investigated and reported, are summarized.*

The tribe Scilleae Bak. (Liliaceae) consists of six genera in West Tropical Africa (*Albuca* L., *Dipcadi* Medic., *Drimia* Jacq., *Drimiopsis* Lindl., *Scilla* L., and *Urginea* Stein). The latest treatment of the Liliaceae in West Tropical Africa (Hepper, 1968) shows that these genera are represented by three (five, Gledhill & Oyewole, 1972), two, one, one, one, and four (six, Oyewole, 1975a) species, respectively. Most of the representatives of each genus show striking morphological similarities as well as population variations within each species, which make their taxonomic treatment difficult. There is evidence that many natural populations of the representatives of the tribe are not yet in herbarium collections, so it is likely that there are more taxa in the tribe than are now known.

In this paper, new reports on chromosome number and morphology are given for five representatives of the Scilleae.

MATERIALS AND METHODS

Populations of each species were sampled during several field trips to different parts of Nigeria (Table 1). The species were identified using specimens at the Herbarium of the Federal Institute of Forest Research, Ibadan (FHI). Plants of each species were cultivated at the University of Ilorin, Nigeria. Voucher specimens are deposited at FHI, Ahmadu Bello University Herbarium (ABUH), and the Herbarium of the University of Ilorin (IUH).

Each plant was investigated separately, but plants of the same species were treated together. Cytological studies were carried out on squash preparations of young root tips following conventional methods as earlier reported (Oyewole, 1972). Chromosome index, *r* (ratio of long chromosome arm to the short arm), was determined according to Levan et al. (1964) as modified by Oyewole (1972), and the values were employed in analyzing the karyomorphology of each taxon.

RESULTS AND DISCUSSION

Table 2 summarizes earlier work on the tribe Scilleae while Table 3 summarizes karyotype data on the new reports.

URGINEA

The basic chromosome numbers of this genus are $x = 5$ and $x = 7$ (Darlington & Wylie, 1955; De Wet, 1957; Jones & Smith, 1967). The four species listed in the *Flora of West Tropical Africa* (Hepper, 1968) are

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TABLE 1. *Sources of materials investigated (Scilleae).*

Taxa	Collection Site	Herbarium Voucher	Habitat
Urginea ensifolia	Fashola Rocks 12 km north of Oyo along Oyo–Iseyin Road	S00/0660, in ABUH, IUH, FHI	marshy foot of rocky hills in deciduous woodland
	also 6 km to Oshogbo along Oshogbo–Gbongan Road	S00/0752 in ABUH, IUH, FHI	in marshy roadside, deciduous woodland
Urginea pauciflora	Chanchagwa Hills, Minna	S00/0764 in ABUH, IUH, FHI	in gravelly soil on hillcrest on the outskirt of Minna, in low grassland savanna
Dipcadi tacazzeanum	Igbetti about 150 km north Oyo	S00/1001 in IUH, FHI	in dark, humus soil in shaded deciduous woodland
	12 km north of Ilorin along Lagos–Kaduna Road	S00/1091, S00/1092 in IUH, FHI	in dark, humus soil in open shallow soil on rock outcrops in grassland savanna
	Shao, 22 km northwest of Ilorin		
Dipcadi longifolium	Babanloma, about 72 km north of Ilorin along Lagos–Kaduna Road	S00/1008, in IUH, FHI	in dark, humus soil in rock inselbergs; deciduous woodland
	about 20 km to Kabba along Kabba–Okene Road	S00/1104–1110, in IUH	in dark gravelly soil at foot of rock hills; deciduous woodland
	Nasarawa Village along Mokwa–New Bussa Road	S00/2174, in IUH	in dark brown, clay–loamy soil; open, seasonally marshy grazing land
Drimiopsis barteri	Tegina, a small junction village along Lagos–Kaduna Road, about 144 km to Kaduna	JMC/79, in IUH	in open, seasonally marshy rock soil in grassland savanna
	Kaduna Airport environment	S00/1221, in IUH	gravelly brown soil on rock outcrops in grassland savanna

FHI—Herbarium of the Federal Institute of Forest Research, Ibandan.
ABUH—Ahmadu Bello University Herbarium (Department of Biological Sciences, Ahmadu Bello University, Zaria, Nigeria).
IUH—University of Ilorin Herbarium (in Department of Biological Sciences).

TABLE 2. *Previous chromosome counts in Scilleae.*

Taxa	Somatic Number	Haploid Karyotype[1]	
1. *Albuca* L. $x = 9$ (Oyewole, 1972)			
A. abyssinica Murray	18	3 L	6 S
A. fibrotunicata D. Gledhill & S. O. Oyewole	36	6 L	12 S
A. scabromarginata De Wild.	36	6 L	12 S
A. sudanica A. Chev.	36	6 L	12 S
A. nigritana (Baker) Troupin			
cytotype I	54	9 L	18 S
cytotype II	54	12 L	15 S
2. *Urginea* Stein $x = 5$ (Oyewole, 1975b, 1987a, c)			
U. altissima Baker sensu stricto ($2n = 20 + 2ff$)	22	4 L	7 S
U. gigantea (Jacq.) Oyewole	22	4 L	7 S
U. viridula Baker	20	4 L	6 S
U. indica (Roxb.) Kunth	20	Variable	

[1] L = long chromosome (> 4.5 μm in length); S = short chromosome (< 4.5 μm in length).

TABLE 3. *Summary of karyotype data (Scilleae) (chromosome length in μm).*

Taxa	Homologues 1	2	3	4	5
Urginea ensifolia					
Chromosome length	7.0	6.88	6.8	6.0	5.63
r-value	6.0	16.0	23.0	5.6	36.0
Centromeric location	subterminal	terminal	terminal	subterminal	terminal
Urginea pauciflora					
Chromosome length	9.13	8.13	5.31	3.94	3.75
r-value	8.6	15.25	4.5	2.94	6.5
Centromeric location	terminal	terminal	subterminal	submedian	subterminal
Dipcadi tacazzeanum					
Chromosome length	7.3	6.3	5.1	3.5	2.6
r-value	13.6	11.6	9.2	6.0	3.0
Centromeric location	terminal	terminal	terminal	subterminal	submedian
Dipcadi longifolium					
Chromosome length	8.88	8.13	7.13	6.38	6.0
r-value	10.85	20.4	13.26	24.52	11.0
Centromeric location	terminal	terminal	terminal	terminal	terminal
Drimiopsis barteri					
Chromosome length	9.13	9.13	7.88	6.75	6.25
r-value	5.62	7.11	3.5	2.38	2.33
Centromeric location	subterminal	terminal	subterminal	submedian	submedian

U. altissima Baker, *U. indica* (R. & B.) Kunth, *U. ensifolia* (Thonn.) Hepper, and *U. pauciflora* Baker. More recent work, however, has shown that *U. altissima* is a complex of three distinct species (Oyewole, 1975a), all of which have been investigated karyotypically (see Table 2). *Urginea indica* has been treated separately on account of its variable nature (Oyewole, 1987b, c) and is included in Table 2.

Urginea ensifolia has a somatic complement of 20 chromosomes. The karyotype is represented by twelve long and eight short chromosomes (Figs. 1A, 2A). Chromosome lengths vary between 1.0 μm and 7.0 μm. The six long pairs have terminal to subterminal centromeres. The first two short pairs have submedian to median centromeres, while the last two pairs are dotlike and without observable second arms: they are telocentric. The third long pair has an inconspicuous second arm and a secondary constriction on the long arm.

Urginea pauciflora also has a somatic complement of 20 chromosomes. The karyotype is represented by three long and seven short pairs. The chromosome lengths vary from 2.5 μm to 9.13 μm. All the long chromosomes have subterminal to terminal centromeres. Three short pairs have subterminal to terminal centromeres; three others have submedian to median centromeres, while the seventh pair has a very inconspicuous second arm (Figs. 1B, 2B).

All *Urginea* species so far investigated have $2n = 20$ except *U. volubilis*, a Madagascan species ($2n = 14$, Jones & Smith, 1967). With a basic number of $x = 5$ or $x = 7$, the West African species of *Urginea* are polyploids. However, from karyotype studies, these species have somatic complements that are resolvable into homologous pairs. *Urginea altissima* sensu stricto, with $2n = 20 + 2\text{ff}$, has been shown to have normal meiosis with ten bivalents (Oyewole, 1987a). The basic number of $x = 5$ therefore applies to the West African *Urginea* species which are thus tetraploids.

TABLE 3. *Continued.*

Homologues						
6	7	8	9	10	11	12
5.0	3.0	2.0	1.5	1.0		
19.0	2.0	1.0	0	0		
terminal	submedian	metacentric	telocentric	telocentric		
3.50	3.13	3.0	3.0	2.5		
1.33	24.0	0	2.0	9.0		
median	terminal	telocentric	submedian	terminal		
2.2						
3.4						
subterminal						
5.75	5.0	4.88	3.0	2.75	2.75	2.25
10.5	15.0	9.52	59.0	2.0	10.0	0
terminal	terminal	terminal	terminal	submedian	terminal	telocentric
6.25	5.38	4.75	4.31	4.0	3.75	3.75
2.90	1.86	2.17	1.16	4.0	1.50	1.14
submedian	submedian	submedian	median	subterminal	median	median

DIPCADI

Two basic numbers, $x = 4$ and $x = 9$, are already reported for this genus (Darlington & Wylie, 1955); Hepper (1968) recognized two species, *D. longifolium* Lindl. and *D. tacazzeanum* (Hochst. ex A. Chev.) Baker, into which he merged Morton's (1961) *D. filamentosa* Medic. as a morphological variant. Several natural populations of individuals identifiable as *D. filamentosa* have recently been encountered during field trips in Nigeria, and the cytogenetic relationship of this group with the other species of the genus is still being investigated at Ilorin, Nigeria.

Dipcadi tacazzeanum (excluding all materials identifiable as *D. filamentosa*) has a somatic chromosome complement of $2n = 12$. Chromosome lengths range between 2.2 μm and 7.3 μm, and the karyotype consists of three long and three short pairs. The fifth pair has a submedian centromere, while all the others have terminal to subterminal centromeres (Figs. 1C, 2C). The third pair has a secondary constriction in the long arm.

Dipcadi longifolium has a somatic complement of $2n = 24$. The complement consists of 16 long and eight short chromosomes, with chromosome lengths ranging from 2.2 μm to 8.9 μm. One pair of short chromosomes is telocentric, another has submedian centromere, while the remaining two short and all the eight long pairs have terminal to subterminal centromeres (Figs. 1D, 2D). One of the short pairs with the centromere in the terminal region varies morphologically in different individuals—one or both members have an extended centromeric region. Four pairs (1st, 3rd, 4th, and 6th) have a secondary constriction each in the long arm. With a somatic complement of 24 chromosomes, this species is a polyploid.

Jones & Smith (1967) reported a somatic chromosome number of $2n = 12$ for a diploid species suspected to be *D. gracillium*. The records of $2n = 8$, 18, and 34 for three different species, by which the basic numbers of $x = 4$, 9 were determined, were from southern African materials (see Darlington &

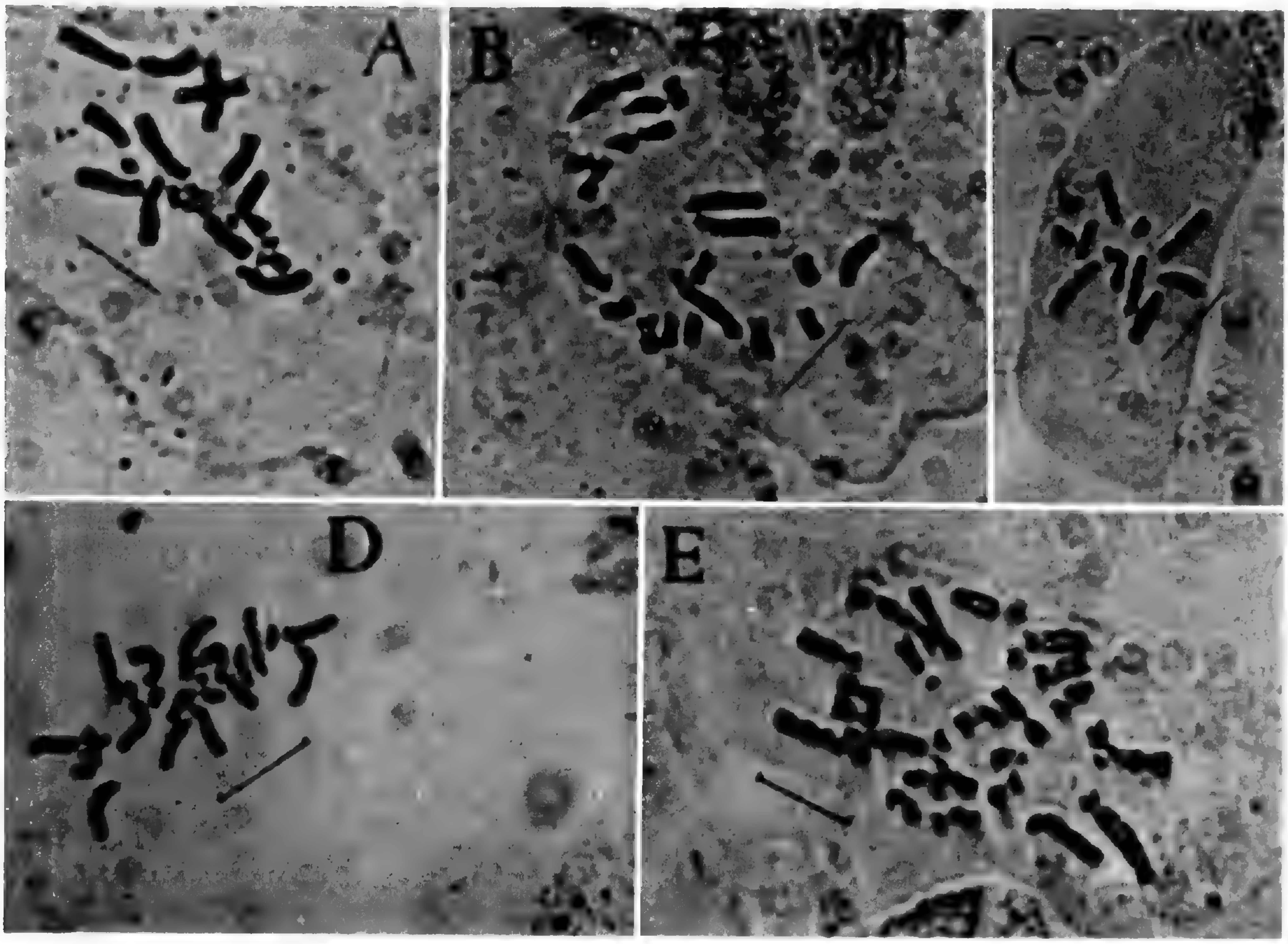

FIGURE 1. *Somatic metaphase complements.* —*A*. Urginea ensifolia.—*B*. Urginea pauciflora.—*C*. Dipcadi tacazzeanum.—*D*. Dipcadi longifolium.—*E*. Drimiopsis barteri.

Wylie, 1955). The two somatic numbers reported here show two ploidy levels and favor a new basic number of $x = 6$, which is supported by chromosome morphology. Thus, one of the two species is a diploid, $2n = 12$ (*D. tacazzeanum*) and the other a tetraploid, $2n = 24$ (*D. longifolium*).

DRIMIOPSIS

This genus is represented by *D. barteri* Baker, as Hepper (1968) recorded. This species has a somatic number of $2n = 24$. The chromosomes fall into twelve morphological pairs, with members of the pairs generally unequal. Chromosome lengths vary between 3.0 μm and 10.0 μm. The complement does not show bimodal categorization into long and short chromosomes. However, seven pairs are longer than 5.0 μm while the other five are shorter than 5.0 μm. Four pairs (1st, 2nd, 3rd, and 10th) have terminal to subterminal centromeres, while the others have submedian to median centromeres (Figs. 1E, 2E). Plants of this species are known to be sexually sterile; meiotic behavior and cause of sexual sterility have been reported (Oyewole, 1984a, b).

Darlington & Wylie (1955) reported a basic chromosome number of $x = 8$ for the genus from South African materials. A somatic chromosome count of $2n = 24$ indicates triploidy. However, Oyewole (1984a, b) showed that a basic number of $x = 6$ rather than $x = 8$ is more consistent with the somatic complement of the West African species of *Drimiopsis*. Two wild and morphologically distinct populations recently sampled in Nigeria have a somatic complement of $2n = 24$ each, as in *D. barteri*, and are sexually reproductive. Their cytogenetic relationship with *D. barteri* and with each other, as well as their taxonomic positions, are being investigated at Ilorin, Nigeria.

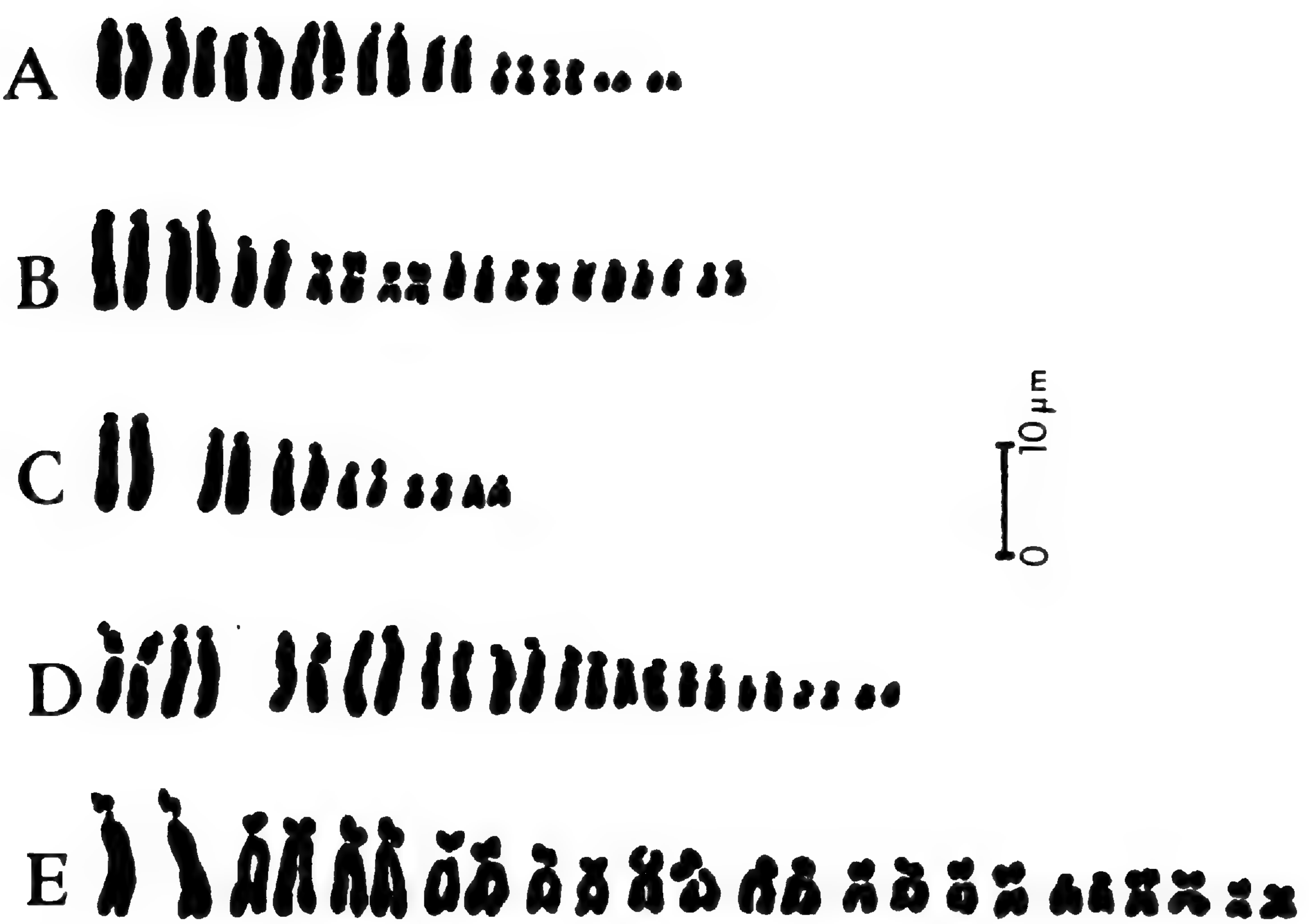

FIGURE 2. *Drawings of the somatic karyotypes.—A.* Urginea ensifolia.—*B.* Urginea pauciflora.—*C.* Dipcadi tacazzeanum.—*D.* Dipcadi longifolium.—*E.* Drimiopsis barteri.

Chromosome length bimodality in certain members of the tribe Scilleae has been reported (Jones & Smith, 1967; Oyewole, 1972, 1975b). This has held true in the present work for the two species of *Urginea* and the diploid *D. tacazzeanum* but not with *D. longifolium* and *D. barteri.* Also, while the West African members of *Albuca, Urginea,* and *Dipcadi* can be said to have a preponderance of chromosomes with terminal to subterminal centromeres, *Drimiopsis* contains a higher number of submetacentrics. It is not possible, therefore, to formulate a common pattern of karyotype evolution in the tribe from mere chromosome morphology.

The morphological similarity among the different genera in this tribe is not correlated with similarity in karyotype morphology. If the morphological similarity is a result of common ancestry for the members of the tribe Scilleae, then karyotypes have evolved along various lines.

Alternatively, morphological similarity in the tribe may be a result of convergent evolution, in which case the tribe would be polyphyletic.

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PRESTOEA (PALMAE) IN CENTRAL AMERICA[1]

Andrew Henderson[2] *and Greg de Nevers*[3]

ABSTRACT

Differences among the morphologically similar Prestoea, Euterpe, *and* Neonicholsonia *are discussed. All species of* Prestoea *occurring in Central America are treated.* Prestoea semispicata *and* P. integrifolia *are described as new species.* Prestoea allenii, P. darienensis, P. decurrens, P. roseospadix, P. sejuncta, *and* P. longipetiolata *are characterized.* E. brachyspatha, E. williamsii, *and* E. simiarum *are placed in synonymy under* P. longipetiolata. Euterpe simplicifrons *is transferred to* Prestoea. *A key and illustrations are provided.*

The neotropical *Prestoea* Hook f. has remained problematic. Moore (1963) argued in favor of keeping *Prestoea* separate from the morphologically similar *Euterpe*. Wessels Boer (1965) argued for uniting the two. Doubts about the characters used by Moore have been expressed by Galeano-Garcés (1986) and Henderson (1986). A third genus, *Neonicholsonia*, is also similar to *Prestoea* but had formerly been distinguished by its spicate inflorescence. Our discovery of a *Prestoea* having usually spicate inflorescences has raised doubts about the distinctness of *Neonicholsonia* from *Prestoea*. Differences between the three genera as understood by us are given in Table 1, which shows that three groups exist. However, any change in ranking should await a study of all species throughout their neotropical ranges.

The Central American species of *Prestoea* are poorly known; too many names are in use; and the regional floras (Standley, 1937, for Costa Rica and Bailey, 1943, for Panama) are outdated. Here we treat all Central American species, based on extensive fieldwork and study of herbarium specimens, including all relevant types. Eight species are recognized. Although *Prestoea carderi* (W. Bull) Hook f. was reported by Hooker (1890) to have come from Guatemala, the description clearly states that the type material came from Colombia.

Although the species are relatively easy to distinguish in the field, this is not so in the herbarium, where the most useful character is the hairs, or their absence, on the rachillae. Sections of rachilla are illustrated for each species, as is the habit. The flowers and fruits of Central American *Prestoea* provide few distinguishing characters. There is substantial variation within species.

KEY TO THE SPECIES OF *PRESTOEA* IN CENTRAL AMERICA

1a. Leaves entire .... (4) *P. integrifolia*
1b. Leaves regularly pinnate 2
    2a. Sheaths closed, forming a green, maroon, or purple-black crownshaft; rachillae at anthesis with sessile, crustose, mostly unbranched hairs (occasionally brown tomentose) .... (1) *P. allenii*
    2b. Sheaths open, not forming a crownshaft; rachillae at anthesis free of crustose hairs (except *P. darienensis*) 3

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[1] *Fieldwork in Panama by Henderson was supported by National Science Foundation Dissertation Improvement Grant BSR 8500989. Herbarium work in Europe by Henderson was supported by a Lawrence Memorial Award. Fieldwork by de Nevers was supported by a Smithsonian Fellowship and by a contract with the Asociación de Empleados Kuna. Loans were received from BH, DUKE, F, and MO. The Latin diagnoses were written by Rupert Barneby. We acknowledge the help of John Dransfield, Gloria Galeano, Michael Grayum, Heraclio Herrera, Gordon McPherson, Ghillean Prance, Robert Read, and Natalie Uhl.*

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TABLE 1. *Comparison of* Neonicholsonia, Prestoea, *and* Euterpe.

	Neonicholsonia	*Prestoea*	*Euterpe*
Leaf sheaths	open and not forming a crownshaft	either semiopen and forming an asymmetric crownshaft or open*	always closed and forming a symmetric tubular crownshaft*
Pinnae	always spreading	spreading to vertical	pendulous, occasionally spreading
Inflorescences	always spicate	usually branched, rarely spicate	always branched
Prophylls	much shorter than the peduncular bract	much shorter than the peduncular bract	more or less equal to the peduncular bract
Rachillae	essentially glabrous, but with groups of hairs, rachillae surface visible	occasionally glabrous, but often with various hairs, rachillae surface visible	never glabrous, densely white- to brown-appressed tomentose or velutinous, rachillae surface not visible
Sepals of staminate flowers	united into a cupule with 3 long-acuminate lobes	free and imbricate or briefly connate at base	free and broadly imbricate
Filaments of staminate flowers	inflexed at apex	inflexed at apex	not inflexed at apex
Staminodes	absent	6, dentate	absent
Pistillate flowers	superficial on rachillae; bracteoles not prominent	superficial on rachillae; bracteoles obscure, rarely prominent	sunken in rachillae; bracteoles prominent
Stigmatic residue positions	subapical	lateral	lateral
Raphe branches	few, large, deeply sunken	numerous, anastomosing to form a network	numerous, anastomosing to form a network

* *Prestoea* inflorescences are more or less terete in bud, and in species with a crownshaft the bud expands before the subtending leaf falls, thereby giving a swollen and open crownshaft. *Euterpe* inflorescences are dorsiventrally compressed and mostly expand after the subtending leaf falls, thus the crownshaft is generally tubular and closed.

3a. Inflorescence spicate or with 2–4 rachillae; pinnae elliptic and abruptly tapered at apex; inflorescence horizontal; endosperm homogenous to slightly ruminate .... (8) *P. semispicata*

3b. Inflorescence usually with many branches; pinnae linear and gradually tapered; inflorescence erect or horizontal; endosperm ruminate 4

  4a. Rachillae at anthesis with short, stiff, simple to branched, white hairs; staminate petals pilose; stem smooth, shiny, with leaf sheaths cleanly abscising and nodes prominent .... (3) *P. decurrens*

  4b. Rachillae at anthesis glabrous, or with sessile, crustose, branching hairs, or densely reddish brown tomentose, or with patches of long, loosely intertwined hairs; staminate petals glabrous; stem mostly rough with persistent leaf sheaths and obscure nodes (occasionally with clean stems and deciduous sheaths in *P. sejuncta* and *P. longipetiolata*) 5

5a. Rachillae at anthesis with sessile, crustose, branching hairs; inflorescence erect, 2–2.5 m long .... (2) *P. darienensis*

5b. Rachillae at anthesis glabrous, or with patches of long, loosely intertwined hairs, or densely reddish brown tomentose; inflorescence erect or horizontal, less than 1.6 m long 6

  6a. Rachillae at anthesis glabrous; stem usually less than 2 m tall; inflorescence erect .... (6) *P. roseospadix*

  6b. Rachillae at anthesis with patches of long, loosely intertwined hairs, or densely reddish brown tomentose; stem usually greater than 2 m tall; inflorescence arching to horizontal 7

7a. Rachillae at anthesis densely reddish brown tomentose; stem thin, often procumbent, less than 2.5 m tall; inflorescence arching; rachis 1–8 cm long with 2–15 rachillae .... (5) *P. longipetiolata*

7b. Rachillae at anthesis with patches of long, loosely intertwined hairs; stem stout, erect, greater than 2 m tall; inflorescence arching to horizontal; rachis 33–50 cm long with (18–)42–48 rachillae .... (7) *P. sejuncta*

1. **Prestoea allenii** H. Moore, Principes 9: 72. 1965. TYPE: Panama. Chiriquí: vicinity of Cerro Punta, 2,000 m, 24

May 1946, *P. Allen 3531* (holotype, BH; isotype, MO). Figures 1, 2.

Stems solitary or cespitose, erect, to 12 m tall, 9–18 cm diam. Leaves 6–8; sheaths deciduous, forming a distinct green, maroon, or purple-black crownshaft 68–75 cm long; petiole 20–60 cm long; rachis 1.8–2.5 m long; pinnae 33–51 per side; middle pinnae 118 cm long, 6 cm wide; apical pinna not wider than others. Inflorescence infrafoliar, horizontal; peduncle ca. 20 cm long, 1.8–2.3 cm diam.; prophyll 40–51 cm long, 10.5 cm wide; peduncular bract ca. 1.1 cm long, 4–6 cm wide, inserted 5–6 cm above base of peduncle; rachis 41–85 cm long; rachillae 23–100, to 73 cm long, at anthesis with sessile, crustose, mostly branched hairs (occasionally brown tomentose); flowers glabrous; fruit 10–11 mm diam.; seeds with ruminate endosperm.

Common name. "Maquenque" (Panama).

Distribution. Eastern Nicaragua to western Panama, in cloud forest 1,000–3,000 m.

Additional specimens examined. NICARAGUA. RIVAS: Isla de Ometepe, NW slopes of Volcán Maderas, 11°26–27'N, 85°30–31'W, 1,000–1,350 m, 24 Feb. 1978, *Stevens 6510* (MO). COSTA RICA. ALAJUELA: Reserva Biológica de San Ramón, road from Las Lagunas to Colonía Palmareña, 10°14'N, 84°32'W, 850–1,100 m, 30 May 1986, *de Nevers et al. 7779* (MO). CARTAGO: above Finca La Florita on road from Cartago to El Generál, 2,450 m, 8 Apr. 1953, *Moore 6677* (BH). HEREDIA: Santo Domingo de Vara Blanca, 2,200 m, 22 Feb. 1937, *Valerio 1597* (F). LIMÓN: Cordillera de Talamanca, Atlantic slope, Valle de Silencio, area just N of Cerro Hoffmann, 4.5 airline km W of Costa Rica/Panama border, 9°08'N, 82°58'W, 2,350–2,450 m, *Davidse et al. 28700* (MO). PUNTARENAS: Cerro Echandi, 3,200 m, "Bocas, Panama, Aug. 1983, Musci, epipetric" (sic), *Gómez et al. 21835* (CAS, MO); Monteverde, 10°17'N, 84°47'W, 1,300 m, 7 June 1986, *Hammel 14872* (NY); 1,800 m, 16 June 1986, *Hammel 14960* (NY); between Sabalito and Finca López above Beneficio de Wa Chong, 1 Feb. 1967, *Moore & Parthasarathy 9440* (BH); Las Cruces ridge, San Vito de Java, 1,200 m, 2 Feb. 1967, *Moore & Parthasarathy 9443* (BH). PANAMA. CHIRIQUÍ: 2.2 km SW of Cerro Punta on road above IDAAN water tank, along ridge trail SW of Quebrada Iglesia above vegetable gardens, 2,100–2,250 m, 7 Aug. 1974, *Croat 26316* (MO); Cerro Pate Macho, Pacific side, 2,150 m, 8°49'N, 82°24'W, 31 Dec. 1985, *de Nevers & Charnley 6685* (MO, NY); road to Cerro Punta from Alto Quiel, above Boquete, 3.5 mi. up Cerro Punta road, 1,850 m, 8°51'N, 82°29'W, 16 Jan. 1986, *de Nevers & McPherson 6800* (MO, NY); path above Cerro Punta to Boquete, 8°50'N, 82°30'W, 2,500 m, moist forest, 16 Mar. 1983, *Hamilton & Stockwell 3392* (CAS, MO, NY).

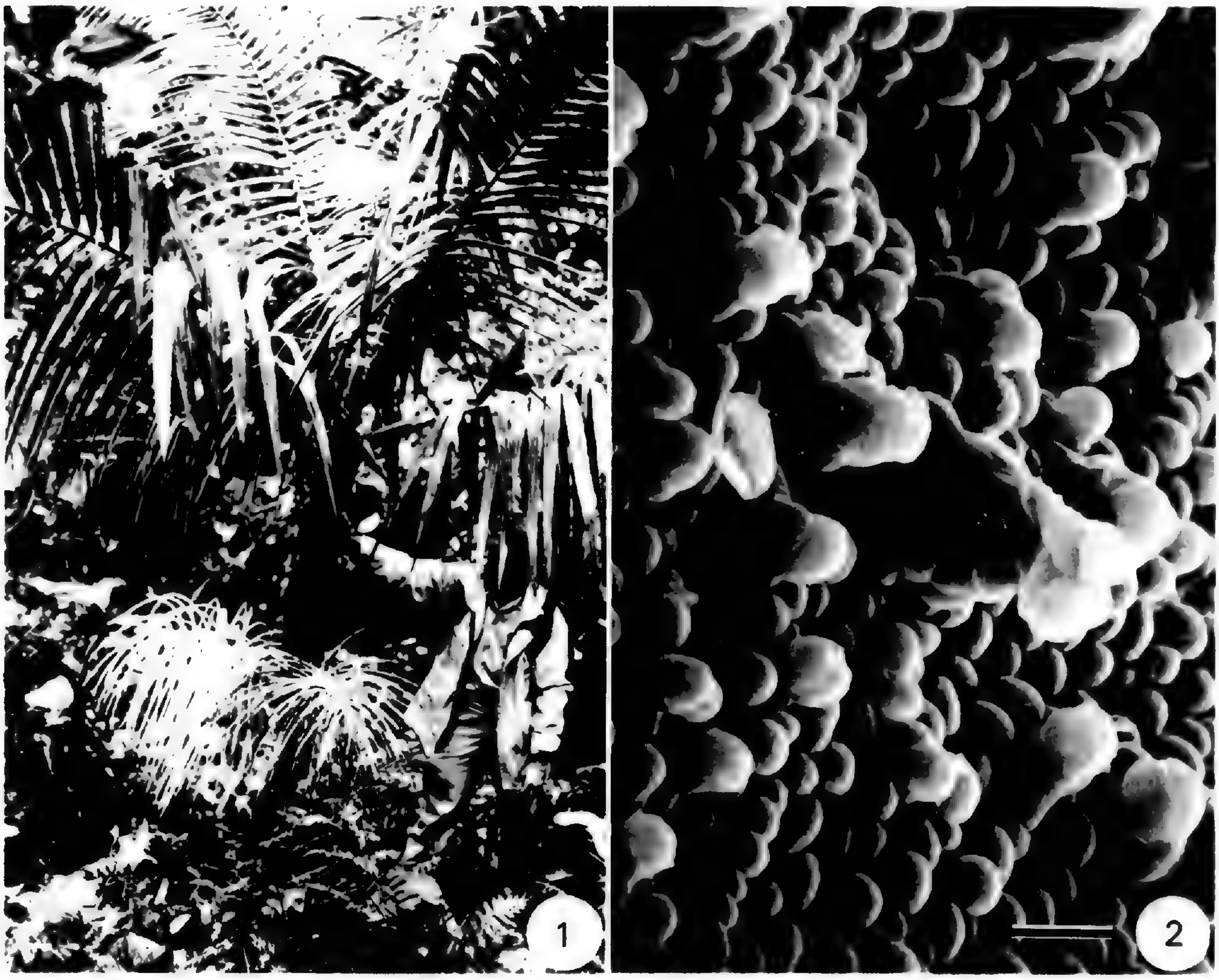
Prestoea allenii varies considerably with altitude. At lower elevations mature plants are sometimes solitary and have green crownshafts, and immature plants can lack crownshafts. At higher elevations the stems are usually cespitose, and the crownshafts maroon or purple-black. In Nicaragua and Costa Rica, lower-elevation populations with green crownshafts may represent a distinct taxon (e.g., *de Nevers et al. 7779*). However, the rachilla hairs are similar to those of *P. allenii*, and such collections are tentatively referred to that species. Robert Read (pers. comm.) reports that color variability in crownshafts of the same species is not uncommon in certain palms.

Prestoea allenii is the largest species of the genus in Central America and occurs at the highest altitude. This is not an uncommon correlation in neotropical palms, occurring, for example, in *Geonoma* and *Chamaedorea.*

2. **Prestoea darienensis** A. J. Henderson, Brittonia 38: 266. 1986. TYPE: Panama. Darién: Serranía de Pirre, on the ridge, 1,130 m, 18 Jan. 1985, *A. Henderson & J. Contraires 97* (holotype, NY; isotype, PMA). Figures 3, 4.

Stem solitary, erect, 2.5 m tall, 10 cm diam. Leaves 6; sheaths persistent, not forming a crownshaft; petiole 80 cm; rachis 165 cm; pinnae 29 per side; middle pinnae 75 cm long, 5 cm wide; apical pinna not wider than others. Inflorescence inter- or infrafoliar, erect; peduncle 75 cm long, ca. 1.5 cm diam.; prophyll 60 cm long, 4 cm wide; peduncular bract 2.23 m long, 2.5 cm wide, inserted 23 cm above base of peduncle; rachis 80–135 cm long; rachillae ca. 60, 45–72 cm long, at anthesis scabrid with crustose, branching hairs; flowers glabrous; fruit 8 mm diam.; seeds with ruminate endosperm.

Distribution. Known only from the type locality.

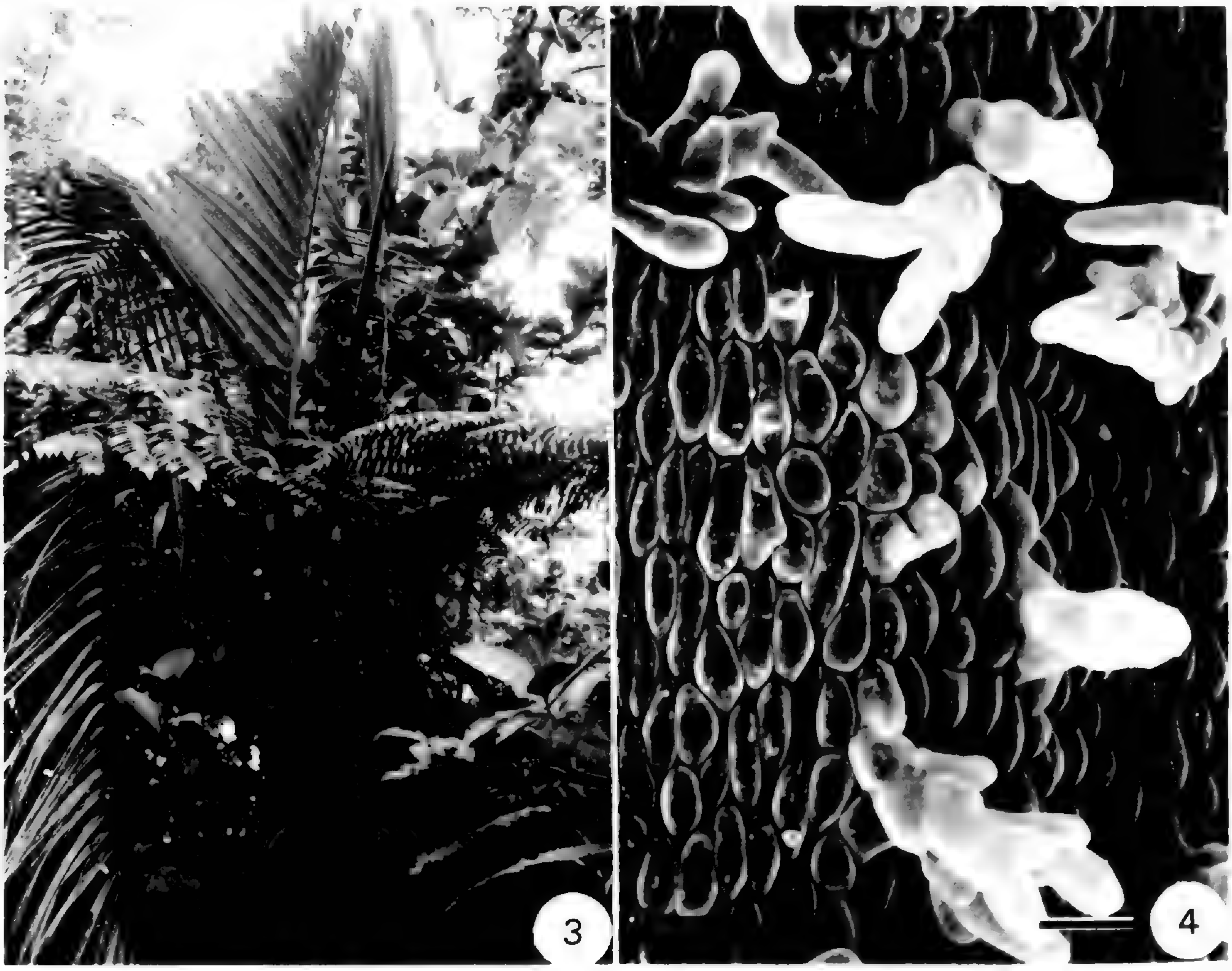


FIGURES 1, 2. Prestoea allenii.—*1. Habit, showing crownshaft and infrafoliar inflorescence (*de Nevers & McPherson 6800*).—2. Part of rachilla, showing sessile, crustose, mostly unbranched hairs (*Allen 3531*). Scale bar = 250 µm.*

Prestoea dariensis can be distinguished from the similar *P. sejuncta* by the rachillae with short, crustose, branching hairs. The inflorescence bud of the type is 2.5 m long, the longest of any *Prestoea* seen, and only approached by some specimens of *P. sejuncta,* which occasionally reach 2.1 m.

3. **Prestoea decurrens** (H. A. Wendl. ex Burret) H. Moore, Gentes Herb. 9: 286. 1963. *Euterpe decurrens* H. A. Wendl. ex Burret, Bot. Jahrb. Syst. 63: 63. 1929. TYPE: Costa Rica. Alajuela: San Carlos, 24 Mar. 1901, *Koschny s.n.* (B, destroyed). Neotype (here designated): Costa Rica. Heredia: Finca La Selva on Río Puerto Viejo just E of its junction with Río Sarapiquí, 12 Dec. 1984, *A. Henderson 50* (NY). Figures 5, 6.

Stems usually cespitose, (1–)2–7, erect, 3–7(–10) m tall, 3.2–10 cm diam., smooth and shiny, green or yellow. Leaves 7–9; sheaths 26–34 cm long, semipersistent, not forming a crownshaft; petiole 50–95 cm long; rachis 1.6–2.3 m long; pinnae 36–50 per side; middle pinnae 52–66 cm long, 3–4 cm wide; apical pinna not wider than the others. Inflorescence infrafoliar, white at anthesis, erect or diagonal; peduncle 15–25(–42) cm long, (0.7–)1–3 cm diam.; prophyll 17.5–19.5 cm long, 3 cm wide; peduncular bract 42–81 cm long, 2.5 cm wide, inserted 2.5–6.5 cm above base of peduncle; rachis 8–27 cm long; rachillae 7–50, 20–56 cm long, at anthesis with short, stiff, simple to branched, white, persistent hairs; staminate petals pilose near apex; fruit 6.5–8 mm diam.; seeds with ruminate endosperm; seedling leaves pinnate.



FIGURES 3, 4. Prestoea darienensis.—*3. Habit, showing long, erect, interfoliar inflorescence bud (*Henderson *97).—4. Part of rachilla, showing sessile, crustose branching hairs (*Henderson 97*). Scale bar = 250 μm.*

Common name. "Palmitillo" (Costa Rica).

Distribution. Throughout Nicaragua, Costa Rica, and Panama, usually between sea level and 1,500 m. This species is also known from northern Colombia (Galeano-Garcés, 1986).

Additional specimens examined. NICARAGUA. MATAGALPA: Comarca Wanawás, beside Río Bilampi, 12°3'N, 85°13'W, 180–200 m, 14 May 1980, *Moreno & Araquistain 2389* (MO, US). RÍO SAN JUAN: near Caño Chontaleño, 20 km NE of El Castillo (Río Indio watershed), 200 m, 7–9 Mar. 1978, *Neill 3320* (MO); 18 Apr. 1978, *Neill & Vincelli 3495* (MO, US). ZELAYA: "Kurinwacito," 13°8'N, 84°57'W, 80 m, 24 Mar. 1984, *Moreno 23880* (US); Mun. Siuna, Caño El Léon, road to Hormiguero, 2 Feb. 1983, *Ortiz 730* (MO); Mina Nueva America, ca. 11.3 km N of main road leading W from 14.3 km N of El Empalme to Rosita, 22 Apr. 1979, *Pipoly 5322* (US); Caño between Cerro La Pimienta and El Hormiguero, ca. 13°45'N, 85°59'W, 800–1,000 m, 15 Mar. 1980, *Pipoly 6018* (MO, US); ca. 6.3 km S of bridge at Colonía Yolonia and ca. 0.8 km S of ridge of Serranías de Yolonia on road to Colonía Manantiales (Colonía Somoza), 11°36'N, 84°22'W, 200–300 m, 29–31 Oct. 1977, *Stevens 4823* (BH, MO, US); 13–14 Feb. 1978, *Stevens 6387* (MO); Caño Costa Riquita, ca. 1.8 km SW of Colonía Naciones Unidas, above road between Colonía Nueva León and Colonía Naciones Unidas, ca. 11°43'N, 84°18'W, 150–180 m, 6–7 Nov. 1977, *Stevens 5034* (BH, MO, US); S slope of Cerro El Inocente down to near Caño Majagua, ca. 13°45'N, 85°0'W, 800–1,000 m, 9 Mar. 1978, *Stevens 6814* (BH, MO); trail from Cerro Saslaya to San José del Hormiguerro, between Caño Majagua and Caño Sucio, ca. 13°45'N, 84°59'W, 600–800 m, 10 Mar. 1978, *Stevens 6838* (BH, MO); 6.3 km S of bridge of Colonía Yolonia on road to Colonía Manantiales of Nueva Guinea, 200–300 m, 13 Feb. 1978, *Vincelli 250* (MO). COSTA RICA. ALAJUELA: E of San Rafael, S of hot springs, W of La Marina, 10°23'N, 84°23'W, 500 m, 19 May 1968, *Burger & Stolze 5021* (F, NY); plains of San Carlos, 100 m, 3 Apr. 1903, *Cook & Doyle 54* (BH, US); Reserva Biológica de San Ramón, road from Las Lagunas to Colonía Palmareña, 10°4'W, 84°32'N, 850–1,100 m, 30 May 1986, *de Nevers et al. 7780* (MO, NY); slopes of Miravalles, above Bijagua, lower montane rainforest, ca. 1,500 m, Nov. 1982, *Gómez et al. 19185* (CAS, CR, MO); vicinity of Guatuso de San Rafael on Río Frío, 10°43'N, 84°48'W, 80–100 m, 4 Aug. 1949, *Holm & Iltis 996* (BH, MO); Río Cuarto, Sarapiquí valley, 1945, *Langlois 12* (BH); beside Laguna María Aguilar, 780 m, 28 Mar. 1969, *Lent 1531* (NY); 2 km N of

Santa Rosa, 15 km N of Boca Arenal on Quesada–Muelle San Carlos–Los Chiles road, 100 m, 10°38′N, 84°31′W, 28 Apr. 1983, *Liesner et al. 15045* (MO, WIS); Río María Aguilar between Cariblanco and San Miguel, valley of Río Sarapiquí, ca. 700 m, 23 Mar. 1953, *Moore 6560* (BH); between Corazón de Jesús and La Virgen, Río Sarapiquí, 340 m, 24 Mar. 1953, *Moore 6576* (BH); 9.1 km before Venado on road from Arenal, 750 m, 1974, *Read & Daniels 74-26* (US). CARTAGO: between Río Pacuare and Grano de Oro, 7 km below Hacienda Moravia, ca. 900 m, 13 Apr. 1953, *Moore 6699* (BH). HEREDIA: Finca La Selva, on Río Puerto Viejo above junction with Río Sarapiquí, 20 Feb. 1981, *Folsom 9056* (DUKE); 27 June 1979, *Holdridge 5107* (BH); 17 Oct. 1980, *Hammel 10189* (DUKE); 5 May 1982, *Hammel 12036* (DUKE); 10 May 1982, *Hammel 12168* (DUKE); 13 June 1984, *Jacobs 2306* (DUKE); 15 July 1984, *Jacobs & Peralta 2883* (DUKE); 28 Jan. 1967, *Moore & Parthasarathy 9407* (BH); 18 Apr. 1972, *Opler 723* (F); 13 May 1984, *Wilbur & Jacobs 34374* (DUKE); 13 May 1984, *Wilbur & Jacobs 34393* (DUKE); 1 June 1985, *Wilbur 37722* (DUKE). LIMÓN: Hacienda Tapezco-Hda. La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, 7 Mar. 1978, *Davidson et al. 6737* (MO). PUNTARENAS: along short cut road to Golfito from Villa Briceño on Interamerican Highway, W side of Fila Gamba, ca. 6 km from Golfito airport, 8°41′N, 83°12′W, ca. 100 m, 6 Mar. 1985, *Croat & Grayum 59925* (CAS, MO); road to Rincón de Osa, 16.5 km W of Chacarita, 83°22′W, 8°45′N, 25 May 1986, *de Nevers et al. 7755* (MO, NY); along the Camino al Pacifico, W of Rincón de Osa, Osa Peninsula, 30 m, 7 Aug. 1967, *Raven 21593* (DS, F, NY). PANAMA. CHIRIQUÍ: above Chiriquí Grande on road to Fortuna Dam, 20 Jan. 1985, *Read et al. 85-20b* (US). COCLÉ: along river leading up mountain to Alto Calvario and trout stream from La Junta near Limón, 800–1,000 m, 12 Oct. 1977, *Folsom 5904* (BH, MO); forest at base of Cerro Pilón above El Valle, 9 Jan. 1972, *Gentry & Dwyer 3655* (BH, MO); 46 km N from Penonomé on road to Coclesito, 30 m, 22 Feb. 1978, *Hammel 1711* (BH, MO). COLÓN: Río Guanche, 3 km upstream of the road, 27 Oct. 1985, *de Nevers & Charnley 6107* (MO, NY); 18 Jan. 1980, *Moore et al. 10515* (BH); 14 Dec. 1974, *Mori & Kallunki 3716* (BH); 15 Mar. 1986, *Hammel & Trainer 14775* (MO); 6 Oct. 1983, *Nee 7253* (CAS, MO); ridge top leading N from Río Escandaloso toward Cerro Bruja, 450 m, 27 Apr. 1978, *Hammel 2707* (MO). COMARCA DE SAN BLAS: El Llano–Cartí road, km 27.6, Río Pingandi, downstream of road, 9°19′N, 78°55′W, 150 m, 9 Mar. 1985, *de Nevers et al. 5065* (CAS, MO); El Llano Cartí road, km 26.5, along Río Cartí Chico, 9°19′N, 78°55′W, 200 m, 12 Apr. 1985, *de Nevers et al. 5346* (MO, NY); 13 Mar. 1986, *de Nevers et al. 7379* (MO, NY); Yar Bired, continental divide between Cangandi and San José, 9°20′N, 79°08′W, 400–500 m, 5 Feb. 1986, *de Nevers et al. 6900* (MO, NY); Río Cangandi at confluence of Quebrada Titamibe, 9°24′N, 79°7′W, 60 m, 8 Feb. 1986, *de Nevers & Herrera 7017* (MO, NY); Río Taindi (Taimdi of maps), 2–3 km above confluence with Río Mandinga, 9°25′N, 79°11′W, 3 Apr. 1986, *de Nevers et al. 7626* (MO, NY); 3 Apr. 1986, *de Nevers & Herrera 7629* (MO); trail to Cerro Obu (Habu of maps) from Río Urgandi (Río Sidra), 9°23′W, 78°48′N, 100–300 m, 24 June 1986, *de Nevers & Herrera 7988* (MO); Cerro Mali, near Colombian border, 1,400 m, 23 Jan. 1975, *Gentry & Mori 13823* (BH, MO, NY). PANAMÁ: pipeline road near Gamboa, 9°10′N, 79°45′W, 100 m, 24 Feb. 1985, *de Nevers & Charnley 4942* (MO).

The type is no longer extant at Berlin. Burret cited a paratype (*Wendland 63*) consisting only of fruit. This is not at Göttingen among Wendland's other specimens, and is apparently lost. We therefore designate *Henderson 50*, from the same general area as the paratype, as neotype. Burret (1929) considered *P. decurrens* to be closely related to *Euterpe macrospadix* Oerst. and placed them in the same subsection (see Henderson, 1986), but they are unrelated. The confusion probably arose because the type of *E. macrospadix* at Copenhagen appears to be a mixture of *Prestoea* leaves (probably *P. longipetiolata*) and a *Euterpe* inflorescence.

Specimens from the Osa Peninsula in Costa Rica (*Raven 21593*, *Croat & Grayum 59925*) and Río Guanche in Panama have the typical tomentum of *P. decurrens*, but the inflorescence is less stout, the peduncle is longer and thinner, and there are 7–20 (vs. 50) rachillae. The strongly cespitose (vs. erect) stems are thinner and weaker than usual for the species.

4. **Prestoea integrifolia** de Nevers & A. J. Henderson, sp. nov. TYPE: Panama. Colón: Santa Rita Ridge, km 21.2, 9°20′N, 79°45′W, 350 m, 24 Feb. 1986, *G. de Nevers 7212* (holotype, MO; isotypes, CAS, COL, K, PMA, NY). Figures 7, 8.

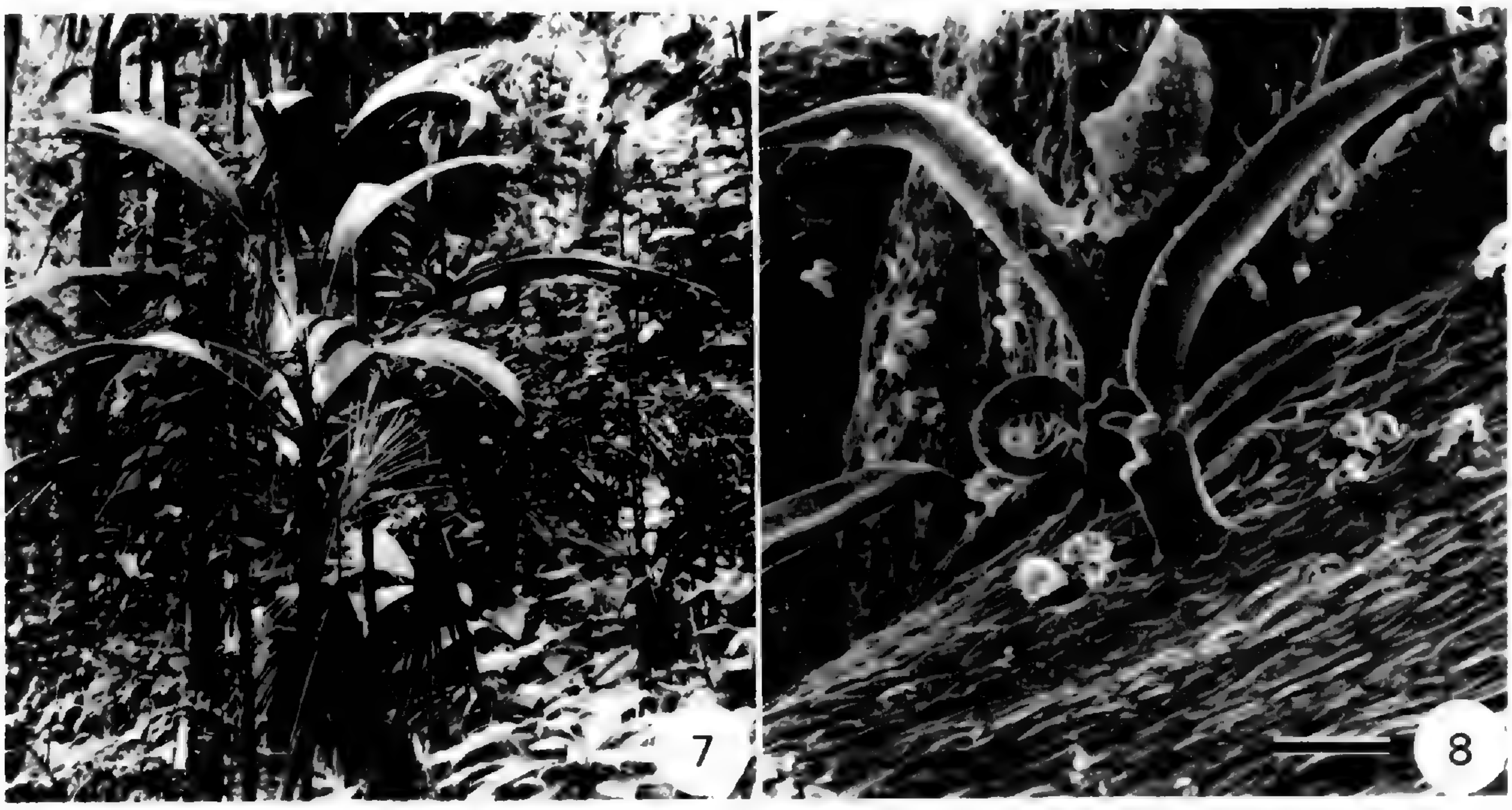
Ab aliis speciebus integrifolius inflorescentia erecta, rachillis tenuibus pilis simplicibus obsitis necnon seminum endospermate ruminato diversa.

Stems cespitose, one well-developed, erect, 2.8–5.8 m tall, 3–4 cm diam.; internodes 3–8 cm long; adventitious roots forming a prominent cone at base of stem, 18–30 cm long, 6–8 mm diam., red, covered with small round projections. Leaves 8–12, spreading; sheaths not forming a crownshaft, 30–38 cm long, closed basally for 15–18 cm, open apically, covered sparsely with closely appressed whit-

FIGURES 5, 6. Prestoea decurrens.—*5. Habit, showing smooth stem, persistent leaf sheaths not forming a crownshaft, erect, interfoliar inflorescence bud, and infrafoliar inflorescence (*Langlois 12*). Photograph courtesy of BH.—6. Part of rachilla, showing short, stiff, simple to branched hairs (*Henderson 50*). Scale bar = 500 µm.*

ish-brown scales; petiole channeled adaxially, rounded abaxially, 30–50 cm long, covered with closely appressed brown scales; rachis 40–65 cm long, ridged adaxially, rounded abaxially and with scales similar to those of petiole; blade entire, 103–113 cm long, 30–35 cm wide, deeply bifid at apex for 60–65 cm; veins prominent adaxially, 14–15 per side, with brown scales proximally. Inflorescence interfoliar, erect at anthesis; peduncle 40–75 cm long, sparsely covered with brown scales; prophyll 21–35 cm long, covered with scales similar to those of peduncle; peduncular bract inserted 5–10 cm above base of peduncle, 80–130 cm long, with scales similar to those of peduncle, at anthesis brown on outside, whitish on inside; rachis 18–32 cm long; rachillae 23–28, 35–54 cm long, 1 mm diam. at middle at anthesis; rachis and rachillae white at anthesis, becoming reddish in fruit, with sparse, hyaline, simple or branched hairs; triads subtended by a low bract; staminate flowers 4 mm long, sessile; sepals 3, free, imbricate, triangular, keeled, membranaceous, hyaline margined, apiculate, 1.5 mm long; petals 3, free, valvate, lanceolate, 4 mm high; stamens 6; filaments unequal, 0.9–1.5 mm long; anthers dorsifixed at center of thecae, introrse; thecae unequal, 0.8–1.2 cm long; pistillode 1 mm long, deeply trifid; pistillate flowers 2 mm long, surrounded by 2 low bracteoles; sepals 3, free, imbricate, glabrous, broadly ovate; petals similar to sepals but slightly smaller; gynoecium ovoid, pseudomonomerous, 1.5 mm long; stigmas sessile; staminodes minute, dentate; immature fruits with ruminate endosperm.

Distribution. Only known from the type locality.



FIGURES 7, 8. Prestoea integrifolia.—7. *Habit, showing entire leaves and interfoliar, erect inflorescence (*de Nevers 7212*).—8. Part of rachilla, showing hyaline, simple and branched hairs (*de Nevers 7212*). Scale bar = 500 µm.*

Additional specimens examined. PANAMA. COLÓN: same locality as type, 13 May 1986, *de Nevers et al. 7738* (MO, NY); km 22, 500 m, 17 Feb. 1986, *Hammel et al. 14473* (MO, NY).

Prestoea integrifolia differs from all other Central American members of the genus by its entire leaves. Three other extra-Central American species have entire leaves: *P. simplicifrons*,[4] *P. simplicifolia* Galeano, and *P. cuatrecasasii* H. Moore.

The holotype of *P. simplicifrons* is no longer extant at B, and no isotypes are known, but there is another collection from at or near the type locality (*Henderson & Bernal 156*). Thus represented, *P. simplicifrons* has relatively short rachillae with a moderate to dense covering of reddish brown hairs, whereas *P. integrifolia* has long rachillae sparsely covered with hyaline hairs.

Prestoea simplicifolia (represented at NY by an isotype and by *Henderson & Bernal 140*) has a stout, pendulous inflorescence with thick rachillae, in contrast with *P. integrifolia*, which has a thin, erect inflorescence with thin rachillae.

Prestoea cuatrecasasii (represented by the original description) has seeds with homogenous endosperm, as opposed to the ruminate endosperm of *P. integrifolia.*

Prestoea pubigera (Griseb. & H. A. Wendl.) Hook. f. is sometimes reported to have entire leaves (e.g., Galeano-Garcés, 1986), but all specimens examined, including the type at Göttingen, have the lower part of the leaf with separate but unequal pinnae, and these are joined in the upper part.

5. **Prestoea longipetiolata** (Oersted) H. Moore, Gentes Herb. 9: 286. 1963. *Euterpe longipetiolata* Oerst., Vidensk. Meddelel. Kjoebenh. 1858: 32. 1859. TYPE: Costa Rica. Cartago: Turrialba, May 1847, *A. S. Oersted 6562* (holotype, C). Figures 9, 10.

Euterpe brachyspatha Burret, Bot. Jahrb. Syst. 63: 57. 1929. TYPE: Costa Rica. Puntarenas: Cañas Gordas, 1,100 m, Feb. 1897, *H. Pittier 11124* (holotype, B destroyed; isotypes, M, US).

Euterpe williamsii Glassman, Fieldiana, Bot. 31: 5. 1964. TYPE: Nicaragua. Matagalpa: Cordillera Central de Nicaragua, along road to La Fundadora, cloud forest area, 1,300–1,400 m, 23 Feb. 1963, *L. O. Williams, A. Molina & T. P. Williams 24922* (holotype, F).

Malortiea simiarum Standley & L. O. Williams, Ceiba 3: 102. 1952. *Euterpe simiarum* (Standley & L.

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[4] **Prestoea simplicifrons** (Burret) A. J. Henderson & de Nevers, comb. nov. *Euterpe simplicifrons* Burret, Engler Bot. Jahrb. 63: 53. 1929.

O. Williams) H. Moore, Principes 1: 145. 1957. TYPE: Nicaragua. Jinotega: vicinity of Finca San Roque, sierra E of Jinotega, 1,300–1,500 m, 5 July 1947, *P. Standley 10923* (holotype, F).

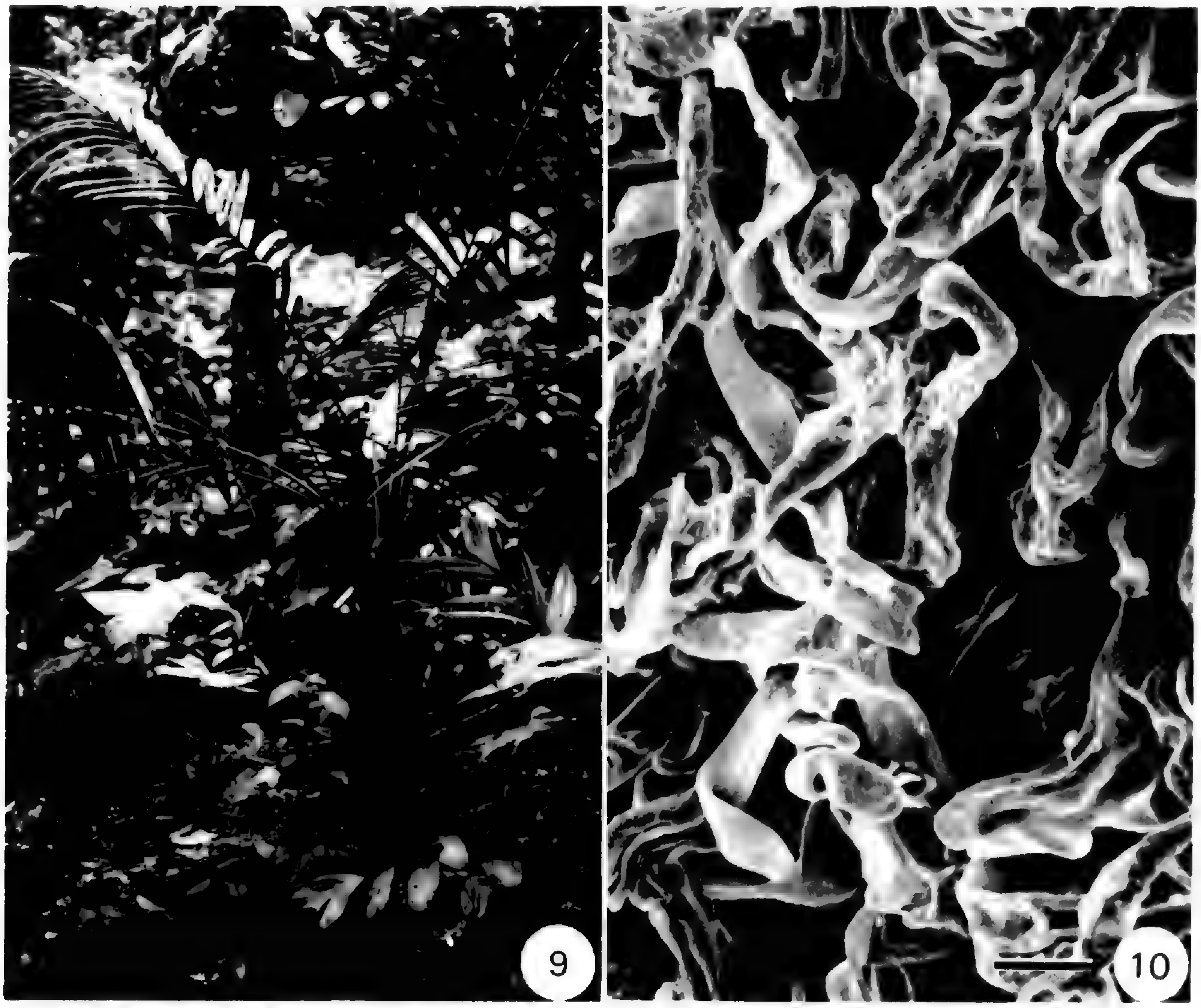
Stems solitary or cespitose, often procumbent, 0.5–3 m tall, ca. 5 cm diam. Leaves 4–8; sheaths persistent, not forming a crownshaft; petiole 80–240 cm long; rachis 116–209 cm long; pinnae 21–33 per side; middle pinnae 45–56 cm long, 1.5–3 cm wide; apical pinna often markedly wider than others. Inflorescence interfoliar or infrafoliar, arching; peduncle 12–100 cm long, 3–6(–11) mm diam.; prophyll (9.5–)15–30 cm long, 1.5–2 cm wide; peduncular bract (32–)56–114 cm long, 2–4 cm wide; rachis 2–9 cm long; rachillae (2–)3–8(–20), (8–)16–35 cm long, at anthesis densely reddish brown tomentose; flowers glabrous; fruit 6–11 mm diam.; seeds with ruminate endosperm.

Distribution. From Nicaragua to western Panama (Chiriquí), 1,000–1,800 m. Contrary to a report by Wessels Boer (1971), this species does not occur in Venezuela (Henderson & Steyermark, 1986).

Additional specimens examined. NICARAGUA. JINOTEGA: Ocotillo near Sta. Lastenia, Cordillera Centrál de Nicaragua, 1,550 m, 17 Jan. 1965, *Williams et al. 27806* (F, NY). MATAGALPA: Cerro Carlota, 12°58′N, 85°52′W, 1,250–1,300 m, 23 Oct. 1982, *Moreno 18129* (MO); Cerro El Picacho, N of Selva Negra, 13°0′N, 85°55′W, 1,500 m, 7 July 1983, *Moreno 21670* (MO, US); 7 July 1983, *Moreno 21671* (MO); Cerro Carlota, 12°58′N, 85°52′W, 1,250–1,300 m, *Moreno 18149* (MO); along Highway 3, ca. 1.9 km W of Aranjuez road entrance, ca. 13°2′N, 85°56′W, 1,460–1,480 m, 30 June 1983, *Stevens 9168* (MO, US); along Highway 3, ca. 1 km NW of La Fundadora entrance, unnamed peak ca. 500 m W of Highway, ca. 13°1′N, 85°56′W, 1,450–1,520 m, 24 May 1981, *Stevens & Henrich 20456* (MO); W slope of summit of Cerro El Picacho, ca. 13°0′N, 85°55′W, 1,350–1,590 m, 3 June 1983, *Stevens & Moreno 22168* (MO, US); Cordillera Central de Nicaragua, along road to La Fundadora, 1,300–1,400 m, 23 Feb. 1963, *Williams et al. 24918* (F); Cordillera Central de Nicaragua, Xelaju, 13°02′N, 85°55′W, 1,500 m, 12 Feb. 1965, *Williams et al. 29266* (F, NY). COSTA RICA. ALAJUELA: Buena Vista, road to San Carlos valley, 600 m, 11 Apr. 1903, *Cook & Doyle 38* (US); Juan Viñas, Reventazón valley, near Juan Viñas River, 1,000 m, 21 Apr. 1903, *Cook & Doyle 173* (US); along Camino Raíz de Hule, SE of Planatillo (Tsipiri), 1,200–1,400 m, 1 July 1976, *Croat 36792* (MO); Reserva Biológia de San Ramón, road from Las Lagunas to Colonía Palmareña, 10°4′N, 84°22′W, 850–1,100 m, 30 May 1986, *de Nevers et al. 7769* (MO, NY); near Río Naranjo, 2 km W of Orosi, 1,400 m, 16 Jan. 1977, *Lent 4066* (F); slopes of ridge separating Río Paz Grande and Río Paz Chiquita, about halfway between Vara Blanca and Cariblanco, valley of Río Sarapiquí, 1,340–1,500 m, *Moore 6639* (BH); Paraiso, area of Muñeco, 9–10 Mar. 1974, *Read & Daniels 74-80* (US); Guadalupe de Zarcero, 1,200 m, 1 Nov. 1973, *Smith A567* (F); La Peña de Zarcero, Cantón Alfar Ruiz, 1,375 m, 23 Jan. 1939, *Smith 1544* (NY); El Muñeco, S of Navarro, 1,400 m, 8 Feb. 1924, *Standley 33600* (F, US). CARTAGO: Cañón del Río Grande de Orosi y Aluvión, 23 Oct. 1983, *Chacon et al. 1489* (MO); Río Tambor, 3 km SE of Cachí, 1,420 m, 22 Aug. 1971, *Lent 2060* (F); about 5 km beyond Hacienda Moravia, 1,000–1,200 m, 13 Apr. 1953, *Moore 6686* (BH); fords of Las Vueltas, Tucurrique, 635 m, Dec. 1898, *Tonduz 12924* (F, US). PUNTARENAS: Finca Loma Linda, 1 mi. SW of Cañas Gordas, 1,150 m, 26–27 Feb. 1973, *Croat 22232* (CAS, K, MO); foothills of the Cordillera de Talamanca, around Tres Colinas, 9°07′N, 83°04′W, 1,800–1,850 m, 20 Mar. 1984, *Davidse et al. 25609* (MO); Monteverde, along Río Guacimal below Lechería, 10°17′N, 84°48′W, 1,500 m, 11–14 June 1985, *Hammel & Trainer 13822* (CAS, MO); 16 June 1985, *Hammel 13872* (MO); Monteverde area, valley of Río San Luis just S of Monteverde, 10°16′N, 84°48′W, 1,000–1,200 m, 18 June 1985, *Hammel & Haber 13924* (MO); 1,800 m, 16 June 1986, *Hammel 14961* (NY); Finca Las Cruces, on trail to Río Java, ca. 1,000 m, 31 Jan. 1967, *Moore & Parthasarathy 9426* (BH); Monteverde, along foot trail in forest reserve, 3 Nov. 1974, *Moore et al. 10170* (BH); Las Cruces, Finca Kilpauk, 15 Dec. 1961, *Read 655* (BH); San Vito de Coto Brus, Las Cruces Botanical Garden, Jan. 1985, *Wilson s.n.* (BH). SAN JOSÉ: El General, 1,490 m, Feb. 1939, *Skutch 4184* (US); between San Isidro and La Georgina, 17 Nov. 1973, *Moore & McAlpin 10150* (BH); 17 Nov. 1973, *Moore & McAlpin 10150A* (BH). PANAMA. BOCAS DEL TORO: La Fortuna Dam Area, N of dam along continental divide trail W of oleoducto road, 8°47′N, 82°15′W, 1,200–1,300 m, 11 Feb. 1986, *Hammel & McPherson 14458*; near continental divide in vicinity of Cerro Colorado, 9.4 road miles from Chami camp, ca. 8°35′N, 81°45′W, ca. 1,700 m, 15 Apr. 1986, *McPherson 8917* (MO, NY). CHIRIQUÍ: 9 mi. from Río Chiriquí Viejo bridge near Nueva California on road to Río Sereno, 7 Apr. 1979, *Hammel et al. 6829* (MO).

Malortiea simiarum was originally distinguished by its pinnate leaves and little-branched inflorescence when being compared with *Reinhardtia* (*Malortiea*). The size, degree of branching, and pubescence of the type fall within the range of variation observed in Costa Rican material of *P. longipetiolata*.

Euterpe brachyspatha, as judged from the original description, was named after a misinterpretation of the inflorescence. Burret (1929) described the spadix (inflorescence) as 98 cm long and the spathe (peduncular bract) as 17 cm long, which is impossible. The ho-



FIGURES 9, 10. Prestoea longipetiolata.—*9. Habit, showing procumbent stem and arching, interfoliar inflorescence (*Moore 9426*). Photograph courtesy of BH.—10. Part of rachilla, showing dense tomentum (*McPherson 8917*). Scale bar = 250 µm.*

lotype is lost, and the isotypes are incomplete. However, the specimens described by Burret represent *P. longipetiolata.* The Munich isotype has the broad apical pinna typical of most but not all specimens of *P. longipetiolata.* A topotype, *Croat 22232,* is typical *P. longipetiolata.*

Euterpe williamsii was originally contrasted with *E. brachyspatha,* presumably represented by the original description. In Burret's (1929) key, *E. brachyspatha* and *E. longipetiolata* are contrasted in the same couplet. In its protologue, Glassman did not contrast *E. williamsii* with *E. longipetiolata. Euterpe williamsii* agrees in the diagnostic characters of size, branching, and pubescence of the inflorescence with *E. longipetiolata.*

6. Prestoea roseospadix (L. Bailey) H. Moore, Principes 9: 73. 1965. *Euterpe roseospadix* L. Bailey, Gentes Herb. 6: 201. 1943. TYPE: Panama. Chiriquí: vicinity of Bajo Chorro, 1,900 m, 20–22 July 1940, *R. E. Woodson & R. W. Schery 623* (holotype, MO; isotype, BH). Figure 11.

Stems solitary, erect, 0.3–3 m tall, 8–10 cm diam. Leaves 4–6; sheaths persistent, not forming a crownshaft; petiole 61–76 cm long; rachis 120–125 cm long; pinnae 21–27 per side; middle pinnae 38–50 cm long, 2–2.5 cm wide; apical pinna not wider than others. Inflorescence infrafoliar, erect; peduncle 16–38 cm long, 0.5 cm wide; prophyll 20–23 cm long, 2 cm wide; peduncular bract 70–80 cm long, 2 cm wide, inserted ca. 14 cm above base of peduncle; rachis 16–40 cm long; rachillae 9–16, 20–40 cm long, glabrous; flowers glabrous; fruit 9–10 mm diam.; seeds with ruminate endosperm.

Distribution. Western Panama (Chiriquí and Veraguas) at altitudes around 1,500 m.

Additional specimens examined PANAMA. CHIRIQUÍ: Cerro Horqueta, 2,100 m, 24 July 1966, *Blum & Dwyer 2665* (MO); 24 July 1966, *Blum & Dwyer 2671* (MO); 8 Aug. 1967, *Kirkbride 162* (MO); Bajo Chorro, Boquete, ca. 2,000 m, 11 Jan. 1938, *Davidson 100* (F); lower slopes of Cerro Pate Macho, 8°49'N, 82°24'W, 1,600 m, 31 Dec. 1985, *de Nevers & Charnley 6697* (MO, NY); 17 Jan. 1986, *de Nevers & McPherson 6829* (MO, NY); La Fortuna hydroelectric dam project, behind camp, 1,300–1,400 m, 23 Mar. 1978, *Hammel 2255* (BH, MO). VERAGUAS: valley of Río Dos Bocas on road between Alto Piedra (above Santa Fé) and Calovébora, 350–400 m, 29 Aug. 1974, *Croat 27440* (MO).

7. **Prestoea sejuncta** L. Bailey, Gentes Herb. 6: 201. 1943. TYPE: Panama. Canal Area: Madden Lake area, upper Río Pequení, 100 m, 29 July 1941, *A. G. B. Fairchild & D. Jobbins 2635* (holotype, BH; isotype, MO). Figures 12–14.

Stem solitary or cespitose, erect, 5–9 m tall, (4.5–)9–13 cm diam. Leaves 5–8; leaf sheaths persistent or deciduous, not forming a crownshaft; middle pinnae 61–86 cm long, 3–4.5(–6) cm wide; apical pinna not wider than others. Inflorescence interfoliar, erect, or arching, or horizontal, straight or curved; prophyll 13–45(–75) cm long, (1.2–)3–5 cm wide; peduncular bract 69–156(–215) cm long, (2.5–)3.6–5.5 cm wide, inserted (2–)4.5–13 cm above prophyll; peduncle 23–71 cm long, 0.6–1.4 cm wide, narrow, cylindric, not flaring at base; rachis (15–)33–50 cm long; rachillae (18–)42–48, 30–70 cm long, essentially glabrous but with patches of long, loosely intertwined hairs; flowers glabrous; fruits 7–10 mm diam.; seeds with ruminate endosperm.

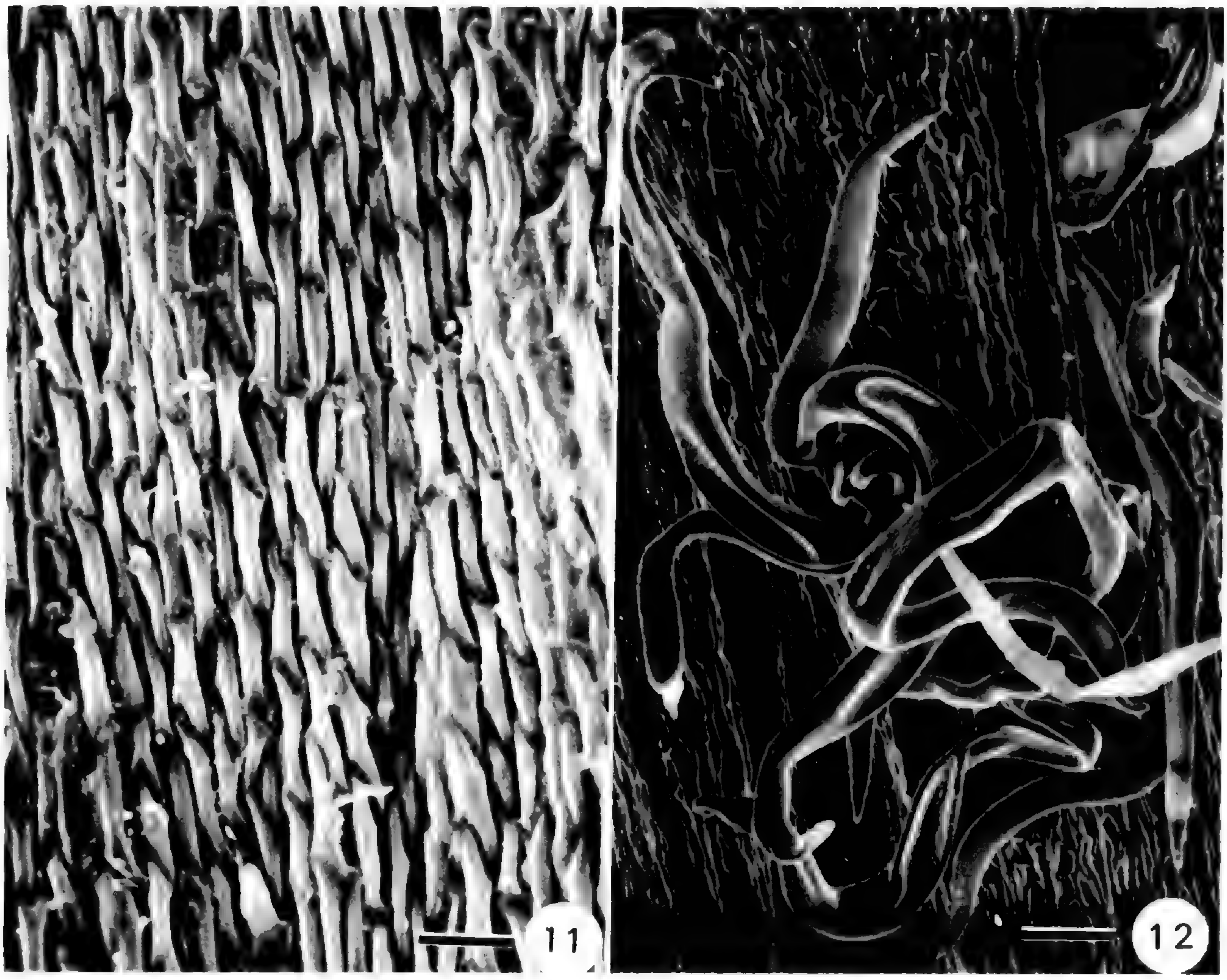
Distribution. Known from central Panama (Chiriquí, Coclé, Comarca de San Blas, Colón), 100–1,100 m. This species is also reported from coastal Ecuador by Dodson & Gentry (1978). Other specimens from Ecuador (e.g., *Balslev & Henderson 62107*) are clearly referable to this species, and it presumably occurs in intervening Colombia.

Additional specimens examined. PANAMA. CHIRIQUÍ: Fortuna dam area, road from Gualaca to Chiriquí Grande, continental divide trail west of road, 1,150 m, 8°45'N, 82°15'W, 18 Jan. 1986, *de Nevers & McPherson 6849* (MO, NY). COLÓN: trail from Alto Pacora to Cerro Brewster, 9°18'N, 79°16'W, 700 m, 18 Nov. 1985, *de Nevers et al. 6223* (MO, NY). COCLÉ: El Valle de Antón, La Mesa, ca. 1,000 m, 2 Sep. 1941, *Allen 2740* (paratype) (BH, MO). COMARCA DE SAN BLAS: Cerro Brewster, 9°18'N, 79°16'W, 850 m, 25 Apr. 1985, *de Nevers et al. 5541* (MO, NY). PANAMÁ: 3 mi. N of Cerro Azúl, 26 July 1970, *Croat 11589* (MO); Cerro Jefe, ca. 700 m, 20 Jan. 1980, *Moore et al. 10522* (BH); Río Pequení, slopes of Cerro San Francisco, 150–300 m, 9°22'N, 79°31'W, 29 Nov. 1985, *de Nevers & Henderson 6411* (CAS, MO, NY); road to Alto Pacora from Cerro Jefe, 700 m, 28 Nov. 1985, *Henderson & Brako 505* (MO, NY); Gorgas Memorial Lab's yellow fever research camp, ca. 25 km NE of Cerro Azúl on Río Piedras, 550 m, 20–22 Nov. 1974, *Mori & Kallunki 3454* (BH, MO).

Among the specimens examined, there appear to be two ecotypes, which may turn out to represent distinct taxa. At higher altitudes (900–1,200 m) in premontane rain forest (Holdridge et al., 1971), the inflorescence is straight and erect in bud (Fig. 13) and relatively long and thick (1.5–2.1 m × 3–5 cm). At lower altitudes (10–200 m) in tropical moist forest and tropical wet forest (Holdridge et al., 1971), the inflorescence is curved and horizontal in bud (Fig. 14) and is relatively short and thin (75–80 × 1.2–2.5 cm). When Bailey described *P. sejuncta*, he cited two specimens, one of each ecotype. The holotype is the short-inflorescence ecotype, and the paratype, *Allen 2740*, is the long-inflorescence ecotype. Although letters accompanying *Allen 2740* from Paul Allen to Bailey clearly outlined this variation, Bailey included only the dimensions of the smaller Madden Lake plant.

8. **Prestoea semispicata** de Nevers & A. J. Henderson, sp. nov. TYPE: Panama. Comarca de San Blas: Cerro Brewster, 9°18'N, 79°16'W, 800 m, premontane rain forest, 19 Nov. 1985, *G. de Nevers, A. Henderson, H. Herrera, G. McPherson & L. Brako 6290* (holotype, MO; isotypes, AAU, BH, CAS, COL, FTG, K, NY, PMA). Figures 15, 16.

Ab omnibus congeneribus inflorescentia simplice vel pauciramosa necnon seminum endospermate subruminato diversa.



FIGURES 11, 12. Prestoea.—*11.* P. roseospadix, *part of rachilla, showing absence of hairs (*Woodson 623*).* *Scale bar = 400 µm.*—*12.* P. sejuncta, *part of rachilla, showing long, loosely intertwined hairs (*de Nevers & Henderson 6411*). Scale bar = 500 µm.*

Stems cespitose, only one well-developed, to 145 cm long, 3.5–9 cm diam., often procumbent and partly subterranean; roots visible above ground, spiny and occasionally swollen. Leaves 4–10, arching to erect; sheaths not forming a crownshaft, 17–20 cm long, brown, persistent; petiole 29–100 cm long, densely covered with closely appressed, brown hairs; rachis 52–180 cm long; pinnae 12–20 per side, elliptic, abruptly and asymmetrically long-apiculate, glossy green adaxially, lighter green abaxially; middle pinnae 19–51 × 2.5–6 cm. Inflorescence infrafoliar, protandrous, arching, borne at or near ground level; peduncle 6–50 cm long, 1.5–3 mm diam., terete, with scattered brown scales; prophyll erect and persistent in leaf axil, inserted at base of peduncle, (1.2–)4.5–19 cm long, 1.1–1.8 cm wide, dorsiventrally compressed, ancipitous, splitting apically; peduncular bract (9–)29–90 cm long, 1–2 cm wide at middle, inserted (0.7–)1.5–7 cm above insertion of prophyll, terete in bud, apically pointed, brown at anthesis, soon dropping; rachillae 1(–4), 8–30 cm long, glabrous; peduncle and rachis white at anthesis and becoming red in fruit; triads densely crowded and borne to apex of rachillae, slightly sunken, subtended by a low bract; staminate flowers 4 mm long, sessile or borne on a short, flattened pedicel, white; sepals 3, triangular, gibbous, imbricate below, 1 mm long, ciliate; petals 3, free, lanceolate, valvate, 4 mm long; stamens 6; filaments slightly flattened, with long reflexed apex in bud, 3 mm long; anthers dorsifixed, latrorse, 2 mm long; pistillode prominent, as long as stamens in bud, briefly trifid at apex; pistillate flower 3 mm long, surrounded by 2 low bracteoles; sepals 3, free, imbricate, minutely ciliate; petals 3, free, val-

FIGURES 13, 14. Prestoea sejuncta.—*12. Straight inflorescence bud and long inflorescence with elongate peduncle and numerous rachillae (*Henderson & Brako 505*).—14. Curved inflorescence bud and small inflorescence with short peduncle and few rachillae (*de Nevers & Henderson 6411*).*

vate above, imbricate below; gynoecium ovoid, pseudomonomerous, 2 mm long, the ovule attached laterally; stigmas sessile, elongate, not recurved at anthesis; staminodes dentiform; fruit spherical, 8 mm diam., with lateral stigmatic residue, black; epicarp smooth; mesocarp fleshy; seed spherical, 7 mm diam., the endosperm homogenous to slightly ruminate; embryo basal.

Common name. "Siler burwi" (Kuna, Panama).

Distribution. Known only from the low mountains of Central Panama, from the western end of the Serranía de San Blas to El Copé in Coclé, where it is uncommon between 350 and 850 m. It grows on steep slopes and ridge tops in premontane rainforest and tropical wet forest.

Additional specimens examined. PANAMA. COCLÉ: El Valle de Antón, Cerro Gaital, 8°37′N, 80°6′W, 1,000 m, 26 Nov. 1985, *de Nevers et al. 6351* (CAS, MO, NY); continental divide above El Copé, 900 m, 19 Jan. 1978, *Hammel 967* (MO); 27 Nov. 1985, *de Nevers et al. 6381* (MO, NY, PMA, other duplicates to be distributed). COMARCA DE SAN BLAS: same locality as type, 16 Oct. 1984, *de Nevers et al. 4027* (MO, NY); 25 Apr. 1985, *de Nevers et al. 5550* (MO, NY); 19 Nov. 1985, *de Nevers et al. 6242* (MO, NY); 21 Dec. 1985, *Hammel & de Nevers 13560* (CAS, MO); El Llano–Cartí road, km 16.5, 9°19′N, 78°55′W, 350 m, 13 Mar. 1985, *de Nevers & Herrera 5153* (MO); 12 Mar. 1986, *de Nevers et al. 7371* (MO); 22 Nov. 1985, *de Nevers & Henderson 6312* (MO, NY); 8 Mar. 1986, *de Nevers & Herrera 7260* (MO, NY); 18 June 1986, *de Nevers & Herrera 7945* (CAS, MO); trail from Cerro Camucañala to Río Titamibe, 9°24′N, 79°8′W, 60–100 m, 28 Jan. 1985, *de Nevers et al. 4719* (CAS, MO, NY); trail from Río Esadi to Cerro Banega, 300–530 m, 9°23′N, 78°51′W, 21 Dec. 1985, *de Nevers & Herrera 6671* (CAS, MO, NY); Yar Bired (Cerro San José), continental divide between Cangandi and San José, 9°20′N, 79°8′W, 400–500 m, 7 Feb. 1986, *de Nevers & Herrera 6961* (MO, NY); trail to Cerro Obu (Habu of maps) from Río Urgandi (Río Sidra), 9°25′N, 79°11′W, 100–300 m, 3 Apr. 1986,

FIGURES 15, 16. Prestoea semispicata.—*15. Habit, showing procumbent stem, arching, infrafoliar inflorescence, and abruptly tapering pinnae (*de Nevers et al. 6290*).—16. Part of rachilla, showing absence of hairs (*de Nevers 5550*). Scale bar = 250 µm.*

de Nevers & Herrera 8029 (CAS, MO); Cerro Obu, 78°48'W, 9°23'N, 25 June 1986, *de Nevers & Herrera 8055* (CAS, MO).

Prestoea semispicata is unusual in the genus by the usually spicate inflorescence, seeds with homogenous to slightly ruminate endosperm, and shape of the pinnae. In populations where individuals with branched inflorescences occur, spicate inflorescences are also found. In fact, branched and spicate inflorescences form on the same plants. *Prestoea semispicata* appears morphologically similar to that group of *Prestoea* characterized by a weakly developed stem, absence of crownshaft, markedly unequal prophyll and peduncular bract, short rachis with few rachillae, and seeds with either homogenous or ruminate endosperm (Henderson, 1986). In this group, *P. semispicata* shares with *P. cuatrecasasii* and *P. schultzeana* (Burret) H. Moore seeds with homogenous endosperm but differs in the shape of the pinnae and in having usually spicate inflorescences. Some specimens of *P. longipetiolata* from Nicaragua and *P. pubens* H. Moore from Colombia have two or three rachillae on the inflorescence, but these are densely tomentose and not glabrous as in *P. semispicata*.

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KARYOTYPE VARIATION IN *PANCRATIUM HIRTUM* A. CHEV. (AMARYLLIDACEAE)[1]

S. O. Oyewole[2]

ABSTRACT

Natural populations of Pancratium hirtum *A. Chev. from different ecological niches show definable morphological variation. Samples were grown in an experimental garden and investigated karyotypically. Five morphological variants (morphotypes) were identified and were confirmed as showing karyotype differences. Karyotype differentiation involves at least: (1) chromosomal breakages, and (2) differences in the total length of chromatin material per nucleus. The chromosome basic number of x = 11 is confirmed for the species, while the presence of accessory chromosomes in one morphotype is reported for the first time in the genus. Population divergence is less pronounced than karyotypic divergence.*

Pancratium L. is represented in West Tropical Africa by two species, *P. hirtum* A. Chev. and *P. trianthum* Herb. Their taxonomy was well documented by Morton (1965), who reported the somatic chromosome number of $2n = 22$ for them. Morton did not include analysis of the karyotypes. *Pancratium hirtum*, with large chromosomes, is especially suitable for study of chromosome morphology.

MATERIALS AND METHODS

Pancratium hirtum grows in a variety of niches in savanna vegetation, where it exhibits minor but definable differences in leaf size, leaf color, extent of pubescence, length and form of the peduncle, and texture of the outermost tunic of the bulb (Table 1).

Five morphological groups (morphotypes, Fig. 1) were recognized during field study and samples were collected. Not fewer than 40 bulbs of each morphotype were grown separately on adjacent beds in the experimental garden. Their habitats are described in Table 2.

Each bulb in each morphotype was examined cytologically using root tip squashes as outlined in Darlington & LaCour (1969). Chromosome counts were made from several metaphase plates in each preparation. Measurement of chromosomes using calibrated micrometer eyepiece graticule was impracticable due to their unusual lengths. Photographs of metaphase plates were taken at ×7.5 ocular and ×40 objective of the Olympus (Vanox model) Research Microscope. Chromosomes were measured from the photomicrographs. The measurements were pooled from 15–20 complements for each morphotype, and average lengths were determined. Chromosome morphological determinations were according to Levan et al. (1964) as modified by Adhikary (1974). Evidence of chromosomal changes was manifested in unequalness of members of homologous chromosome pairs (such changes usually affect one arm of a member). In such instances, the unaffected arm length was employed to identify the members, and the chromosome index was based solely on the length of the longer member of the pair. Idiograms were constructed from enlarged photomicrographs.

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RESULTS

Karyotype data are summarized in Table 3. Figure 2 shows metaphase plates of the somatic complements, and Figure 3 presents the idiograms. All morphotypes have a somatic chromosome number of $2n = 22$, except E, in which the complement is $2n = 22 + 4$ B-chromosomes.

Morphotype A. The chromosomes vary in length from 5.5 μm to 19 μm, with a total length of chromatin material of 216.5 ± 6.5 μm. The complement (Figs. 4A, 5A) consists of four pairs with median to submedian centromeres (1st, 2nd, 3rd, and 11th), one telocentric pair (8th), and six pairs with terminal to subterminal centromeres (4th–7th, 9th and 10th). The longest two pairs have unequal members, one member of each having lost a portion of its long arm.

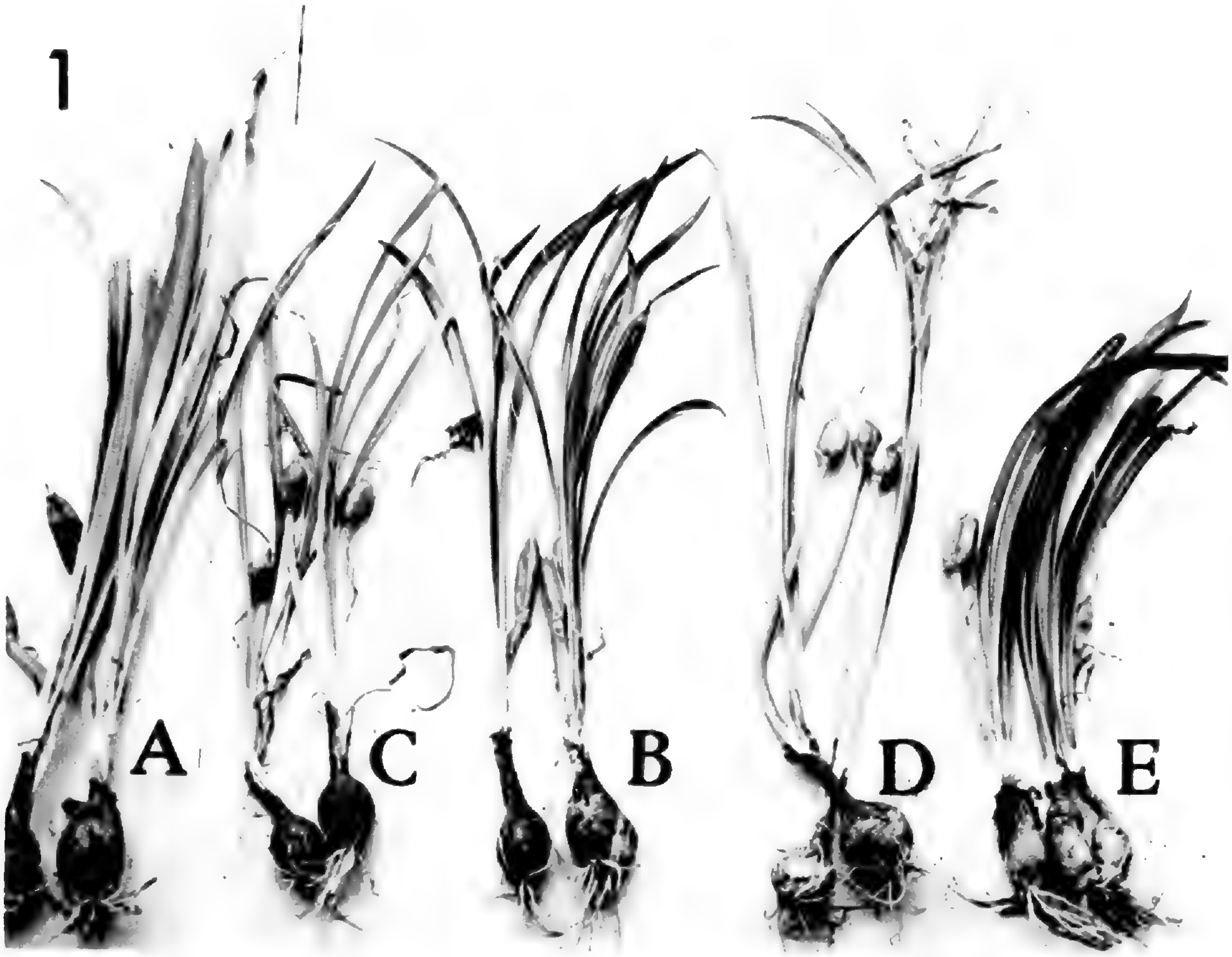
Morphotype B. Chromosomes vary in length from 11.38 μm to 41.75 μm, with an average total chromatin length of 439.5 ± 18.5 μm. The complement (Figs. 4B, 5B) consists of three pairs (1st, 2nd, and 11th) with median to submedian centromeres, and eight (3rd–10th) with terminal to subterminal centromeres. The second- and third-longest pairs have unequal members: a member of the former having lost a portion of the long arm, while one member of the latter lost a portion of its short arm.

Morphotype C. Chromosomes vary in length from 6.3 μm to 19.14 μm, and the total chromatin length averages 237.3 ± 23.3 μm. The complement (Figs. 4C, 5C) consists of three pairs (1st, 2nd, and 11th) with median to submedian centromeres and eight pairs (3rd–10th) with terminal to subterminal centromeres. The third-longest pair has unequal members—the shorter member has a shorter second arm. One member of the shortest pair also shows loss of a portion of one arm.

Morphotype D. Chromosome length varies between 8.6 μm and 27.3 μm, with an average total chromatin length of 340.4 ± 49.8 μm. The complement (Figs. 4D, 5D)

TABLE 1. *Summary of the external morphology of* Pancratium hirtum *morphotypes.*

	A	B	C	D	E
Peduncle	4–7 cm long, flattened, puberulous	2–4.5 cm long, elliptic, fluted, faintly puberulous	4–7 cm long, cylindrical, glabrous	10–13 cm long, cylindrical, glabrous	4–6 cm long, slightly flattened, shortly puberulous
Fruit	2.5–3.5 cm long, 3–3.6 cm circumference, oblong-elliptic, obtuse apex, trigonal in transverse section, green, glabrous, receptacle 1–3 mm high	2–4 cm long, 2–3.3 cm circumference, lanceolate, obtuse apex, trigonal in transverse section, green, glabrous, receptacle 1–3 mm high	1.7–2 cm long, 2–3.6 cm circumference, oblong, apex 4–5 mm high, trigonal in transverse section, green, glabrous, receptacle 1–3 mm high	1.4–2 cm long, 2.5–3.5 cm circumference, cylindrical, apex 2–4 mm high, trigonal in transverse section, green, glabrous, receptacle 1–3 mm high	2–2.5 cm long, 3–4 cm circumference, spindle shaped, apex 1–5 mm high, obtusely trigonal, green, glabrous, receptacle 1–3 mm high
Leaf	light green, 26–33 cm long, 9–15 mm wide	dark green, 21–30 cm long, 4–9 mm wide	light green, 22–31 cm long, 5–9 mm wide	light green, 24–35 cm long, 5–9 mm wide	dark green, 20–26 cm long, 7–14 mm wide
Bract	single, deciduous, about half-encircling, single lipped, yellowish green	single, deciduous, half-encircling, single lipped, green	single, deciduous, half-encircling, single lipped, light green	single, persistent until fruit ripening, fully encircling, 2-lipped, green	single, deciduous, half-encircling, single-lipped, dark green



FIGURES 1, 2.—*1.* Pancratium hirtum *morphotypes with mature fruits, ×0.2.—2. Mature fruits, with peduncles, of* Pancratium hirtum *morphotypes, ×0.4.*

consists of five pairs (1st–3rd, 10th, and 11th) with median to submedian centromeres and six pairs (4th–9th) with terminal centromeres. Five of the eleven pairs (1st, 2nd, 3rd, 8th, and 10th) show evidence of loss of portions from one member of each pair. First and 10th pairs show loss in the long arm; the second and third pairs show loss in the short arm, and the eighth shows loss in one of the two equal arms.

Morphotype E. The autosomes vary in length from 5.6 μm to 17.9 μm, and the B-chromosomes vary between 1 μm and 1.5 μm. The average total chromatin length is 219.14 ± 2.5 μm. The complement (Figs

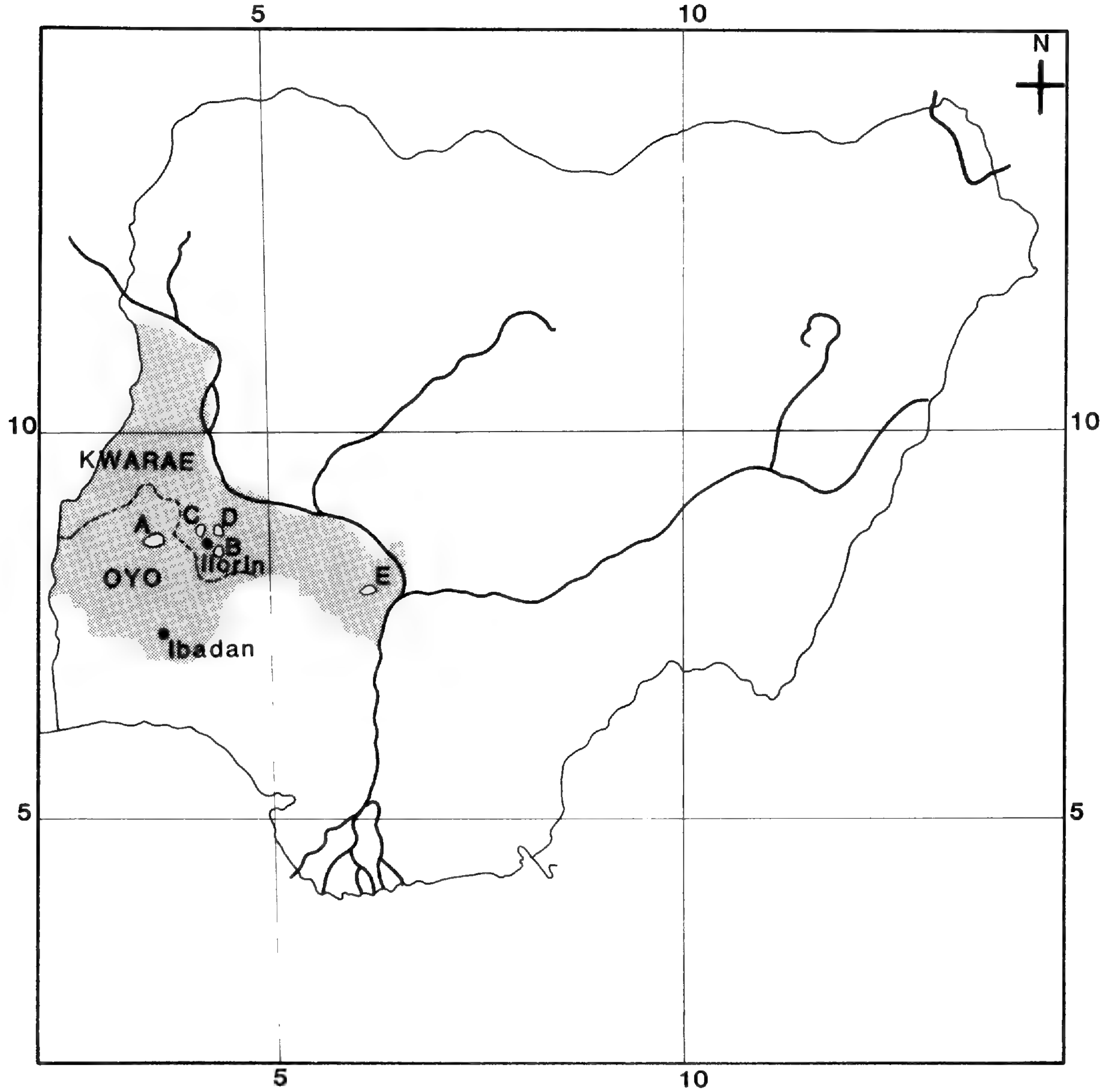


FIGURE 3. *Map of Nigeria showing locations where* Pancratium hirtum *populations were sampled in Oyo and Kwara States. Broken line = state boundary; circles = state capital city; solid lines = rivers.*

4E, 5E) consists of five pairs (1st, 2nd, 4th, 8th, and 11th) with median to submedian centromeres, and six pairs (3rd, 5th, 6th, 7th, 9th, and 10th) with terminal to subterminal centromeres. All the B-chromosomes are telocentric. One member of the second-longest autosomal pair has chromosome loss in the long arm, while one member of each of the eighth and ninth pairs shows loss in the short arm.

DISCUSSION

Previous chromosome counts in *Pancratium* show a chromosome number of $2n = 22$ (Ponnamma, 1978; Lakshmi, 1980). This number is confirmed here except that the presence of accessory chromosomes had not been reported previously in the genus.

The five karyotypes share a basic plan: the largest two and the smallest pairs of chromosomes are metacentric while all the others are acrocentric. Deviations from this plan consist of increase in the number of metacentrics (A, D, and E with an increase of one, two, and two pairs, respectively). Apart from these, there is evidence of structural changes in the chromosomes as a result of loss or gain of segments. This is common to all the karyo-

TABLE 2. *Sources of material of* Pancratium hirtum.

Morphotypes	Collection Site	Herbarium Voucher	Habitat
A	Iseyin–Igbetti about 150 km northwest of Ibadan	S00/2106 in University of Ilorin Herbarium (IUH)	deciduous woodland, in dark humus, under the shade of trees such as *Butyrospermum paradoxum*, *Lophira lanceolata*, etc.
B	Affon, 25 km southeast of Ilorin	S00/2199 in IUH	disturbed woodland, in dark humus soil on shallow inselbergs and foot of rocky hill under the shade of *Parkia biglobosa*
C	Shao, 22 km northwest of Ilorin	S00/2200 in IUH	open and exposed brown soil of old mats of *Afrotrilepis pilosa* on rock outcrops in savanna grassland
D	Oke-Oyi, about 20 km north of Ilorin	S00/2201 in IUH	open brown humus soil among rock boulders in savanna grassland
E	Okene–Lokoja Road, about 50 km from Okene	S00/2202 in IUH	dark brown gravelly clay–loam in floodplains in savanna woodland under stands of *Khaya senegalensis*

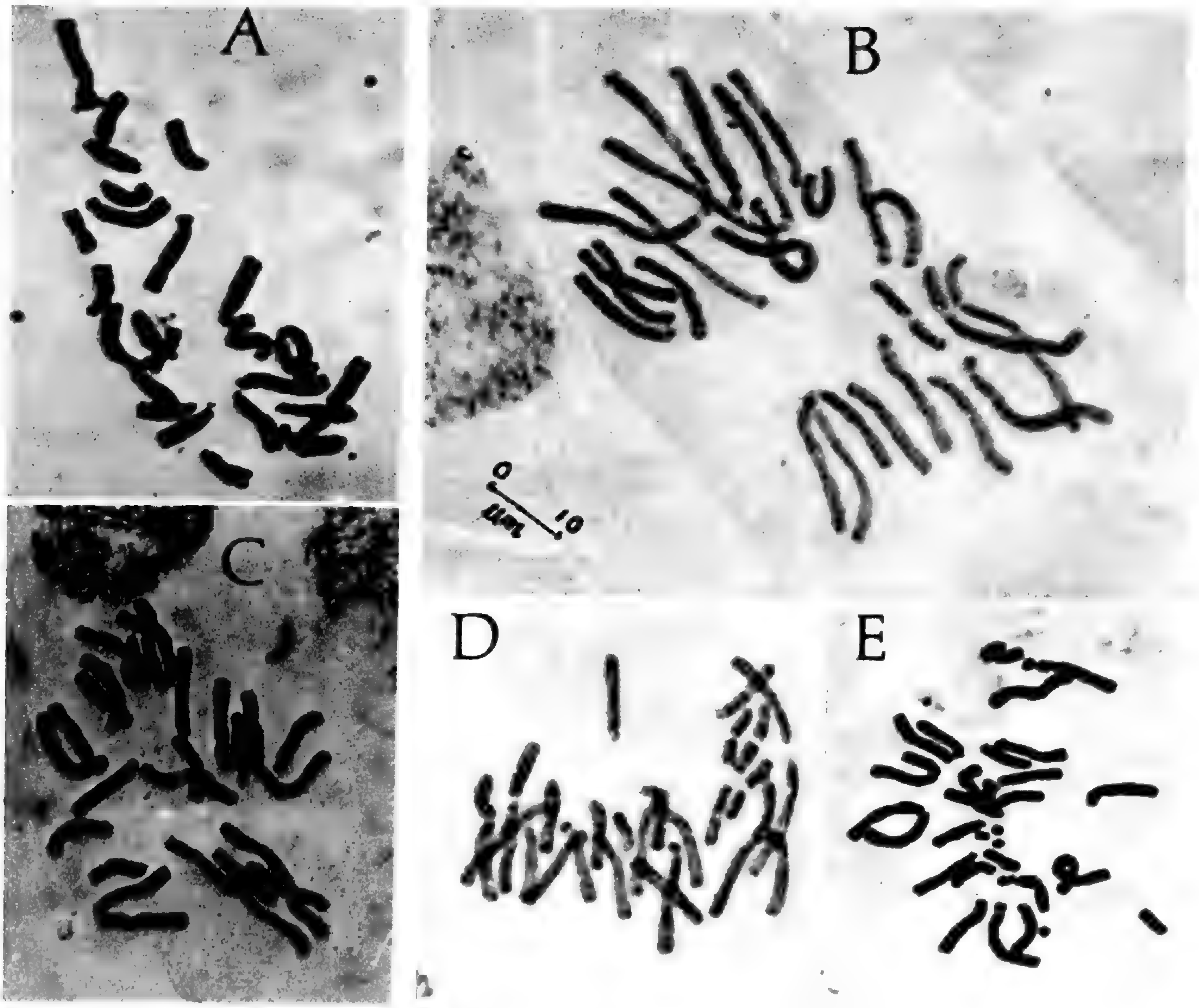


FIGURE 4. *Somatic metaphase complements of* Pancratium hirtum *morphotypes.*

TABLE 3. *Karyotype data for* Pancratium hirtum *(chromosome length in μm).*

Homologues		A	B	C	D	E
1	chromosome length	19.0	41.75	19.14	27.25	17.88
	r-value	1.1	1.2	1.0	1.17	1.37
	centromere location	median	median	median	median	median
2	chromosome length	16.0	27.25	15.42	25.80	14.5
	r-value	1.0	1.37	1.76	1.48	1.7
	centromere location	median	median	median	median	median
3	chromosome length	12.25	25.75	13.92	21.06	12.63
	r-value	2.3	3.29	3.64	2.56	11.25
	centromere location	submedian	subterminal	subterminal	submedian	terminal
4	chromosome length	10.75	21.25	11.92	17.75	11.88
	r-value	9.75	13.17	10.92	10.83	1.97
	centromere location	terminal	terminal	terminal	terminal	submedian
5	chromosome length	9.0	18.75	9.75	15.0	9.0
	r-value	8.0	14.0	13.63	10.25	35.0
	centromere location	terminal	terminal	terminal	terminal	terminal
6	chromosome length	7.5	16.0	9.25	13.0	8.25
	r-value	14.0	15.0	21.2	11.0	15.5
	centromere location	terminal	terminal	terminal	terminal	terminal
7	chromosome length	7.5	15.5	9.0	12.0	8.25
	r-value	14.0	14.5	8.0	13.4	7.25
	centromere location	terminal	terminal	terminal	terminal	terminal
8	chromosome length	7.0	15.0	8.58	10.92	7.38
	r-value	0	9.0	7.58	17.71	2.04
	centromere location	terminal	terminal	terminal	terminal	submedian
9	chromosome length	7.0	14.0	8.0	10.75	6.63
	r-value	6.0	13.0	11.0	13.33	3.0
	centromere location	subterminal	terminal	terminal	terminal	subterminal
10	chromosome length	6.75	13.13	7.33	10.0	6.25
	r-value	26.0	16.5	21.0	1.07	4.0
	centromere location	terminal	terminal	terminal	median	subterminal
11	chromosome length	5.5	11.38	6.33	8.67	5.67
	r-value	1.2	1.12	1.0	1.0	1.2
	centromere location	median	median	median	median	median
Accessory chromosomes		—	—	—	—	1.5, 1.0
		—	—	—	—	1.0, 1.0
	total chromatin length	216.5 ± 6.5	439.5 ± 18.5	237.3 ± 23.3	340.4 ± 49.8	219.14 ± 2.5

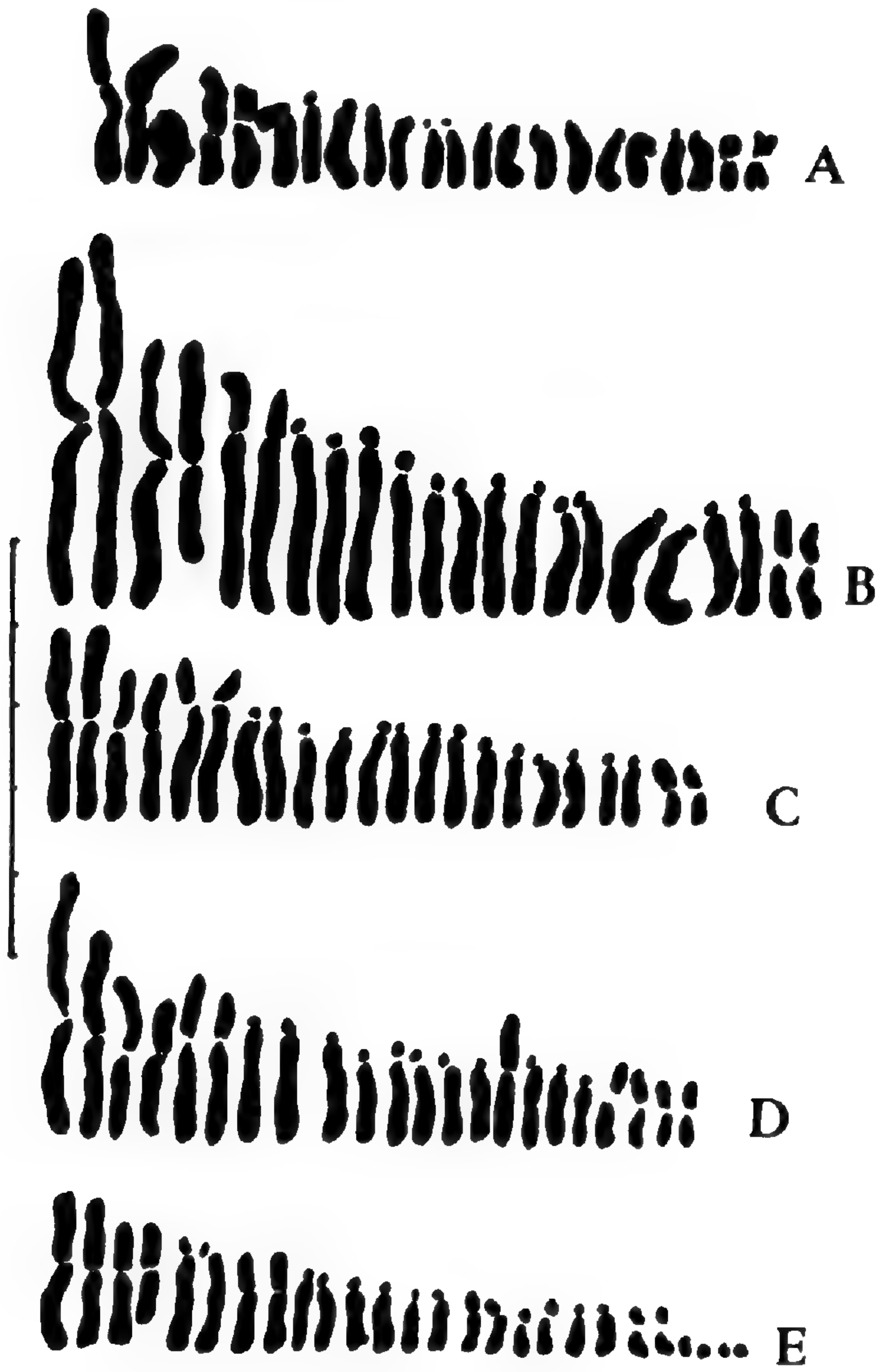


FIGURE 5. *Idiograms of the somatic chromosome complements of* Pancratium hirtum *morphotypes.*

types. Further deviation is the presence of B-chromosomes in E.

One way of generating genetic variation is by changes in chromosomal morphology, which are reflected in the karyomorphology of the population or the species (Coates, 1979; Coates & James, 1979). Another way is by genic changes that may not be immediately detectable (see Linhart et al., 1981). Thus, while genic changes may not be as immediately detectable as changes in the karyotype, karyotype variation may not be immediately accompanied by morphological divergence.

Karyotype variation in *P. hirtum* is associated with population differentiation and ecological preference. Dickinson & Antonovics (1973) maintained that karyotypic differentiation is a direct response of various biotypes to differing habitat pressures. White (1973) opined that chromosome rearrangements underlie reproductive isolation and, hence, speciation. It is probable that the ancestral population of *P. hirtum* in West Africa was at some time afflicted by some drastic environmental events that left survivors whose genetic systems suffered some changes. Such survivors occupied different ecological niches to which each had adapted for continued survival. Each has thus become ecologically isolated. Such a situation would be reinforced further by environmental barriers to long-distance pollen dispersal. The smallness of the population that would initially inhabit each ecological niche would enhance both chromosomal evolution and speciation, as asserted by Wright (1940), Bush et al. (1977), and Bengtsson (1980). These events would lead to reproductive isolation and thereby lay the foundation for further divergence of the population, culminating, in time, in the formation of several species. Again, the effects of the environment, especially edaphic factors, may be the major driving force in the karyotypic differentiation in this species. For instance, Morton's (1965) pl. 14, fig. 1 is similar to the karyotypes reported here, but it is not identical with any of them. All of Morton's materials were collected from Ghana. It is therefore possible that other karyotypes may still be encountered within the tropical West African region.

In conclusion, karyotype differentiation in *P. hirtum* has involved: (i) changes in chromosomal morphology resulting from loss or gain of chromosomal segments, which might have been accompanied by changes involving rearrangements of genes and/or gene blocks in inversions and translocations; and (ii) variations in the length of total chromatin material per somatic nucleus. Therefore, it seems likely that ecotype differentiation at the morphological level appears genetically fixed, and this is accompanied by varying degrees of karyotypic change, which presumably originated once the ecotypes had become established.

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THE ARCHITECTURE OF INFLORESCENCES IN THE MYRTALES[1]

Focko Weberling[2]

In Memory of Dorothea Weberling,
April 25, 1928–February 2, 1988.

ABSTRACT

In the Myrtales a great variety of inflorescences are found. In some families such as Oliniaceae or Alzateaceae (formerly included into Lythraceae) the inflorescences are exclusively of the more primitive monotelic type. In others gradual transitions from the monotelic to the polytelic type can be observed. Within the Lythraceae the genera Lawsonia, Lagerstroemia, *and* Galpinia *and—if included as subfamilies—the Punicoideae and Sonneratioideae still represent the monotelic type, whereas in the majority of the genera polytelic inflorescences are found. These often show a botrytic ramification, although the basic type of ramification is a thyrse. Among the great diversity of forms the gradual specialization of a short shoot–long shoot system can be observed, especially in the genus* Ginorea. *The same can be seen within the Combretaceae, which are polytelic throughout. As in most Myrtales families, phylloscopic accessory buds or branches are frequently occurring and sometimes form a determinating factor for the shape of a flowering plant. In Onagraceae polytelic structure of inflorescences is also manifested throughout the family and florescences as botrya or spikes are known. On this basis an impressive diversity exists, especially in the variations of the proportions between the terminal main florescence and the extension of the enrichment zone, the number and size of paracladia, the length of the internodes, and the possibility of a reversion of the inflorescence apex to vegetative growth, commonly called proliferation. The latter often occurs in the inflorescences of Myrtaceae in which the "central type" and perhaps the phylogenetically primitive form is a monotelic thyrsoid or a panicle. Even in proliferating or in truncate synflorescences the monotelic character is evident by the fact that all paracladia, including those with more than one pair of flower-bearing branches, are provided with a terminal flower. The efforation of the proliferating inflorescence can be delayed for such a long time that the proliferating shoot may even form branches above the flower-bearing zone. Thus inflorescences of this shape sometimes were regarded as "intercalary inflorescences." In some cases (some species of* Eugenia*) the transition to the polytelic type seems to be complete. In the majority of the Penaeaceae the inflorescences forming thyrsoids or stachyoids follow the monotelic type. Some facultatively or constantly truncate synflorescences form a transition to taxa with polytelic synflorescences. In Psiloxylaceae the flower-bearing systems are brachyblasts reduced to their botrytic florescence and inserted on older axes. Variety of inflorescences in Melastomataceae corresponds to the size of the family but shows less diversity than Myrtaceae. The inflorescences are monotelic. Cases of complete transitions to polytelic structures were not found. Even truncation seems to be rare and only a single case is reported for* Medinilla magnifica. *On the other hand, proliferation is not rare.*

FUNDAMENTAL FEATURES OF INFLORESCENCE MORPHOLOGY

Since differences and conformities in the arrangement of flowers are characteristic for smaller or larger taxonomic groups, these criteria have been used in many ways since the very beginning of systematic botany. For this purpose an elaborate descriptive terminology is in use designating the different modes of foliation and especially of ramification by well-known terms such as raceme, spike, umbel, panicula, etc. Many efforts have been made to establish a natural system for the immense diversity of inflorescences. The results, however, remained insufficient, primarily because the empirical basis was too small. Above all, it does not follow that the flower-bearing parts

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to which a term such as "spike," "umbel," or "dichasium" is applied are necessarily homologous. For that reason, one cannot achieve correct interpretation of the morphology of inflorescences by focusing exclusively on those flower-bearing ramification systems that by some conspicuous quality appear to be "units." One must also consider the position of these entities within the structural plan of the whole plant. Only in this way it is possible to ascertain which flower-bearing elements may legitimately be compared as identical structures. This, however, is connected with the elucidation of the structural plans of flowering plants and therefore needs a broad empirical basis. According to Troll (in Troll & Weber, 1955; Troll, 1964, 1969), the great diversity of inflorescences is due to the variation of two types only: the polytelic and the monotelic types.

In the *monotelic* inflorescence (Fig. 1 I), the apex of the inflorescence axis commonly ends with a *terminal flower*. This also applies to all the floral branches below the terminal flower. All of these branches, whether branched or not, are homologous elements, and they are all referred to by the term *paracladia* (pc; singular: paracladium), because these branches repeat the structure of the main axis of the flowering system. Accordingly, their ramifications are called paracladia of the second to n^{th} order. The whole area that produces flowering paracladia (Bereicherungstriebe, "enriching branches") may be designated as the *enrichment zone* (Bereicherungszone, "paracladial zone"). In the lower part of the flowering shoot this zone is commonly preceded by an *inhibition zone*, within which the development of paracladia is inhibited more or less abruptly (Figs. 1, 3 I). The same zonation can be recognized in the individual paracladia if these are not reduced in any way. In perennials the axillary buds at the base of the whole stem do not develop within the same season but will give rise to innovation shoots at the beginning of the following season. Therefore, this area has to be distinguished as an *innovation zone*.

In the *polytelic* type of inflorescence (Fig. 1 II), which is no less frequent in angiosperms, there is no terminal flower at the summit of the primary axis. The shoot apex remains *indefinite* after developing a smaller or greater number of lateral flowers, the last of which often do not complete their development but atrophy in the same way as the end of the axis. This apical flowering system, which is composed of lateral flowers only (or cymes, see below), is a characteristic feature of this type of inflorescence and is now referred to by the special term *florescence*. The term "florescence" should not be confused with the term "*in*florescence," which has no specified morphological signification and may be used to designate any flower-bearing ramification system. (The same applies to the term "partial *in*florescence," which can designate without any morphological relevance any part of a flowering system, while the term "partial florescence" means a distinct part of a florescence, namely a cymose branch.) Instead of ending in a single flower, as in the monotelic inflorescence, the floral axis here terminates in a multiflowered so-called polytelic florescence.

If the lateral flowers composing the florescences are provided with prophylls (Fig. 2 I), these may produce secondary flowers or dichasial or monochasial flowering systems from their axils (Fig. 2 II). This mode of ramification, in which the production of branches is restricted to the axils of prophylls of consecutive order, is called cymose (see Schimper, 1835; Wydler, 1851a: 305 ff.; Eichler, 1875: 34 ff., but not in the strict sense; Troll, 1957: 234 ff.; 1964: 63). The diverse sympodial ramification systems resulting from this mode of branching (Fig. 2 III–VI) are often briefly called cymes (cymae, see p. 231). In such cases the florescence consists of cymose *partial florescences* (pf) as, for example, in the inflorescences of most Scrophulariaceae and Labiatae (Fig. 3 III). Within both families, the derivation given here is verified by many transitional forms.

Below the florescence terminating the main axis there may be some branches that repeat the structure of the main stem by producing

FIGURE 1. *Diagrams of a (I) monotelic and (II) polytelic inflorescence. T, terminal flower; pc, paracladium; pc', pc", paracladia of second and third order; mf, main florescence ("Hauptfloreszenz"); cof, co-florescence; bi, basal internode ("Grundinternodium"); fi, final internode ("Endinternodium"); pz, paracladial zone ("Bereicherungszone"); inh.z. inhibition zone ("Hemmungszone"). From Troll (in Troll & Weber, 1955), slightly modified.*

florescences themselves and that therefore are also called *paracladia.* Their florescences are termed *co-florescences* in order to distinguish them from the main florescence of the main axis. The apices of the co-florescences remain *indefinite* like those of the main florescence. Thus the whole flower-bearing ramification system appears as a system of florescences: a (polytelic) *synflorescence.* In the case of a monotelic inflorescence, the synflorescence consists of a terminal flower and (monotelic) paracladia.

Within the polytelic synflorescences, the same zonation can be observed as in monotelic flowering systems (Fig. 3 II, III): an *enrichment zone* (Bereicherungszone: Troll), which precedes the main florescence, an *inhibition zone* (Hemmungszone: Troll), and in perennials, an *innovation zone.* The three zones together form the so-called *hypotagma.* The florescence is separated from the paracladial zone by a *basal internode* (Grundinternodium: Troll), which may be of remarkable length.

It also proved to be useful to designate the ultimate internode preceding the terminal flower of a monotelic system by a special term: *final internode* (Grundinternodium, Fig. 1 I).

The polytelic type probably has been derived repeatedly from the monotelic during the evolution of angiosperms *by reduction of the terminal flower* and *specialization of the paracladia* of the monotelic system into either single lateral flowers or lateral cymes, which then constitute elements of the florescences, whereas the others are differentiated as par-

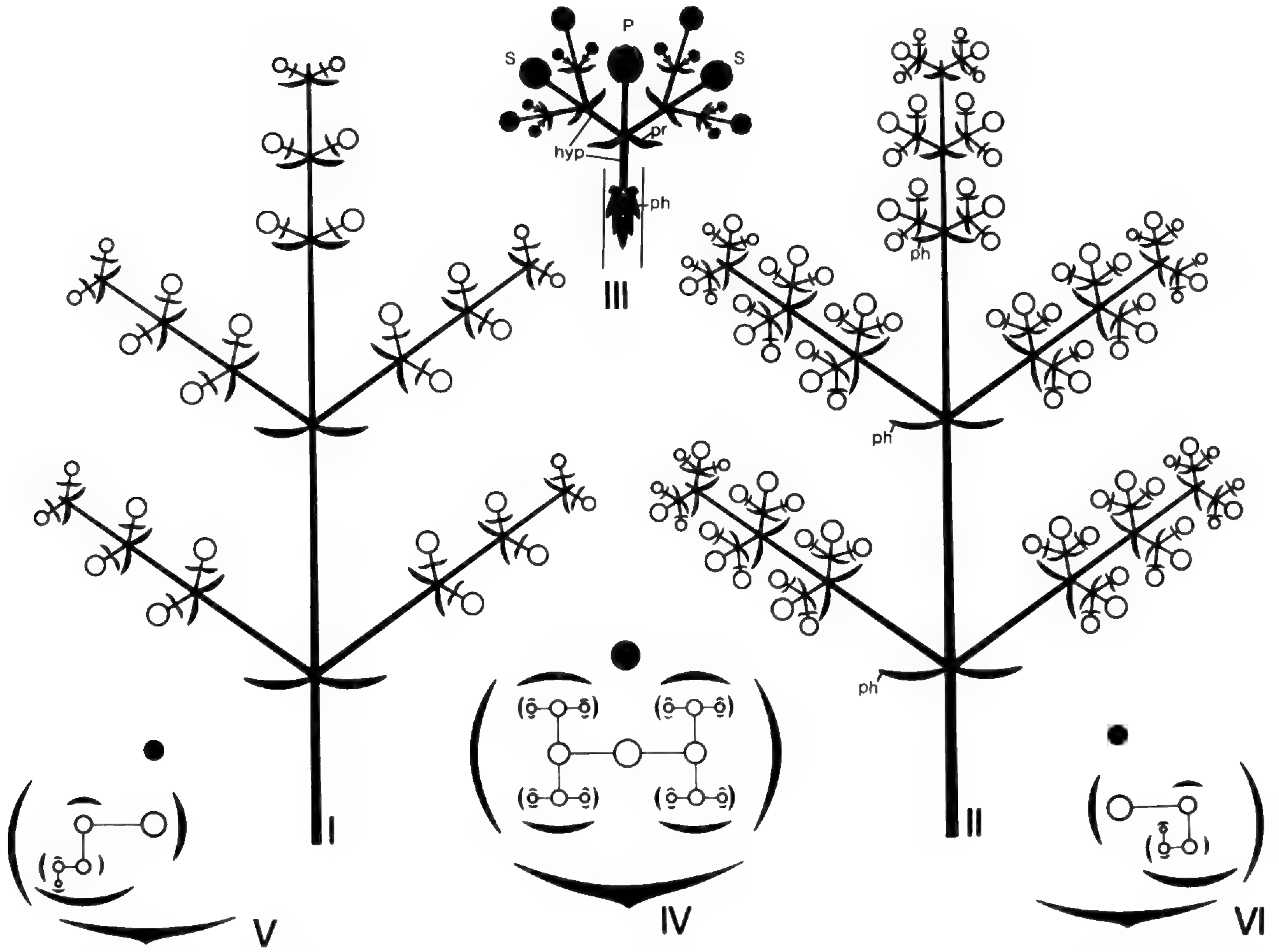


FIGURE 2. *I, II. Vertical diagrams of polytelic inflorescences.—I. Heterothetic diplobotrys.—II. Diplo-thyrse; this inflorescence can be deduced from the diplobotrys in I by the assumption that the prophylls of second order are fertile. III–VI. Vertical (III) and transverse (IV) diagrams illustrating diverse forms of cymose ramification.—III, IV. Dichasium.—V, VI. Monochasia.—V. Scorpioid cyme (cincinnus).—VI. Helicoid cyme (bostryx). P, primary flower; S, secondary flower; ph, pherophyll ("Tragblatt," "Deckblatt"); pr, prophyll; hyp, hypopodium. III–VI from Troll (1959b), modified.*

acladia (of the polytelic type), which themselves form florescences (Weberling, 1961, 1965, 1983a, b; Troll & Weberling, 1966).

In both monotelic and polytelic types, the different elements may vary in many different quantitative respects according to the principle of variable proportions: in polytelic synflorescences, the main florescence may be extended and the number of its flowers may be increased in many ways, or it may be reduced or even be missing altogether (truncate polytelic synflorescences). In both cases the paracladia may be well developed or reduced, their number may be increased, or they may be missing or modified in different ways. The development of paracladia may be basitonic or acrotonic (see below). Variation also exists in the diversity of phyllotaxis and foliation, shortening or lengthening of the internodes in different parts of the plant, different intensity and different modes of ramification, and so on. Especially in woody plants the zonation of flowering systems can be altered extremely by, for example, the complete reduction of the inhibition zone.

An essential difference between the types seems to be that in inflorescences of the polytelic type the shoot apex of the inflorescence axis remains indeterminate. This also occurs, however, in some monotelic inflorescences in which the terminal flower aborts. In such *truncate monotelic synflorescences,* however, the paracladia usually end in terminal flowers, thus demonstrating the monotelic character of the whole system.

In many lianas, the growth of the main

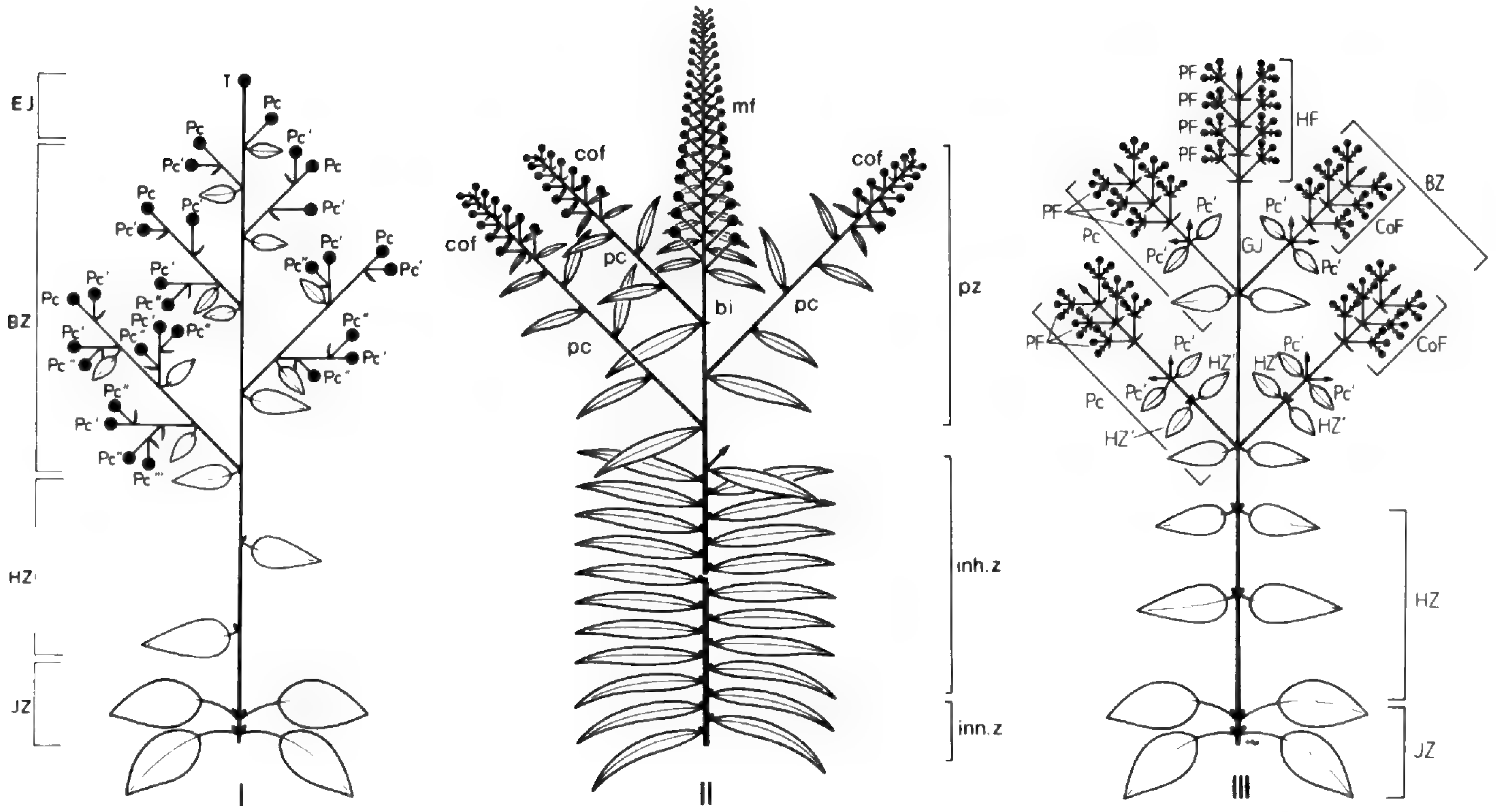


FIGURE 3. *I. Diagram of a monotelic inflorescence in form of a panicle. T, terminal flower; Pc, Pc′, Pc″, Pc‴, paracladia of first to fourth order; EJ, final internode ("Endinternodium"); BZ, pz, paracladial zone (enrichment zone); HZ, inh.z., inhibition zone; JZ, inn.z., innovation zone.—II, III. Diagrams of polytelic inflorescences with the main florescence (HF, mf) and the co-florescences (cof) in form of botrya (II) or of thyrses (III). GJ, bi, basal internode; pc, pc′, paracladium of first and second order; HZ′, inhibition zone of pc; PF, partial florescence; the rest as in I.*

axis is indefinite. Therefore the main axis, though it may produce lateral flower-bearing branches, never ends in a terminal flower. The sample applies to rosette geophytes with indefinite main axes, as in *Plantago* or *Phyllactis* (Valerianaceae). In the latter, the apex of the rosette changes periodically from the formation of absolutely sterile zones to the formation of fertile regions, in which thyrsoid "partial inflorescences" originate from the axils of the rosette leaves. (The same applies to the so-called *proliferating inflorescences* of many Myrtaceae.) In cases like these, the monotelic or polytelic character of the inflorescence is revealed by the monotelic or polytelic character of the paracladia.

Thus the question of whether the terms monotelic and polytelic correspond to the old classification of inflorescences into two groups called "indeterminate" (indefinite, racemose) and "determinate" (definite, cymose) must be answered in the negative. Apart from this answer, the statement given by Rickett (1955: 419), that "current usage" of this classification, "at least in English, is both confused and inaccurate," still refers to this classification in general. To a great extent this is due to the fact that the "cymose type" is often equated with an "overtopping" of the (somewhat sympodial) branching system (Rickett, 1955: 426; Goebel, 1931: 81 ff.).

However, it is neither necessary nor possible to renounce all the classical descriptive terms used for the description and distinction of flower-bearing ramification systems. Many of these terms can be used without any change, and some need to be clarified and specified in their application. This also has been done by Troll (1964: 33 f.), who partly referred to Eichler (1875: 34 f.) in his classification of descriptive terms, which may be repeated here:

I. *Simple inflorescences:* botrys (raceme), spike (stachys), spadix, umbella, capitulum.
II. *Complex (compound) inflorescences*
    a. with racemose partial inflorescences: diplobotrys (and related forms: bispica, bi-umbella, etc.), panicula.

b. with cymose partial inflorescences: thyrse (including thyrsoid), cymoid.

Among the compound inflorescences the panicle is distinguished by the main axis ending in a terminal flower (as do all of the branches). Thus the panicle is a determinate inflorescence, and this term never refers to any indeterminate inflorescence, as it often is used by English language authors.

If all branches of the panicle are reduced to single flowers (uniflorous paracladia), a botryslike system results that, however, still ends in a terminal flower and therefore is termed a "botryoid"; if the flowers are sessile, a spicoid. Complete reduction of all lateral flowers (all paracladia) leads to a uniflorous system (single terminal flower).

The term thyrse, which was often confused with the term panicle (Čelakovský, 1893: 45), needs some further comments too. (There is, of course, some connection between panicles and thyrsoids, as seen, e.g., in the so-called thyrso-paniculate systems of *Sambucus* and *Viburnum*: Troll & Weberling, 1966.) The term, used by Linnaeus for a "coarctate panicle of ovate form" (Rickett, 1955: 443), was specified by De Candolle (1827: 417) as "compound of small cymes along an axis of indefinite growth" (Rickett, 1955: 443; Bravais & Bravais, 1837: 197: "groupe de cimes disposées d'après l'évolution centripète comme les fleurs le sont dans l'épi"). It was applied, however, to determinate thyrsic branching systems as well (see Troll, 1964: 63 f.).

Briggs & Johnson (1979: 177, 247) restricted the term thyrse to a "blastotelic inflorescence with a multinodate main axis that bears lateral cymes"; thus a determinate thyrselike ramification system should be termed a thyrsoid (which appears consequent, as this term is comparable with terms such as botryoid, spicoid, cymoid in the terminology of Troll). Although we fear that a change of terminology used hitherto in so many publications might cause new confusion, we hesitantly follow this suggestion of Briggs & Johnson. Consequently, and in accordance with these authors, the adjective "thyrsoid" must be replaced by "thyrsoidal" (thyrsusartig), while the adjective thyrsic (thyrsisch) should be used now for a thyrse in the restricted sense.

The terms used here are illustrated by Figure 2 II–VI. The vertical diagram in Figure 2 II shows a diplo-thyrsic inflorescence. The distal part of it, comprising three pairs of lateral cymes, forms a simple thyrse (monothyrsus, haplothyrsus), whereas the branches originating from the two proximal nodes are thyrses themselves (named "Spezialthyrsen" by Troll, "special thyrses," infrathyrse). In this diagram, the lateral cymes are triadic, i.e., comprising three flowers only. They may, however, produce more flowers by continuous branching from the consecutive axes (Fig. 2 III). The characteristic trait of this mode of ramification is that each axis before ending in a terminal flower produces two and only two leaves: the *prophylls*, which are mostly transversal-opposite and identical with the prophylls (the first two leaves) of other branches. In monocotyledons there is frequently only one prophyll, often in adaxial position. The internode preceding the prophyllar node is the *hypopodium*, the internode following the prophyllar node and terminating in the flower is the *epipodium*. If the two prophylls are separated by another internode, this is called the *mesopodium*. From the axils of the prophylls of the primary flower arise branches that end in the secondary flowers and bear two prophylls of second order. From the axils of the prophylls of second order the ramification can continue in the same way. This mode of cymose ramification can result in a complete symmetrical dichasium as shown in Figure 2 IV. In many cases, however, the continuation of the ramification is limited at a certain stage to one of the two prophyllar axils, thus resulting in the formation of a monochasium, either a scorpioid cyme (cincinnus, Fig. 2 V) or a helicoid cyme (bostryx, Fig. 2 VI). In the monocotyledons a rhipidium or a drepanium can be formed.

In thyrsoidal inflorescences, as displayed in a great variety of forms within the Caryophyllaceae for example, a high degree of diversity can result from differences between paracladia in vigor of development. In many cases the paracladia are more extensively developed toward the base of the plant (*basitonic* ramification) or, if the paracladial zone is preceded by an inhibition zone, toward the middle of the plant (*basi-mesotonic*; in *mesotonic* ramification, vigor of the paracladia increases from both ends to the middle part of the flowering system), whereas in others the distal paracladia are the most vigorous (*acrotonic* ramification). Examples for these models can be found within the genus *Silene*.

In thyrsoids with decussate foliation and ramification (as in *Silene*), extreme acrotonic branching results in the exclusive development of the uppermost pair of cymose paracladia, which far overtop the main axis by vigorous development and copious branching. Such dichasia as represented, e.g., by *Silene vulgaris* (Moench) Garcke often have been regarded as ideal "cymose inflorescences." They are, however, connected by many transitional forms with basi-mesotonic thyrsoids as represented, e.g., by *Silene nutans* L. In other plants transitions can even appear in the same individual, if the subdistal pair of paracladia develops at a later stage. Thus these "dichasial" inflorescences do not represent an inflorescence type of their own but must be regarded as thyrsoids with acrotonic ramification. The complete inflorescence only simulates a cymose ramification, which actually takes place in the cymose paracladia. This induced Troll (1959a: 115; 1964: 102) to name this extreme form of an acrotonic thyrsoid a cymoid. In similar fashion, monochasial or pleiochasial overtopping of the main axis can be included in this term.

As is well known, foliation and phyllotaxis often change in the transition from the vegetative to the flower-bearing parts of a plant. The foliage leaves may be diminished from leaflike *frondose* to smaller *frondulose* organs or even convert by change of diverse proportions into *bracteose* organs (*bracts*), which are often more or less scalelike. The subtending leaves of the flower-bearing branches, the *pherophylls* (Briggs & Johnson, 1979: 179, 246; "Tragblatt," "Deckblatt"), may thus be frondose, frondulose, or bracteose.

The *mode of efflorescence* can, but need not be characteristic for the diverse forms of inflorescences. One should expect that anthesis of flowers follows the way of their initiation, advancing from, for example, the oldest flowers at the base of a botryoid to the top of this flowering system. In monotelic synflorescences, however, the terminal flower usually blooms before the neighboring laterals. To some extent this dominant position results from the fact that the organs of the terminal flower arise from the inflorescence apex immediately, whereas the lateral flowers are formed by lateral apices. Thus the terminal flower is somewhat in advance in relation to the ultimate lateral flowers. It is not rare for the flowers or partial inflorescences in the axils of the ultimate leaves preceding the terminal flower to be retarded or even to abort. Thus the terminal flower can be preceded by sterile leaves that are called "Zwischenblätter" (Nordhagen, 1937: 12; Troll, 1964: 15) or *metaxyphylls* (Briggs & Johnson, 1979: 179, 244). Beyond that, cases of a complete basipetal efflorescence—advancing from the top to the base of a flowering system—are not rare (*Meconopsis*). In the florescences of polytelic inflorescences, the efflorescence usually advances from base to apex (acropetal). For thyrses this means, of course, that an acropetal sequence of primary flowers that open first is followed and overlapped by a secondary sequence of the secondary flowers of the cymose partial florescences (Troll, 1957: 380 f.). There are also florescences with divergent effloration, the best known example may be *Dipsacus*. However, the sequence of paracladia in polytelic systems mostly unfolds in a basipetal order. Starting with the paracladia immediately below the main florescence, the progression of unfolding usually depends on the vigor of the individual and the length of the flowering period, thus determining the extension of the paracladial zone and the inhibition zone (Troll, 1950). Nevertheless, in annual or hapaxanthic plants this progression can reach the base of the plant, and the most basal paracladia can, if they are fully developed, be the most vigorous.

ONAGRACEAE

Polytelic structure of inflorescences is manifested throughout the Onagraceae. The florescences are botrya or spikes. Even when the pedicels remain undeveloped, the inflorescences frequently (e.g., *Oenothera biennis* L., Fig. 4) look like botrya, because pedicels are simulated by the long gynoecium of the epigynous flowers. In some taxa, e.g., *Epilobium alsinoides* Cunn. subsp. *tenuipes* (Hook. f.) Raven & Engelhorn, the pedicels lengthen after anthesis. Plants in the flowering state, as shown for the case of *Epilobium angustifolium* (Fig. 3 II), usually show a clear zonation: below the main florescences there is a more or less extended enrichment zone (paracladial zone, pz) which stretches down the primary axis until the development of paracladia is inhibited. Transition between this "inhibition zone" (inh.z., Hemmungszone) and the paracladial zone may be more or less abrupt. In perennials the axillary buds at the base of the whole stem do not develop within the same season but will give rise to innovation shoots at the beginning of the following season ("innovation zone," inn.z., Innovationszone).

Diversity in appearance of the different genera and species depends highly on quantitative variations of these zones, different lengths of the internodia, and different foliation of the florescences.

The phyllotaxis can be alternate or decussate, sometimes even verticillate mostly with three leaves at the same node. It is not rare to find that in the transition from the hypotagma to the main florescence the position of the leaves changes from decussate to alternate (e.g., *Epilobium montanum* L.).

The subtending leaves of the flowers can be quite different within the same genus. They can be bracteose as in *Fuchsia arborescens* Sims (Fig. 15 II) or foliaceous as in *Fuchsia magellanica* Lam. (Fig. 14), giving the inflorescence a "naked" or "leafy" shape. In many species of *Epilobium* or, for example, in *Oenothera biennis* (Fig. 4), they are leafy in the basal part of the florescences, diminishing distally, and finally becoming bracteose (frondo-bracteose foliation). Only in *Circaea* are the subtending leaves of the flowers missing. With the exception of the genus *Ludwigia*, the flowers do not bear prophylls.

Many representatives of the family are half-rosette plants, which means that the primary

FIGURE 4. *Onagraceae.* Oenothera biennis.—*Top, left. Flowering plant.—Top, center. The same plant with the flowers cut off to show the frondo-bracteose foliation.—Top, right. With developing paracladia.—Bottom, left. Plant with fully developed paracladia zone.—Bottom, right. Proliferation apex of the main florescence. (Original photographs from Troll.)*

FIGURE 5. *Onagraceae.*—*I.* Oenothera rosea.—*II.* O. stricta.—*III.* O. fruticosa.

axis starts with the formation of a leafy rosette and continues its development with elongated internodes. In *Oenothera biennis*, *O. muricata* L., and some other species, the rosette leaves that develop during the first year of the biennial life cycle do not persist until the plant is flowering. This plant in full development shows a large main florescence, a preceding paracladial zone, and a long zone of inhibition. This basi-mesotonic support of ramification is shown for *O. biennis* in Figure 4. In vigorous plants of *O. biennis* the paracladia can develop strongly and in great number (Fig. 4). In species forming typical half-rosette plants, such as *O. indecora* Cambess., *O. rosea* L'Hér., and *O. stricta* Ledeb., the development of vigorous "rosette shoots" (Rosettentriebe) can be observed (Fig. 5). They form a second series of paracladia separated from the upper paracladia by the zone of inhibition.

Usually the extension and the stoutness of the p.z. depends on the vigor and age of the plants. In the annual *Camissonia scapioidea* (Torrey & A. Gray) Raven and *C. walkeri* (A. Nelson) Raven subsp. *tortilis* (Jepson) Raven, the paracladial zone can be extended over the whole elongated part of the main shoot, leaving no residuum of the zone of inhibition between the upper paracladia and the rosette shoots ("simple or branching from the base . . . the stems quite simple above," Abrams, 1951: 206). These plants show a pronounced basitonic support in the development of the paracladia and a scapelike prolonged internode that precedes the main florescence. Especially within the *Oenothera* alliance (in tribe Onagreae), the proportions of the main florescence, the paracladial zone, and the inhibition zone and the development of the internodes can be modified in different ways and can be very characteristic for some taxa. Sometimes, in *Camissonia cheiranthifolia* (Hornem. ex Sprengel) Raven, for example, the development of paracladia can be restricted to the basal rosette. The reason is often that this rosette comprises the whole hypotagma while the main florescence is the only part of the axis with elongated internodes. The early development of these basal paracladia is shown for *O. fruticosa* L. in Figure 5.

FIGURE 6. *Onagraceae.* Oenothera laciniata, *showing a small main florescence, a short inhibition zone, and vigorous rosette shoots. (USA. Texas: Brazos Co.,* N. Bean 331 *(M, as* O. sinuata*).)*

In some species, for example, *Oenothera laciniata* (L.) Hill (Fig. 6), *Camissonia hirtella* (Greene) Raven, and *Calylophus hartwegii* (Benth.) Raven, even the main florescence often or always remains relatively short and few flowered. In *O. caespitosa* Nutt., *Camissonia palmeri* (S. Watson) Raven, and many other species, the internodes of the primary axis, including the main florescence, are undeveloped throughout ("Caespitose perennial, acaulescent or nearly so," Abrams, 1951: 195). Among these species, *O. triloba* Nutt. (*O. rhizocarpa* Sprengel, *Lavauxia triloba* Spach), a hapaxanthic taprooted plant, is of special interest because of its basicarpous hygrochastic capsular fruits (Sernander, 1927: 73 ff.). In such cases the paracladia, however, can be well developed, forming plagiotropic (Figs. 7, 8) or ascendent branches with frondose (co-)florescences.

In other rosette plants, for example, *Camissonia graciliflora* (Hook. & Arn.) Raven (Fig. 15 III), even the paracladia, if developed, remain short, the whole plant forming a single rosette (also *Oenothera ovata* Nutt., *O. xylocarpa* Cav., *O. nana* Griseb., Figure 9, *C. tanacetifolia* (Torrey & A. Gray) Raven, Figure 10, *C. subacaulis* (Pursh) Raven, and *O. formosa* Brandegee), or a cespitose tuft.

In contrast to *Oenothera triloba*, which always retains its rosette stage, *O. macrocarpa* Nutt. subsp. *macrocarpa* (*O. missouriensis* Sims) is a perennial tap-rooted geophyte. After the juvenile rosette stage, it grows with slightly prolonged internodes and can develop innovation shoots, which can innovate secondarily. The same could possibly apply to *O. californica* (S. Watson) S. Watson, which Abrams (1951: 195) described as "perennial from underground rootstalks, rather coarse stemmed, rarely simple."

In the fruiting plant of *Oenothera triloba* (Fig. 8), the top of the primary axis is crowned by a bunch of foliage leaves as a result of the proliferating growth of the florescence axis. This proliferation may occur repeatedly in the same primary axis, thus forming zones with buds of paracladia alternating with single flowers in the axils of more or less foliaceous leaves. Proliferation can be observed in many additional species of *Oenothera*, for instance, *O. macrocarpa* and *O. biennis* (Fig. 4), and in many other members of the family, since the predisposition if frequently given by a strong florescence axis with more or less leafy pherophylls.

FIGURE 7. *Onagraceae.* Oenothera triloba. *(USA. Texas: Tarrant Co., Fort Worth,* A. Ruth 70 *(M).)*

In *O. triloba*, *O. macrocarpa*, and *O. biennis*, it is the apex of the main florescence that returns to vegetative growth (Spätprolifikation, Troll, 1960: 116, prolification of the florescence, retarded proliferation), whereas *O. multicaulis* Cav. (Figs. 11, 12) does not form a main florescence at all. Rather, it develops long paracladia from the axils of rosette leaves (Frühprolifikation), which can grow straight upright (Fig. 11) or more or less ascendent (Fig. 12).

In most herbaceous genera of Onagraceae the same architecture and zonation as described for the basi-mesotonic ramified *Epilobium angustifolium* (Fig. 3 II) and for *Oenothera biennis* (Fig. 4) can be observed. This applies to many species of *Epilobium* and all or most species of *Boisduvalia*, *Clarkia* (except species with decumbent or prostrate stems), *Gaura* and allied genera, *Lopezia*, and *Circaea*, although some species of *Boisduvalia*, e.g., *B. densiflora* (Lindley) S. Watson (Troll, posthumous notices), can be branched from the base.

Plagiotropic growth, often connected with proliferation, is also characteristic for *Clarkia*

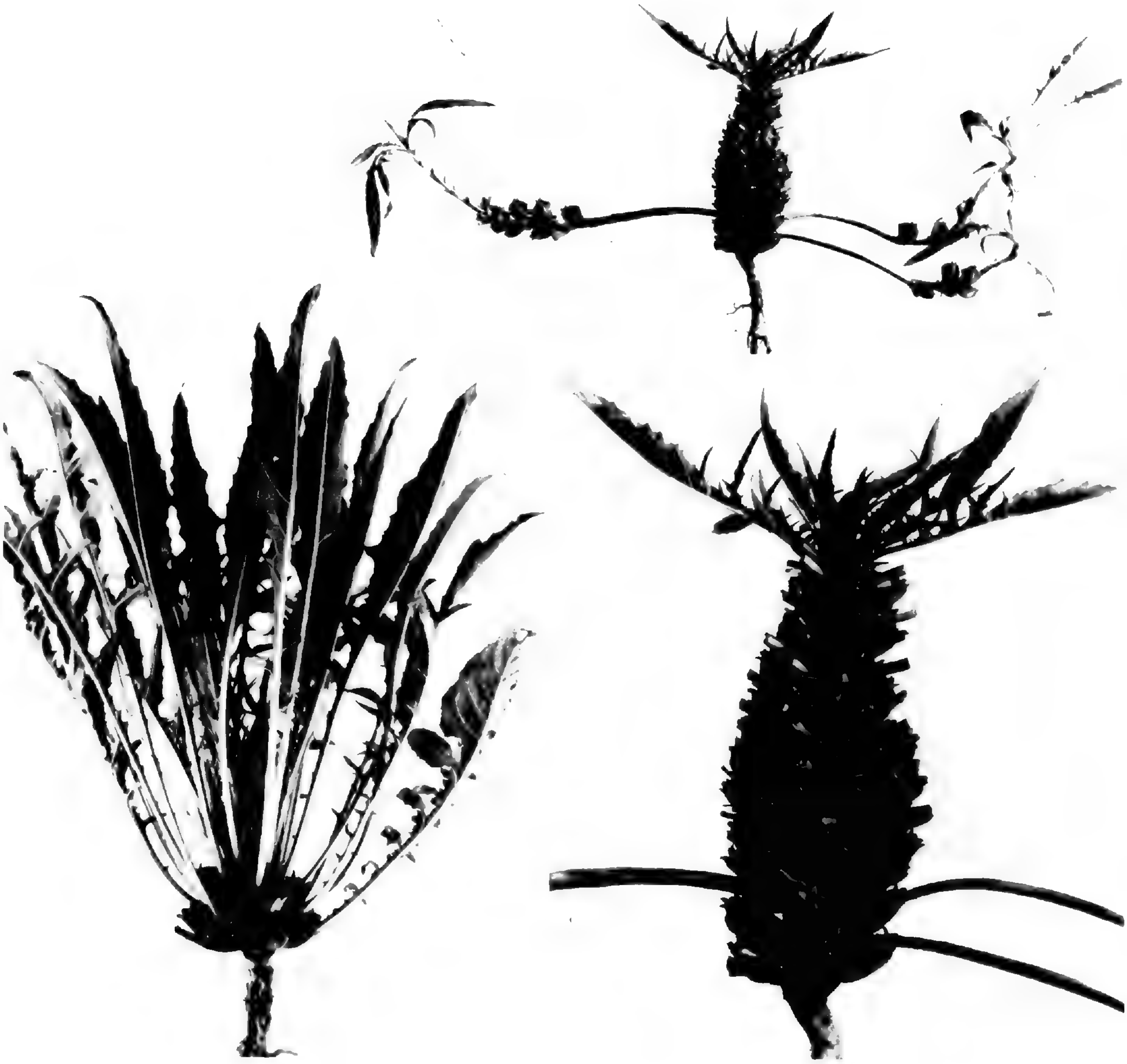


Figure 8. *Onagraceae.* Oenothera triloba.—*Left. Fruiting plant with proliferating main axis.—Top, right. Fruiting plant with terminal vegetative rosette and stolonlike fruiting and proliferating paracladia.—Bottom, right. Detail. (Original photographs from Troll.)*

prostrata Lewis & Lewis, *C. davyi* (Jeps.) Lewis & Lewis (Lewis & Lewis, 1955, fig. 11b, c), *Camissonia strigulosa* (Fischer & Meyer) Raven, and many species of *Ludwigia.*

Plants growing under severe environmental stresses may develop reduced inflorescences only. This is especially common in annuals. Often only the main florescence is formed, and in extreme but not uncommon cases only the lowermost flower of the main florescence comes to anthesis. *Clarkia bottae* (Spach) Lewis & Lewis (Fig. 13 I) is an example. In such cases this lowermost flower can be erected in pseudoterminal position, which also is characteristic for *Epilobium alpinum* L. f. *pusillum* Hausskn. The same occurs facultatively in *E. montanum* (Fig. 13 II).

For the genus *Epilobium* two features must be mentioned, each of them characteristic for a great number of species. In many species the buds of the innovation zone develop more or less proleptically into epigeal or subterranean stolons. If these stolons creep at the surface of the soil, their leaves are more or less foliaceous, as in *E. alpinum* L. The subterranean stolons bear scalelike cataphylls.

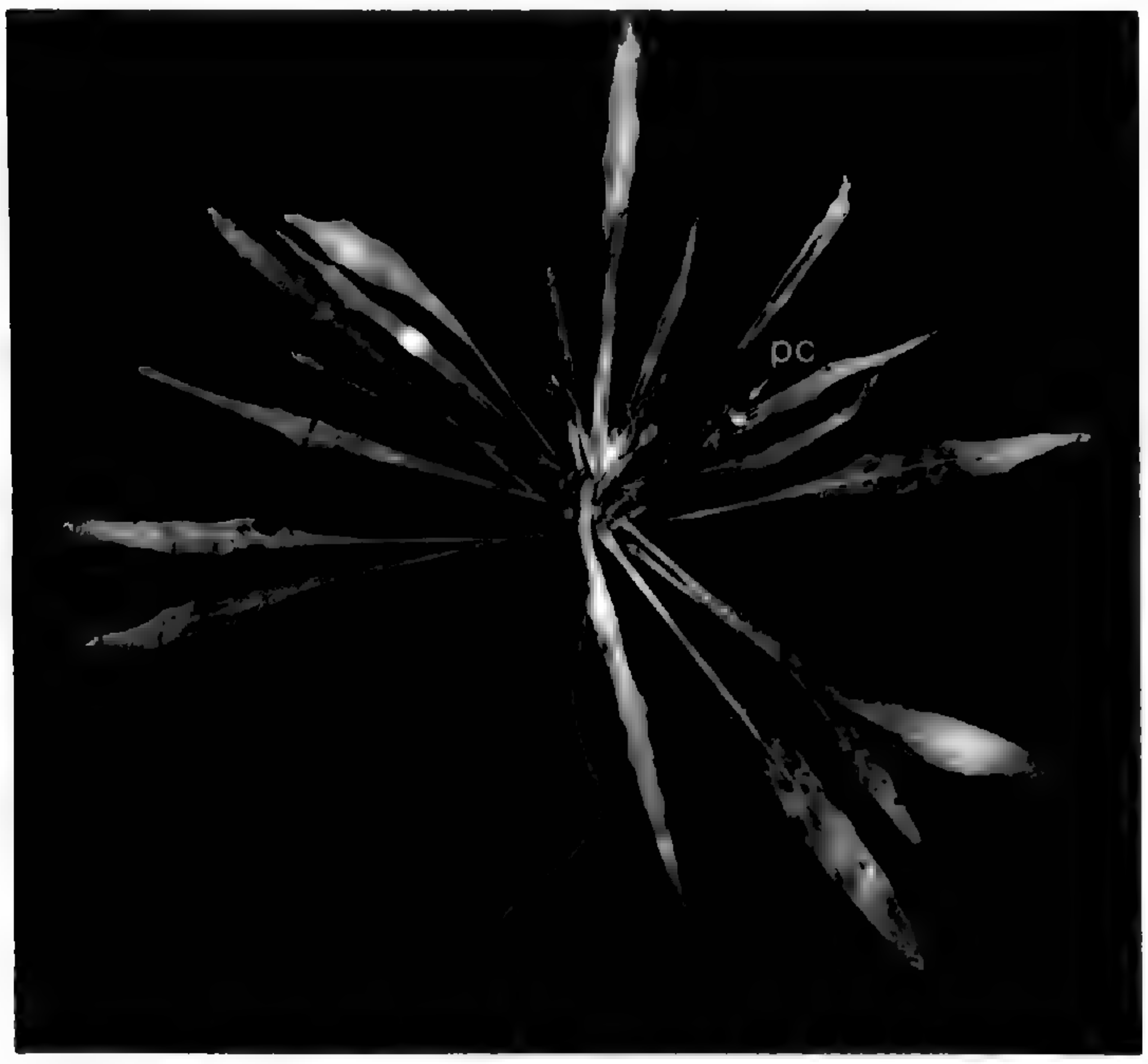


FIGURE 9. *Onagraceae.* Oenothera nana. *All internodes of the primary axis, including the main florescence, remain short; this also applies to the paracladia (pc). (Peru. Puno: above Chimu,* K. A. Santarius 2056/364 *(M).)*

FIGURE 10. *Onagraceae.* Camissonia tanacetifolia. *(USA. Washington: Spokane Co., July 1884,* Suksdorf s.n. *(M).)*

FIGURE 11. *Onagraceae.* Oenothera multicaulis. *Plant with rosette-leaved proliferating main shoot and flowering paracladia. (Peru: between Huancayo and Jarpa,* Müller 2345/75 *(M).)*

Their internodes may be very slender (*E. lineare* Muhlenb., *E. obscurum* Schreber) and often form small bulbs at their ends, especially well developed in *E. palustre* L. (Irmisch, 1847; Warming, 1918: 348; Troll, 1937: 811, fig. 639). In others the stolons are somewhat thickened, forming storage organs in this way (*E. hirsutum* L., Fig. 14). There are also many transitional forms between subterranean and epigeal stolons, which then develop foliaceous leaves in place of scales (*E. hirsutum*), and between stolon-forming innovation buds and those that remain short (the latter in *E. montanum*, *E. collinum* Gmelin, *E. roseum* Schreber, transitional in *E. parviflorum* Schreber, and *E. lanceolatum* Seb. & Mauri). In *E. palustre* there occur also transitional ascendent shoots with foliaceous leaves coming to flower in the same year as the main shoot and thus forming proleptical-

FIGURE 12. *Onagraceae.* Oenothera multicaulis. *Plant with proliferating main shoot with rosetted leaves and ascendent paracladia with co-florescences. (Peru: Huancayo.* Santarius 2204/717 *(M).)*

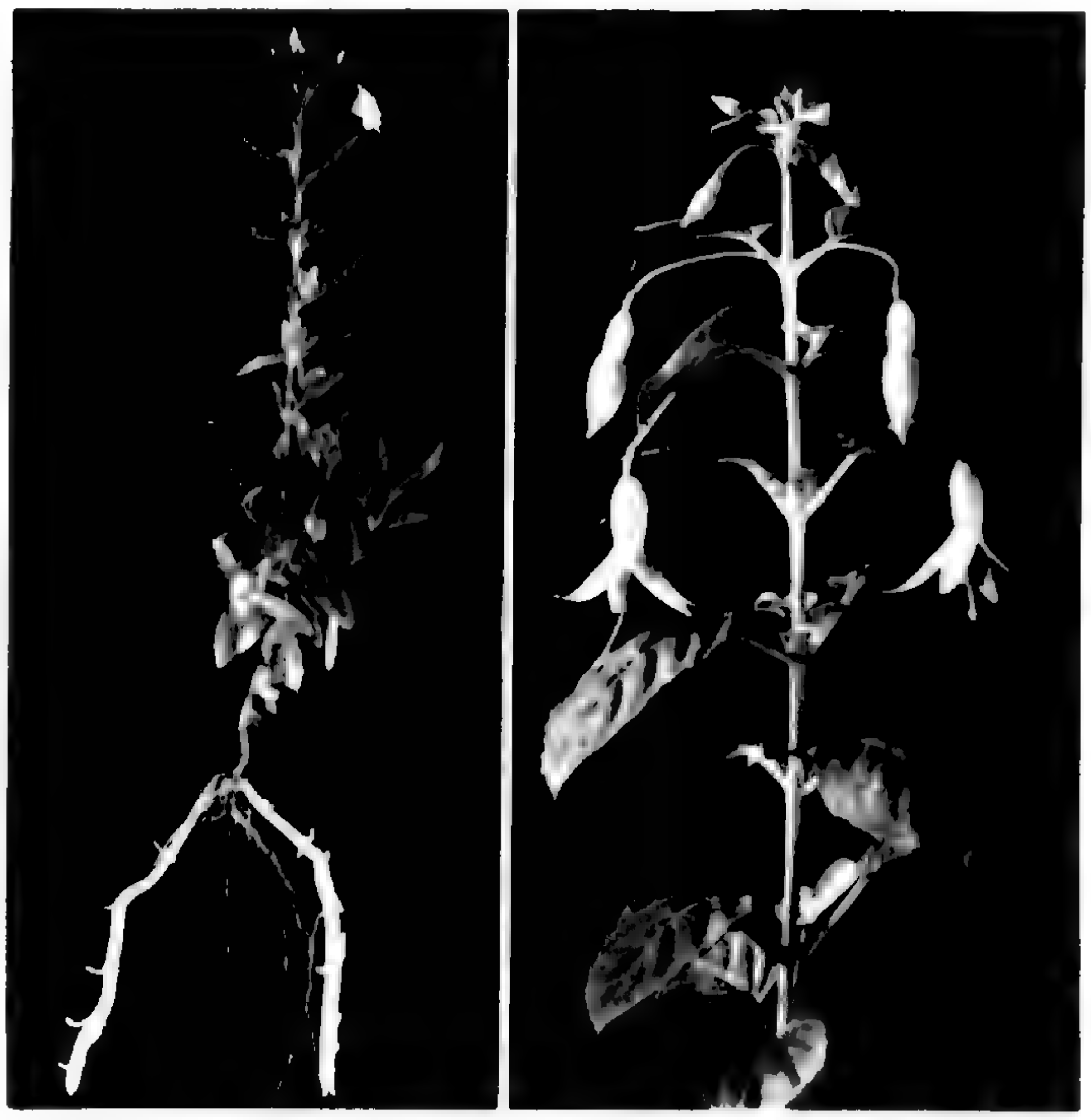


FIGURE 14. *Onagraceae.—Left.* Epilobium hirsutum; *plant with vigorous subterranean stolons.—Right.* Fuchsia magellanica; *inflorescence. (Original photographs from Troll.)*

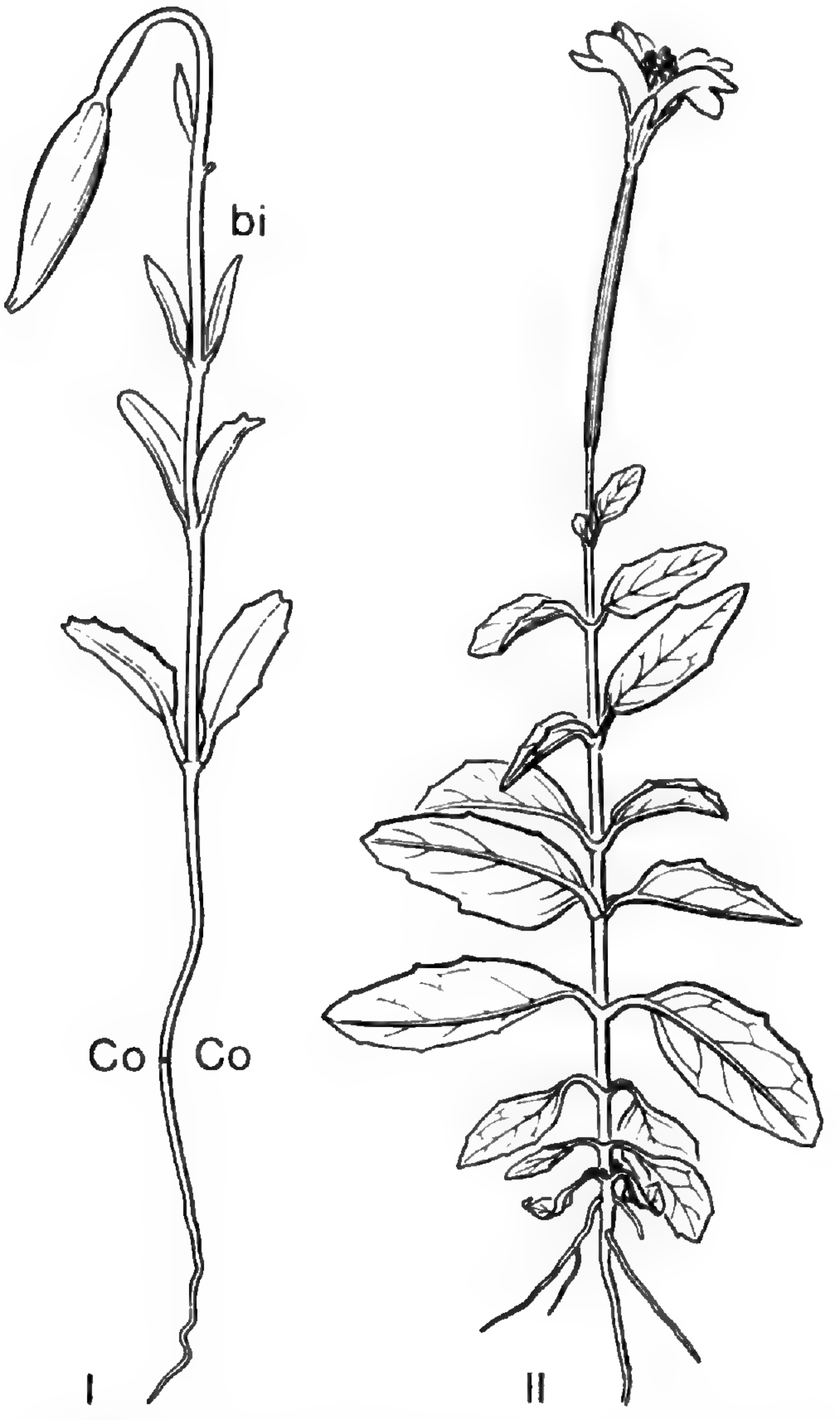


FIGURE 13. *Onagraceae. One-flowered dwarf forms of* Clarkia bottae *(I) and* Epilobium montanum *L. (II). bi, basal internode; Co, scars of the cotyledons. (Original drawings from Troll.)*

anthetical (see Müller-Doblies & Weberling, 1984) innovation shoots, while normally it takes until the next season for the stolonlike or short remaining innovation shoots to develop into a new flowering system. (For discussion of different modes of perennation in *Epilobium*, see Keating et al., 1982.)

A second peculiarity is especially characteristic for a number of species belonging to the series Similes, Microphyllae, and Sparsiflorae Hausskn., distributed in Australia, Tasmania, and New Zealand. These species show a more or less plagiotropic growth correlated with proliferation of the florescence apex, which seems to be a constant feature within the three series. "All of the leaves are opposite" (Raven & Raven, 1976: 15), and "the stem creeps and roots at the nodes, and continues growing vegetatively beyond the area where the flowers are produced." Thus the apex of the florescence regularly returns to a vegetative phase in which paracladia are developed and returns again to the production of a certain number of flowers. In *Epilobium nummulariifolium* R. Cunn., a node bearing a pair of flowers may be followed by two nodes with paracladia, but more frequently one of the axils of a pair of leaves produces a flower,

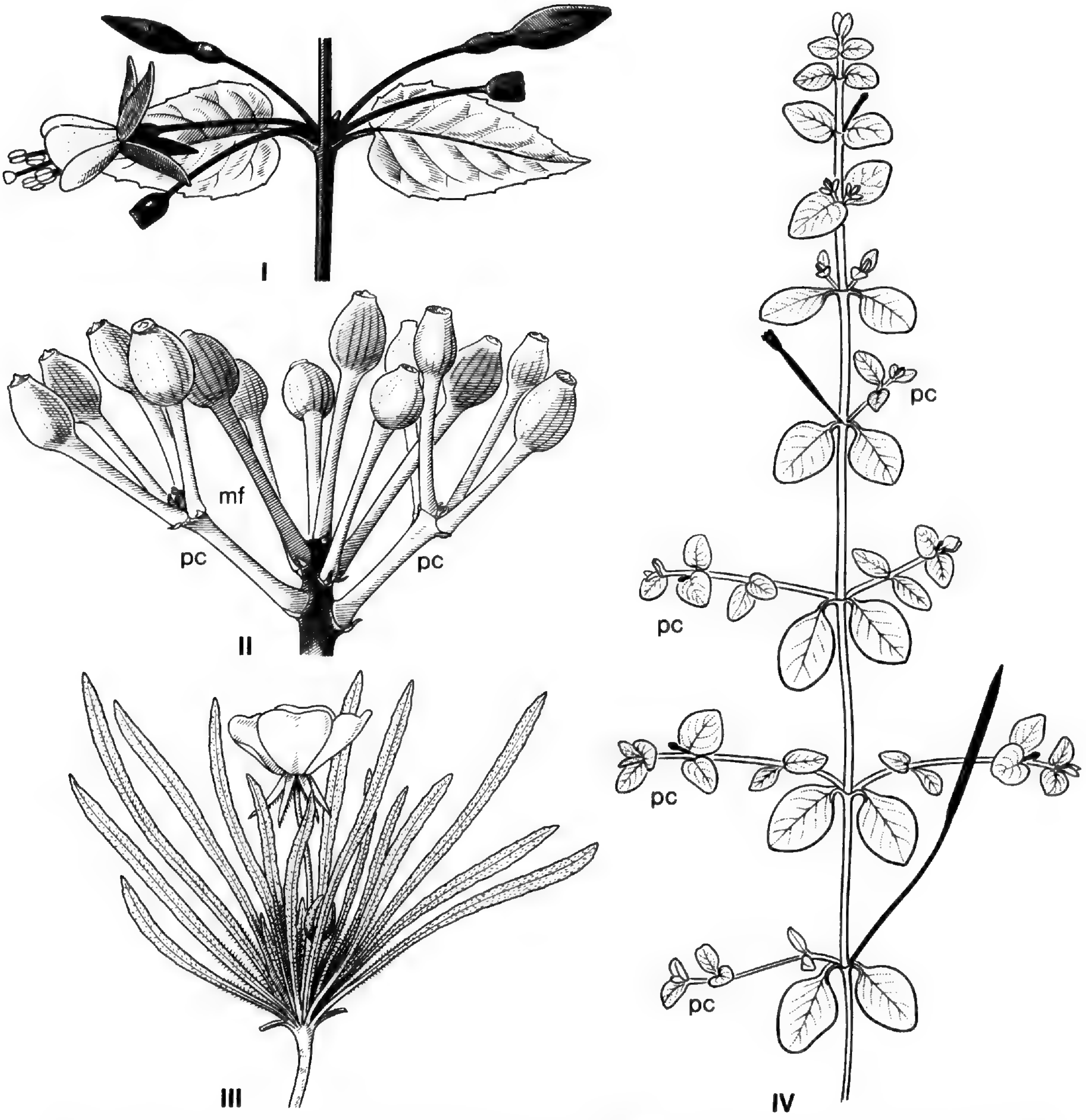


FIGURE 15. *Onagraceae.—I.* Fuchsia coccinea; *node of the florescence with regular and accessorial flowers.—II.* F. arborescens; *inflorescence with main florescence (mf) and paracladia (pc).—III.* Camissonia graciliflora; *habit (after J. W. Hook.).—IV.* Epilobium nummulariifolium. *(I, II, IV original drawings from Troll.)*

while the other one bears a paracladium (Fig. 15 IV). Troll (unpubl. notes) found the primary axis passing over to plagiotropic growth after the unfolding of the cotyledons. The axils of the cotyledons produced paracladia. According to Raven & Raven (1976: 15) this "habit has evolved independently on at least seven occasions among the Australasian species, as indicated by the morphological, genetic, and geographical relationships of the species involved: 1) *E. willisii*; 2) *E. macropus*; 3) *E. pedunculare*; 4) *E. crassum*; 5) *E. margaretiae*; 6) *E. brunnescens*, *E. pernitens*, *E. nerteroides*, and *E. nummulariifolium*; and 7) *E. komarovianum* and *E. angustum*. There is presumably an ecological solution as to why this peculiar plant form, unknown elsewhere in the world, should have evolved repeatedly in Australasia."

Within the genus *Ludwigia* (including *Jussieua)* one can find species that show the typical zonation as described for polytelic

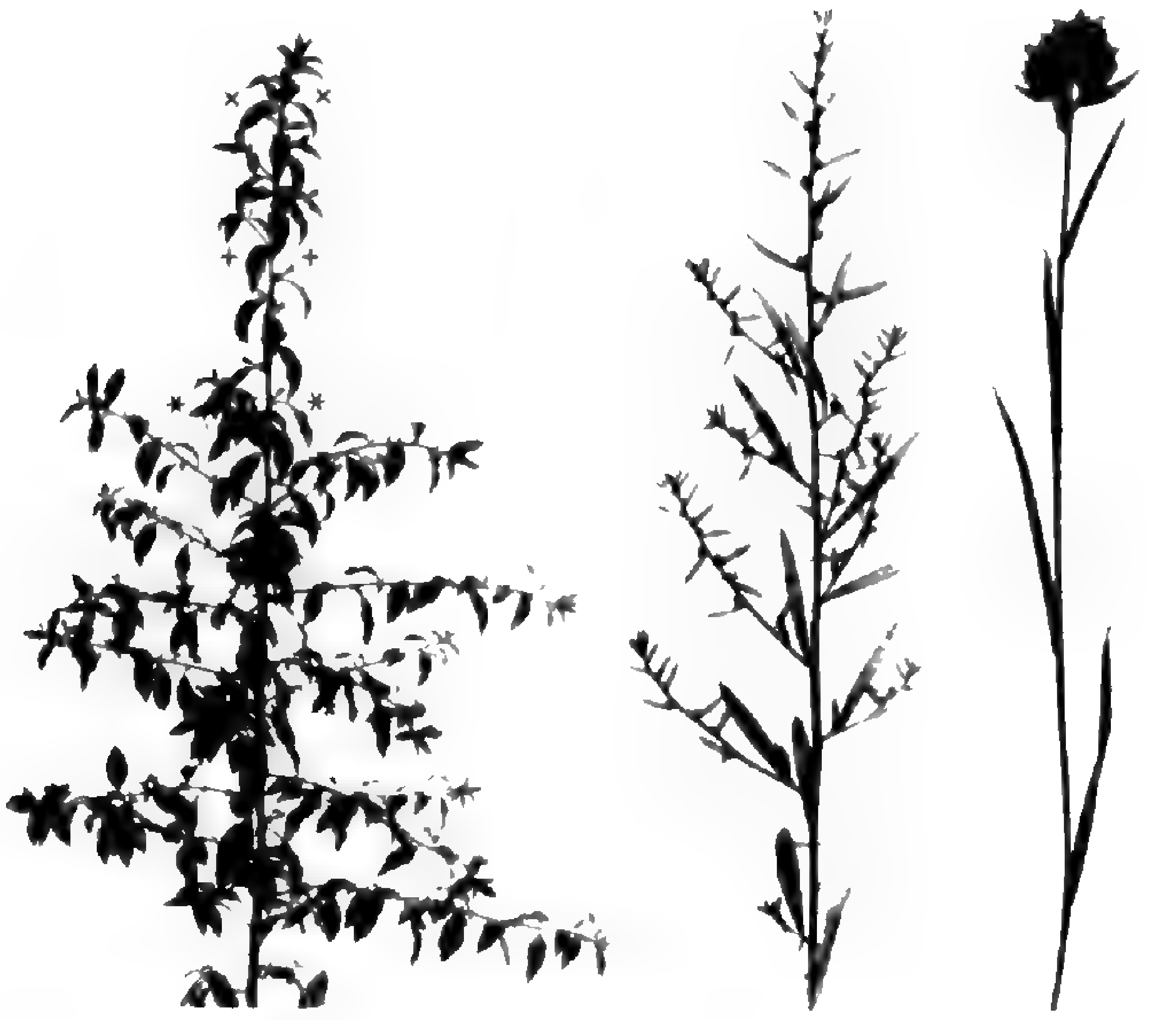


FIGURE 16. *Onagraceae.—Left.* Ludwigia suffruticosa.—*Center.* L. alata.—*Right.* L. octovalvis (L. capitata). *(Original photographs from Troll.)*

plants with botrytic florescences. *Ludwigia suffruticosa* (L.) Gomez serves as an example (Fig. 16). The main inflorescence is a frondose botrys. The same applies to the paracladia, which are preceded by an inhibition zone. Axoscopic accessorial buds can be observed accompanying the paracladia as well as the single flowers of the florescences. The apex of the inflorescence axis proliferates repeatedly: after having produced single lateral flowers forming the main florescence, it develops a paracladial zone and then returns to produce single flowers again. This zonation found in *L. octovalvis* is also found in *L. alata* Ell. (Fig. 16) and *L. perennis* L. In the latter the pherophylls within the florescences are somewhat smaller than in the preceding paracladial zone. Here the paracladia mostly comprise a co-florescence only, since the prophylls bear flowers in their axils already. The axoscopic accessorial buds within the florescence form small flower-bearing branches, while those that accompany the paracladia remain undeveloped.

In *Ludwigia virgata* Michaux, development of the paracladia usually is suppressed. The plants are extremely heterophyllous, bearing lanceolate leaves in the proximal part of the hypotagma and linear leaves in the distal part, whereas the foliation of the main florescence consists of small bractlike leaves. *Ludwigia octovalvis* (Jacq.) Raven resembles *L. virgata* in the suppression of the paracladia, but the flowers of the main florescence of *L. octovalis* (= *L. capitata* Michaux) usually are condensed into a head by suppression of internode development (Fig. 16). At the base of the plants, Troll (unpubl. notes) sometimes observed stolonlike innovation shoots.

FIGURE 17. *Trapaceae.* Trapa natans; *flowering rosette. (Deutsch-Mühlenweiher, Saarbrücken, 1904,* Ruppert s.n. *(M).)*

On the other hand, we could not find a main florescence in herbarium specimens of *Ludwigia abyssinica* A. Rich. The specimens investigated only had paracladia ending in a botrytic florescence, their foliation being bracteose in the upper paracladia and frondobracteose in the lower paracladia. If this preliminary result proves to be true, *L. abyssinica* has a truncate polytelic synflorescence.

Ludwigia palustris Ell. differs from the preceding species by having plagiotropic growth. The plant, which grows in stagnant or slow-flowing water or on muddy soil, develops roots from the nodes and different forms of leaves depending on ecological conditions. In these features *L. palustris* resembles species such as *L. helminthorrhiza* (Martius) Hara (*Jussieua natans* Humb. & Bonpl.) and *L. adscendens* (L.) Hara (*J. repens* L.), which are well known for peculiar respiratory roots that develop at the nodes in addition to normal roots. They also show a more or less pronounced heterophylly. Here again the inflorescence apex regularly proliferates and returns to flower formation. In *L. peduncularis* (Wright ex Griseb.) Gomez (*L. clavellina*) a pair of flowers often is followed by a pair of paracladia. In the picture of *L. helminthorrhiza* given by Humboldt & Bonpland (1805, t. 3, under *Jussieua natans*), each flower is accompanied by a vegetative accessorial branch.

The most interesting species of *Ludwigia* is *L. sedoides* (Kunth) Hara, an aquatic herb in which the branches end in floating rosettes. The rosettes are formed by alternate leaves that gradually differ in the length of their petioles, thus forming a configuration similar to a rosette window.

Usually the flowers are described as solitary in the axils of the foliage leaves. Actually they all form a botrytic main florescence which proliferates, however, after the formation of only a few flowers, forming a vegetative flowerless zone and then returns to flower production. Thus the flower-bearing zones are interrupted by vegetative zones. Paracladia that repeat the architecture of the main shoot seem to develop rarely only from the more remote parts of the stem.

In all of these respects *Ludwigia sedoides* is completely congruent with *Trapa natans* L., Trapaceae (Fig. 17). The submerged leaves of *Trapa*, however, are pinnatifid and thus differ from the floating leaves that have a rhombic lamina and somewhat inflated petioles, which keep the rosette floating.

In the ligneous (*Fuchsia, Hauya*) or suffruticose Onagraceae, the architecture of the inflorescences does not differ fundamentally from that of the herbaceous genera.

In *Fuchsia* the diversity of inflorescences mainly depends on differences of foliation, development of the internodes, and degree of ramification within the flower-bearing parts. As was shown already, the difference between the bracteose and the leafy character of the pherophylls (Figs. 14, 15 II) has a great effect on the appearance of the plants. In *F. magellanica* the leafy botrytic florescences proliferate frequently and often repeatedly, giving the impression that there are "flowers solitary in the axils of leaves." From the vegetative zones of the "interrupted florescences" paracladia can develop. Accessorial flowers can occur in a phylloscopic sequence (Fig. 15 I). Quite a different impression is given by the botrytic florescences of *F. triphylla* L., *F. coccinea* Sol., and *F. fulgens* Mociño & Sessé (see Raimann, 1893b, fig. 94A), the foliation of which is bracteose or frondo-bracteose. In *F. boliviana* Carr. the pendant botrytic frondo-bracteose main florescence and co-florescences are hanging by the inclination of their prolonged basal internodes, while the flower-bearing zone is more or less condensed (Fig. 18). The bracteose inflorescence terminating the foliaceous shoots of *F. arborescens* Sims (Fig. 18) is often called a panicle but comprises a botrytic main florescence and a smaller or greater number of paracladia, which are restricted to their coflorescences. The inflorescences of *Hauya elegans* DC. subsp. *cornuta* (Hemsley) Breedlove & Raven is a leafy proliferating few-flowered spike. Although the structure of the inflorescences within the woody Onagraceae seems to be clear, the position of the flower-bearing branches within the whole ramification system should be examined in comparative investigations regarding the different growth forms of the ligneous plants.

LYTHRACEAE

The diverse forms of ramification found in the inflorescences of Lythraceae have been carefully investigated and described by Koehne (1883). Thus we only need to treat some new fundamental and comparative aspects here. The phyllotaxis is usually decussate, rarely alternate; sometimes verticils with three or many (e.g., species of *Rotala*) leaves are formed. With some exceptions (*Cuphea* sect. *Lythrocuphea* and some other species) prophylls are nearly always present within the inflorescences. Eichler (1878b: 478) named as the only exceptions *Cuphea* subgen. *Cuphea* (subgen. *Lythrocuphea* Koehne) and the secondary flowers within the cymes of *Lythrum* species.

FIGURE 18. *Onagraceae. Inflorescences of* Fuchsia arborescens *(left) and* F. boliviana *(right). (Original photographs from Troll.)*

Within the family only the genera *Galpinia*, *Lagerstroemia*, *Lawsonia*, *Rhynchocalyx* (now treated as Rhynchocalycaceae), and *Woodfordia* are characterized by monotelic inflorescences.

The inflorescence of the ligneous *Lagerstroemia indica* L. (Figs. 19 I, 20 I) is a diplothyrsoid (a diplothyrse with terminal flower) with three- to seven-flowered cymes. A remarkable feature of this inflorescence is that effloration takes place from base to top, though the terminal flower of the whole system precedes the neighboring lateral ones. The same applies to the terminal flowers of the thyrsoid paracladia in the proximal part of the inflorescence. Correlated with this mode of effloration is the delay in the formation of the ultimate lateral flowers below the terminal flower, which can be more or less impeded (Fig. 20 Ia). In case of complete reduction of the uppermost paracladia their subtending bracts appear as metaxyphylls.

Generally *Lagerstroemia tomentosa* Presl shows the same mode of ramification as *L. indica*. In *L. calyculata* Kurz, *L. hypoleuca* Kurz, and *L. speciosa* Pers., however, the distal part of the inflorescence bears a considerable number of uniflorous paracladia forming a botryoidlike zone. This also occurs in the thyrsoid paracladia at the base of the inflorescence, which apparently are more numerous and vigorously developed in these species. In any case, a careful comparative examination of the inflorescences of the numerous species of this genus is needed in order to find out if the peculiarities mentioned here are useful for diagnostic and systematic aims.

The mode of effloration found in *Lagerstroemia indica* can also be observed in *Lawsonia inermis* L. (Fig. 19 II), which differs from *L. indica* in that the ramification of the cymes does not exceed the three-flowered stage (Fig. 20 II). On the other hand, the number of flowers of the inflorescence fre-

FIGURE 19. *Lythraceae.—I.* Lagerstroemia indica.*—II.* Lawsonia inermis; *flowering branches. (After Koehne, 1893.)*

quently is increased by accessory phylloscopic branches of first (as_1) and second (as_2) order. They can form a single flower provided with two prophylls, as in pc_2 to pc_4, or can develop into triads (pc_5) and even into thyrsoids (pc_6). The highest degree of ramification and most vigorous development of accessory branches takes place at the base of the whole inflorescence. The formation of accessory branches can be repeated within the paracladia (pc_5, pc_6) and even within the accessory branches themselves (as_1 in pc_6). The diagrams in Figure 20 III–V give additional information about the serial position of the accessory branches. Accessory branches or flowers are very common within the whole family.

Lagerstroemia parviflora Presl (Fig. 21 I) has advanced to the differentiation of a

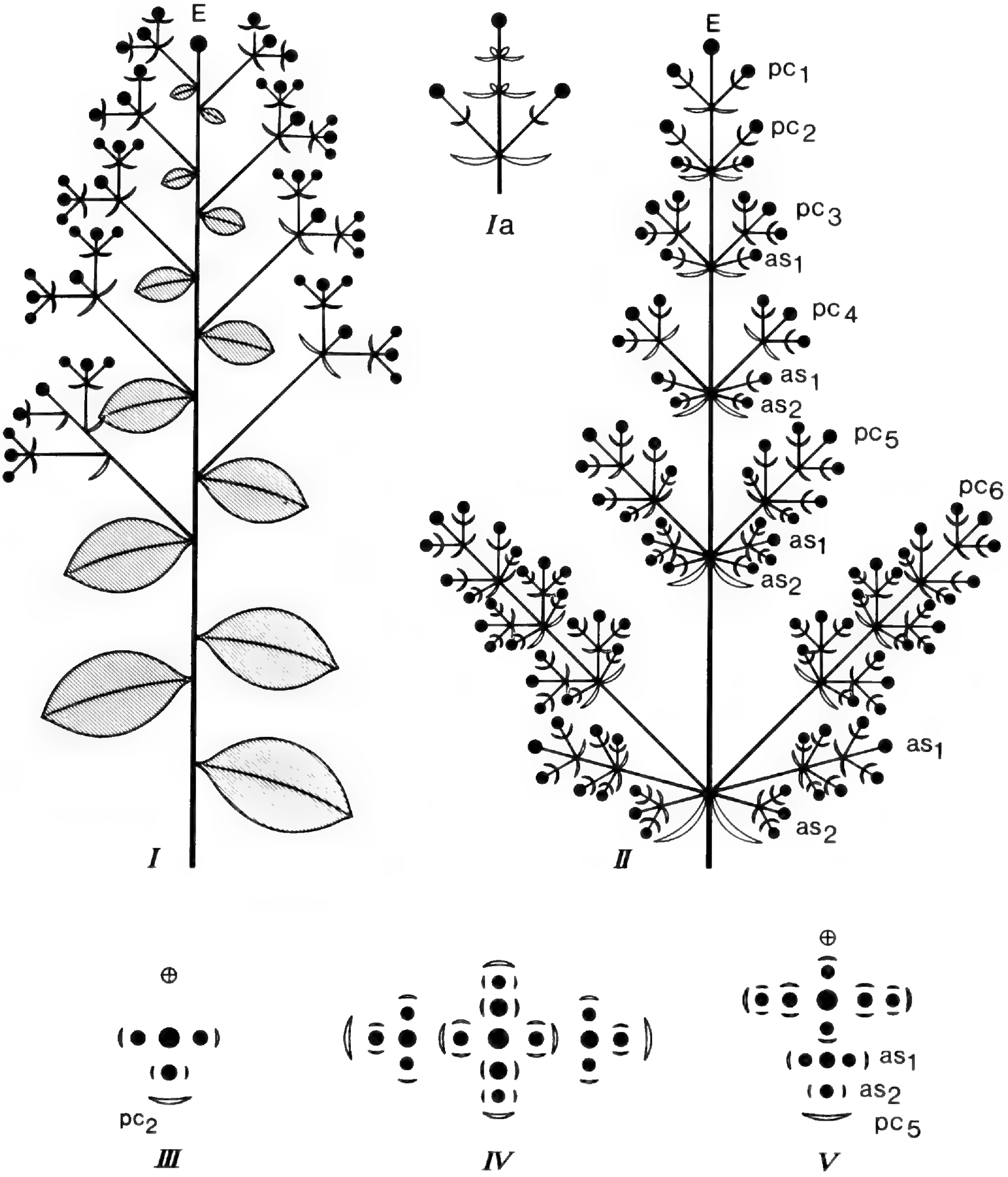


FIGURE 20. *Lythraceae.* Lagerstroemia indica *(I, Ia) and* Lawsonia inermis *(II–V). Vertical projections of flowering branches (I, II) and horizontal projections of* pc_2 *(III),* pc_5 *(V) with accessory branches* as_1 *and* as_2*, the distal part* (pc_1–pc_2) *of the inflorescence in II (IV). Ia is terminal flower of another inflorescence of* Lagerstroemia indica *with two preceding pairs of bracts with undeveloped axillary buds. (From posthumous notices of W. Troll, except Ia.)*

long shoot–short shoot system in which flower formation is restricted to the short shoots (brachyblasts), while the long shoots (macroblasts) continue the vegetative growth. In this case the buds of the short shoots are protected by a series of bud scales and kept undeveloped until the next vegetation period. At the moment of their unfolding and flowering the long shoot has lost its leaves already. The flowering short shoot proliferates. Thus the inflorescence consists of paracladia only, which form botryoids rising from the axils of normally

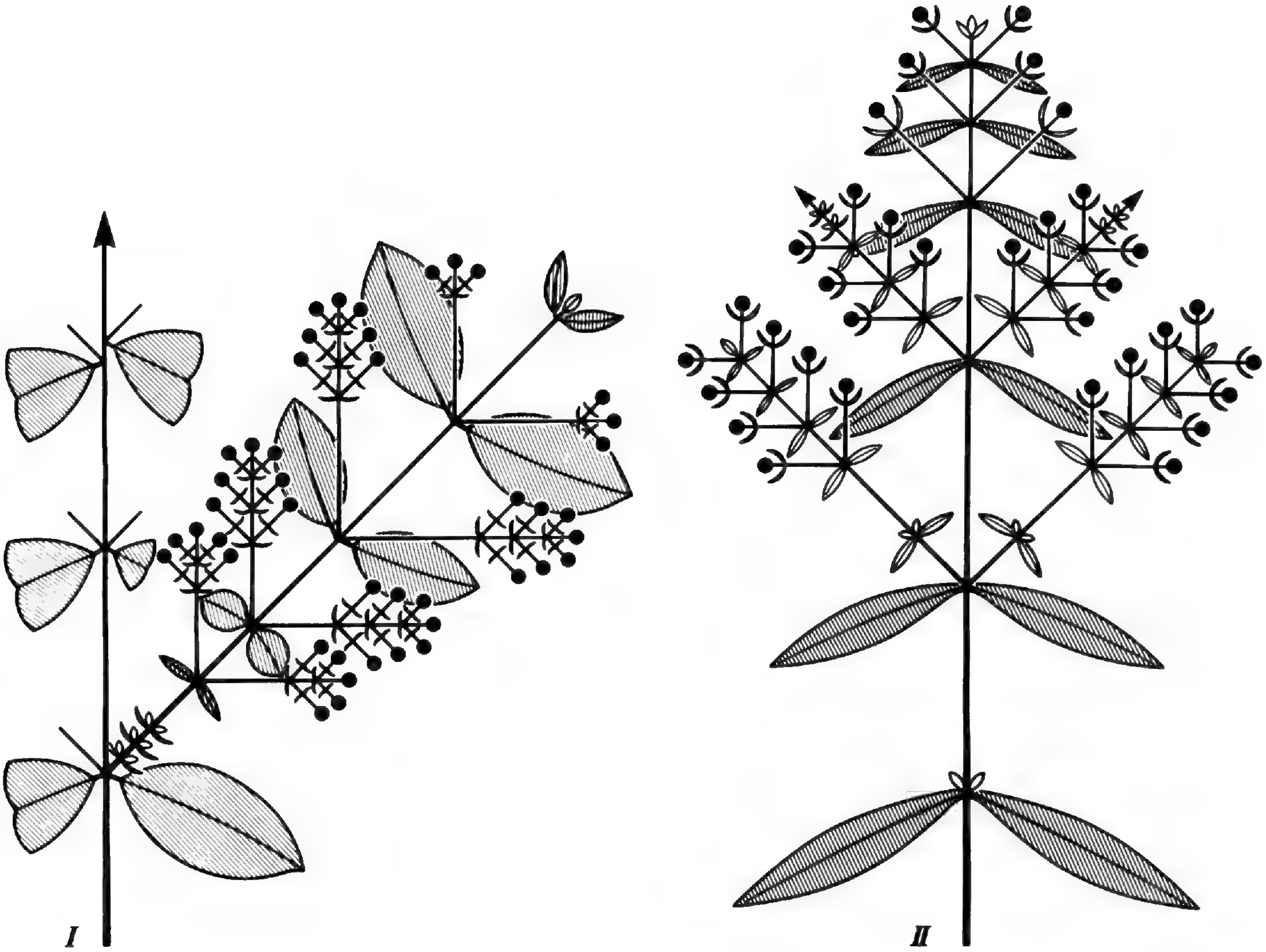


FIGURE 21. *Lythraceae. Vertical projections of flowering branches.—I.* Lagerstroemia parviflora; *piece of a last year's vegetative long shoot with a flowering short shoot.—II.* Lafoensia replicata. *(From posthumous notices of W. Troll.)*

developed or, at the base of the short shoots, very small foliaceous leaves. The basis of the brachyblast that bears bud scales may be interpreted as a zone of inhibition or perhaps also as an innovation zone.

If *Punica* (formerly Punicaceae) ought to be included in Lythraceae, forming subfamily Punicoideae, it could be placed close to *Lagerstroemia* for its monotelic inflorescences. These inflorescences, however, are highly reduced and frequently limited to their terminal flower. They may develop one or two decussate pairs of uniflorous paracladia originating from the axils of bracteose leaves. The uniflorous paracladia bear prophylls that are inserted immediately below the flower. Most of these lateral flowers degenerate sooner or later.

Sonneratia (formerly Sonneratiaceae), which is regarded now to form subfamily Sonneratioideae within the Lythraceae, also has monotelic inflorescences: terminal botryoids with two or three decussate pairs of uniflorous paracladia that bear large prophylls immediately below the flowers. At least the lowermost paracladia arise from the axils of foliage leaves. Sometimes only the terminal flower develops (*S. acida* L. f.).

The genus *Duabanga*, which was formerly included in Sonneratiaceae and now is regarded to represent subfamily Duabangoideae of the Lythraceae, has terminal few-flowered panicles in which ramification only somtimes goes beyond the formation of Pc′.

Crypteroniaceae, formerly sometimes joined with Sonneratiaceae, differ fundamentally from *Sonneratia* by polytelic di- to pleiobotrytic inflorescences of paniclelike appearance with frondo-bracteose (*Axinandra* Thwaites, *Dactylocladus* Oliv.) or mainly bracteose (*Crypteronia* Bl.) foliation and many-flowered botrya. In the axils of the lowermost and foliaceous leaves of the flowering system we could observe well-developed botrytic accessory branches.

Sometimes we found the terminal flower of the inflorescence of *Lagerstroemia speciosa* missing, though terminal flowers still were present in all paracladia. One might overestimate this fact, however, if one interprets this occurrence of truncate monotelic inflorescences as first indication of a gradual transition to the polytelic type within the family. In any case polytelic inflorescences occur in most Lythraceae.

The inflorescence of *Galpinia transvaalica* N. E. Br. resembles those of *Lagerstroemia* in the terminating leafy branches and in its paniclelike structure: the inflorescence axis and all floriferous branches end in terminal flowers. Its foliation, however, is frondulose to bracteose.

In contrast to *Galpinia*, *Lawsonia*, and most species of *Lagerstroemia*, the flower-bearing systems of the shrubby genus *Woodfordia* (*W. floribunda* Salisb., *W. uniflora* (A. Rich.) Koehne) are brachyblastlike branches originating in the axils of foliaceous leaves that are still present during anthesis. They are thyrses or diplo-thyrses (in the narrow sense, cf. Fig. 2 II) with frondulose leaves on their main axes. Since they often bear a series of cataphylls at their bases, it seems likely that they do not unfold immediately after initiation but remain as buds for a while, perhaps to endure an unfavorable season. Frequently these brachyblasts are accompanied by phylloscopic accessory branches of similar shape.

In the flowering systems of *Lafoensia*, another ligneous genus comprising large trees or shrubs, all axes bearing more than one pair of leaves proved to be auxotelic or anauxotelic (see p. 290). The inflorescence of *L. replicata* Pohl, which may serve here as an example (Fig. 21 II), shows a complete reduction of cymose branching. Thus a terminal and several pairs of lateral botryslike structures with acropetal effloration are formed. They can be interpreted as the terminal main florescence and the co-florescences of a polytelic system. The same applies to *L. acuminata* DC., *L. pacari* St. Hil., *L. punicifolia* DC., and *L. densiflora* Pohl. The deciduous prophylls of the flowers are situated immediately at the base of the flowers. In other species, as in *L. nummulariifolia* St. Hil., the number of flowers is diminished.

While in the *Lafoensia* species treated here the subtending leaves within the inflorescences are more or less foliaceous, *Physocalymma scaberrimum* Pohl is characterized by bracteous foliation throughout the whole flower-bearing system that terminates vegetative branches. This system is a diplo- or pleiobotryum with a large paracladial zone (Fig. 22 I). The axes of all botrya end in a vegetative bud. According to Koehne (1893), flowering of this tree takes place when the plants have lost their leaves. In the shrubby *Pemphis madagascariensis* (Baker) Koehne, the production of flowers seems to be limited to brachyblastlike branches which, however, proliferate like the macroblastic main axis. The botrytic flower-bearing zones comprise a few flowers only (Fig. 22 II). *Pemphis acidula* Forster, the second species of the genus, is similar.

A gradually progressing differentiation of the ramification system into flower-bearing short shoots and vegetative long shoots can be seen within the genus *Ginoria* Jacq. As reported by Koehne (1883: 115) in *G. americana* Jacq., the flower-bearing branches arise from the axils of foliaceous leaves. After the appearance of a pair of bud scales, these twigs develop several pairs of foliaceous leaves that bear single flowers in their axils (Fig. 23 I). At a later stage the twigs pass over to vegetative growth. *Ginoria spinosa* and *G. glabra* Griseb. are reported to be similar, but the flowering branches are shorter with fewer flowers and do not proliferate regularly.

In *Ginoria curvispina* Koehne, the flower-bearing brachyblasts unfold in the season after their initiation, when their pherophylls are already lost (Fig. 23 IIa). Their foliation begins with one to three pairs of cataphylls

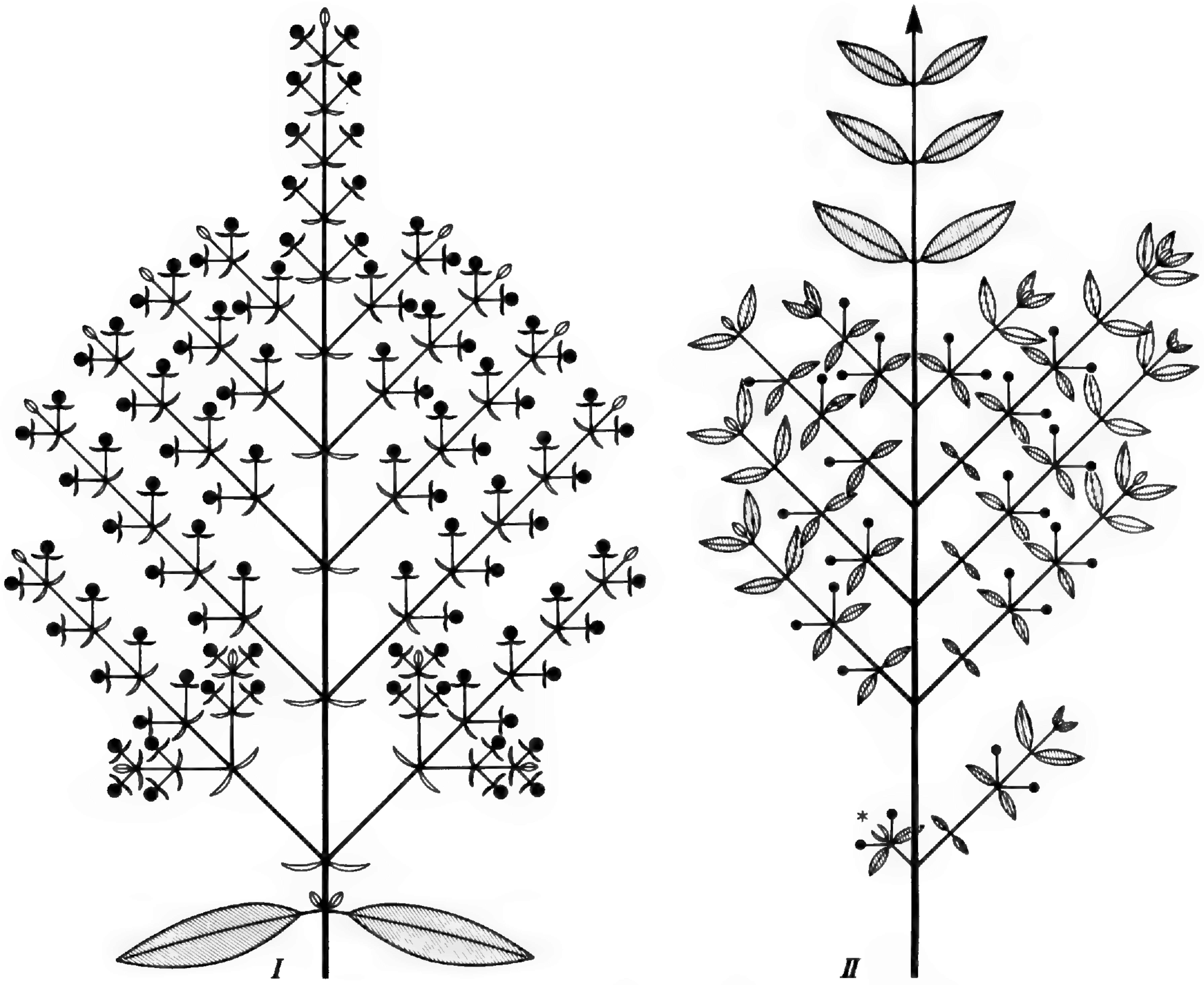


FIGURE 22. *Lythraceae. Vertical projections of flowering branches.—I.* Physocalymma scaberrimum.—*II.* Pemphis madagascariensis. *(From posthumous works of W. Troll.)*

followed by foliaceous leaves. The whole brachyblast can bear one to four pairs of single flowers that can originate in the axils of the cataphylls as well as in the axils of the foliaceous leaves. Finally the brachyblasts proliferate.

According to Koehne (1883: 116), the foliaceous leaves of the brachyblasts resemble those of the macroblasts but measure only one-fourth of their size.

Thus the brachyblasts with their botrytic main florescences contrast conspicuously with the vegetative macroblasts, which at their distal end can continue growth with the development of a new annual shoot. According to the observations of Koehne, these new shoots can also bear single flowers in the axils of their lowermost foliaceous leaves (Fig. 23 IIb). Koehne also reported that two similar long shoots can originate at the very base of the annual shoot and also bear up to four pairs of flowers (Fig. 23 IIc). Thus the limitation of flower production to the short shoots seems not to be complete yet.

In *Ginoria diplusodon* Koehne (Fig. 23 III), the brachyblasts remain shorter, their foliation consists of scales, one to three pairs of which can bear flowers in their axils, thus forming a short botrys. (Sometimes the prophylls of these flowers bear secondary flowers.) Even here the annual shoots continuing the macroblasts (Fig. 23 V) develop one to three pairs of single flowers originating in the axils of cataphylls at the base of the annual shoots (Koehne, 1883). *Ginoria rohrii* (Vahl) Koehne is similar, but the brachyblasts are shorter and the two- to eight-flowered florescence is umbel-shaped (Figs. 23 IV, 24);

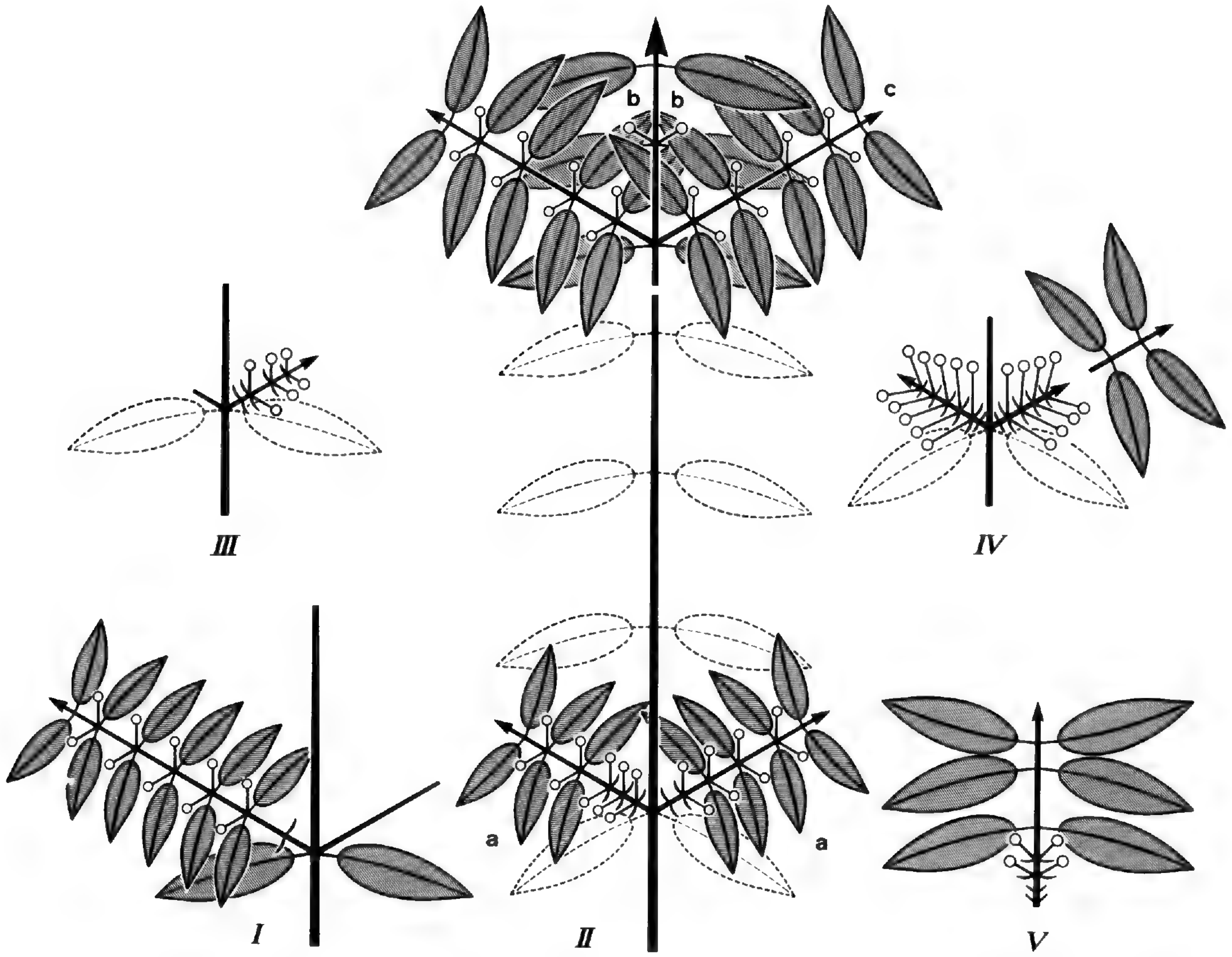


FIGURE 23. *Lythraceae. Vertical diagrams of flowering shoots.—I.* Ginoria americana; *proliferating brachyblast.—II.* G. curvispina; *last year's macroblast with flowering and proliferating brachyblasts (a), single flowers in the axils of proximal foliaceous leaves of the new annual shoot (b), and lateral macroblasts (c) developing from the axils of proximal foliaceous leaves of the new annual shoot. These lateral macroblasts can also bear single flowers in the axils of their proximal foliage leaves.—III.* G. diplusodon; *bracteose flowering brachyblasts in the leaf axils of a last year's macroblast.—IV.* G. rohrii; *brachyblasts which later can proliferate.—V.* G. diplusodon; *base of an annual shoot (macroblast) with flowers in the axils of the uppermost (bud) scales. Prophylls of the flowers omitted. (Construction according to report by Koehne (1883) and to our results.)*

the prophylls are sterile. The brachyblasts unfold when the macroblast is already defoliated. The uppermost brachyblasts are reported to proliferate occasionally. According to Troll (unpubl.), the terminal bud of the macroblast often fails. Then the macroblast is continued by the development of the uppermost lateral buds. Their foliation begins with two or three pairs of bud scales. The distal pair can be frondulose; according to Koehne (1883: 117), the flowers originating in the axils of the bud scales may bear a second flower in the axil of one of their prophylls.

Although the florescences of the ligneous Lythraceae such as *Ginoria*, *Lafoensia*, *Pemphis*, and *Physocalymma* present themselves as botrya or spikes, the basic form of the florescence in the polytelic Lythraceae is a thyrse (in the narrow sense, i.e., without terminal flower). Among the ligneous taxa this is demonstrated by *Adenaria*: in *A. floribunda* Kunth, the flower-bearing twig is a foliaceous, proliferating thyrse with many-flowered cymes, which by abbreviation of all internodes except the epipodia become umbel-shaped or headlike (Fig. 25). *Pehria* (= *Grislea*), as seen in *P. compacta* (Rusby) Sprague, is said to be similar in this respect (Koehne, 1893); the same applies to *Decodon verticillatus* (L.) Ell.

Within the suffruticose and herbaceous taxa

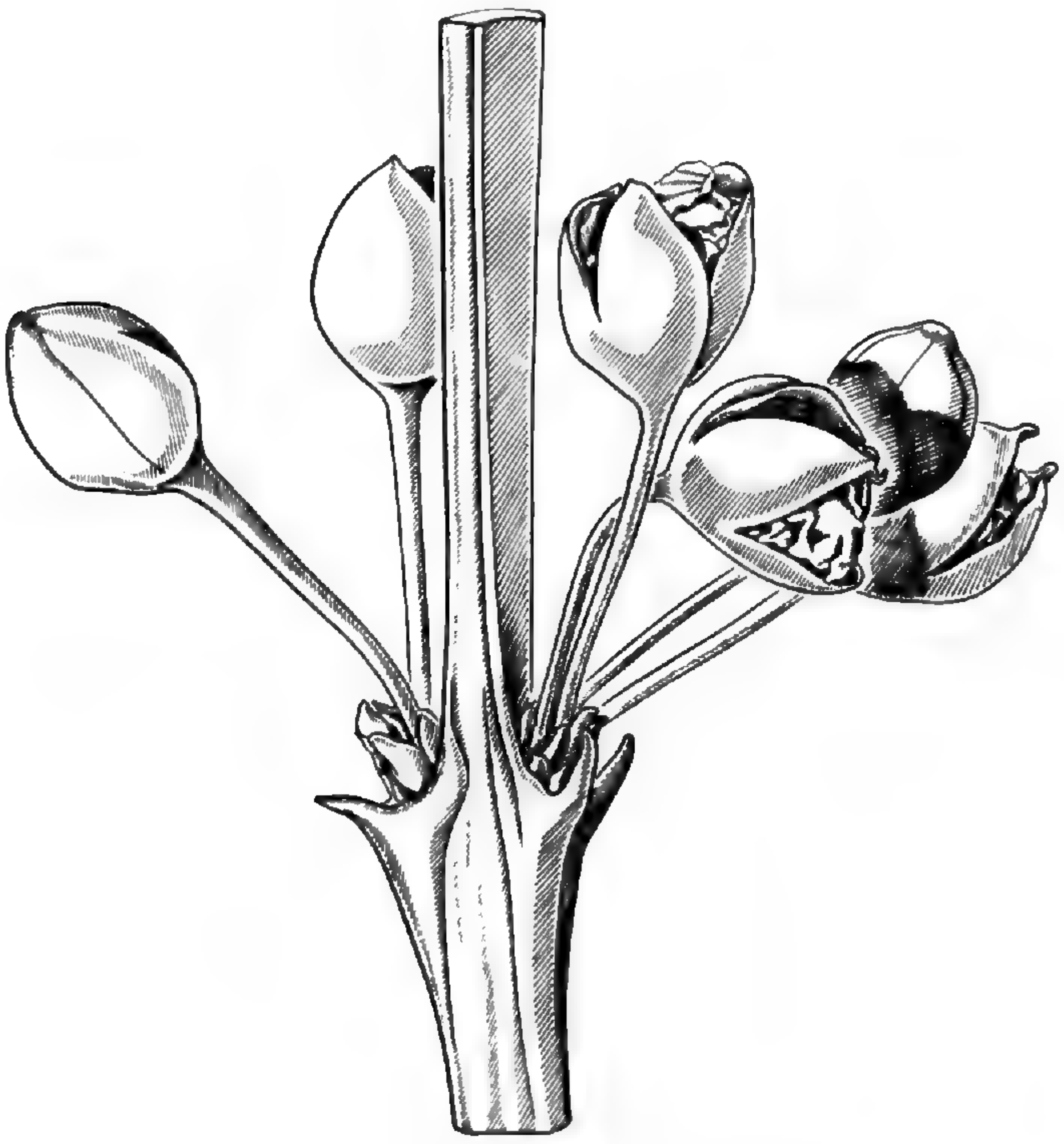


FIGURE 24. *Lythraceae.* Ginoria rohrii; *macroblast with two brachyblasts. (June, 1907,* Eichinger s.n. *(M).)*

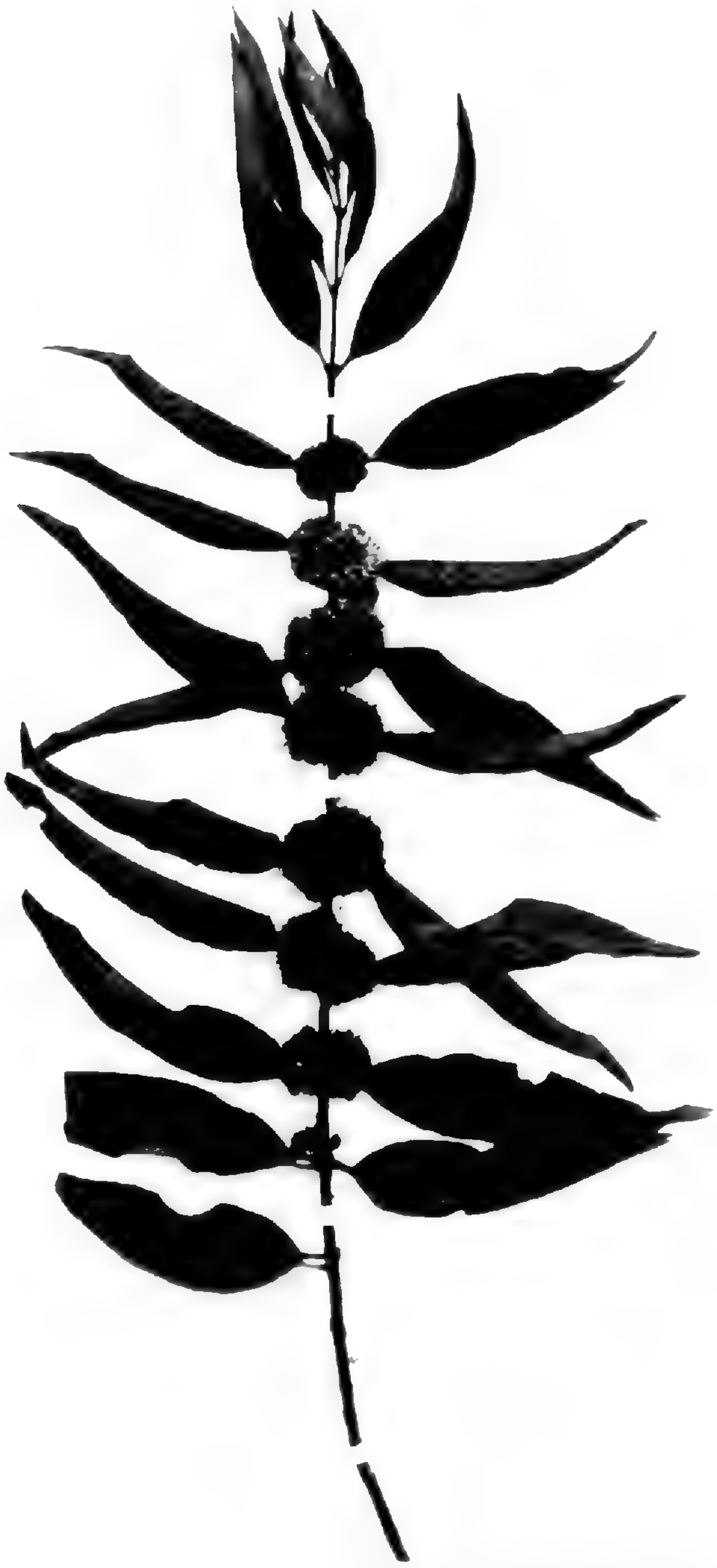


FIGURE 25. *Lythraceae.* Adenaria floribunda; *flowering branch. (Bolivia: Vic. Sorata,* M. Bang 1311 *(M).)*

there are also many groups with copiously branched thyrses. As an example, *Nesaea crassicaulis* (Guill. & Perr.) Koehne (Fig. 26 I) may be mentioned. Its partial florescences are loosely branched with only the hypopodia remaining relatively short, whereas in others, for example, *N. pedicellata* Hiern, even the hypopodia are prolonged and form long peduncles. In *N. aspera* (Guill. & Perr.) Koehne all internodes remain short, and the partial florescences form many-flowered glomerules (see also *N. sarcophylla* Koehne in Koehne, 1903: 227, fig. 43E).

Frequently the partial florescences are reduced to uniflory, thus converting the thyrse into a botrys or spike. This applies to some species of *Nesaea* (e.g., *N. linifolia* Hiern (Fig. 28 III) and *N. baumii* Koehne), most species of *Lythrum,* and all species of *Pleurophora, Cuphea, Heimia, Peplis,* and *Diplusodon.* In *Rotala,* only one species, *R. serpiculoides* Hiern, is reported to have 3–12 flowered dichasia (Koehne, 1883: 124), while in *Ammannia* reduction of the cymes to uniflorous elements occurs facultatively in many species.

A remarkable arrangement of flowers within the botrytic florescences can be observed in *Rotala wallichii* Koehne. It was reported by Koehne (1883: 118) for the verticillate species of the genus that in each whorl the number of flowers equals the number of leaves, i.e., the axil of each leaf bears a single flower. In *R. wallichii* (Fig. 26 II), however, the proximal verticils of a florescence comprising six or seven leaves bear only two or three flowers. The number of flowers increases distally, until each leaf axil of a verticil bears a flower. The disposition of the flowers in the lower whorls can be quite different, without any obvious rule. During the development of a shoot the number of leaves in the consec-

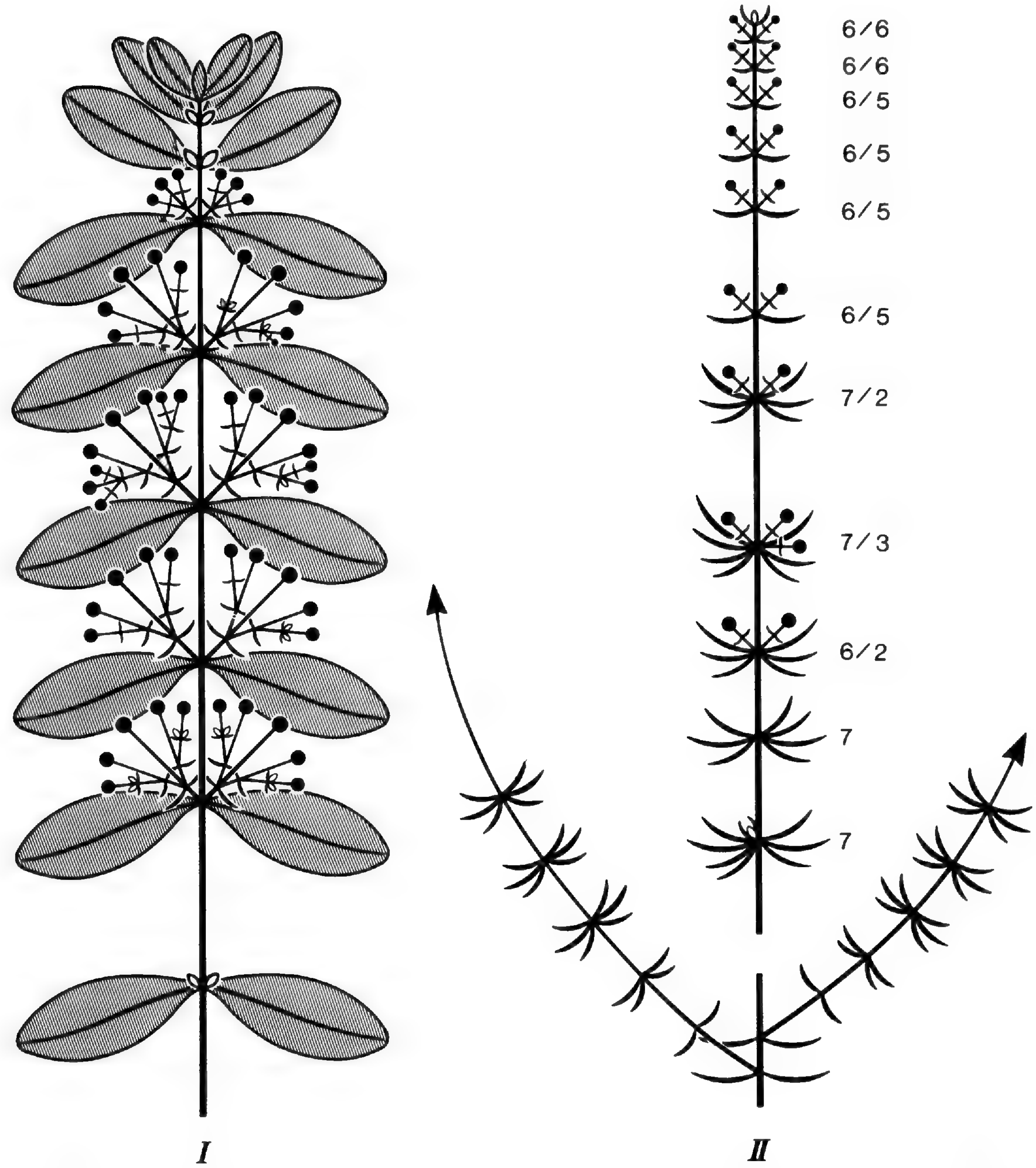


FIGURE 26. *Lythraceae.—I.* Nesaea crassicaulis; *diagram of a flowering shoot.—II.* Rotala wallichii; *flowering branch. (For each verticil of the main axis the number of leaves and of axillary flowers is added.)*

utive verticils increases gradually from two to four and six, then perhaps up to seven and decreasing to six again.

Among the taxa with copiously branched cymose partial florescences, the species of *Nesaea* sect. *Nesaea* (= sect. *Typonesaea* Koehne) subsect. *Tolypeuma* (E. Meyer) Koehne are remarkable. By shortening of the internodes of all consecutive ramifications the cymes are contracted to small headlike aggregations of flowers enveloped by an involucrum that is formed by the large cordate-lanceolate prophylls. The corollae of the flowers rise slightly above the border of these prophylls, which often are somewhat whitish and violet-nerved basally. The hypopodia of the capitulate partial florescences are prolonged. Since the main axis of the thyrsic florescences—the main florescence and the co-florescences—is anauxotelic, the flores-

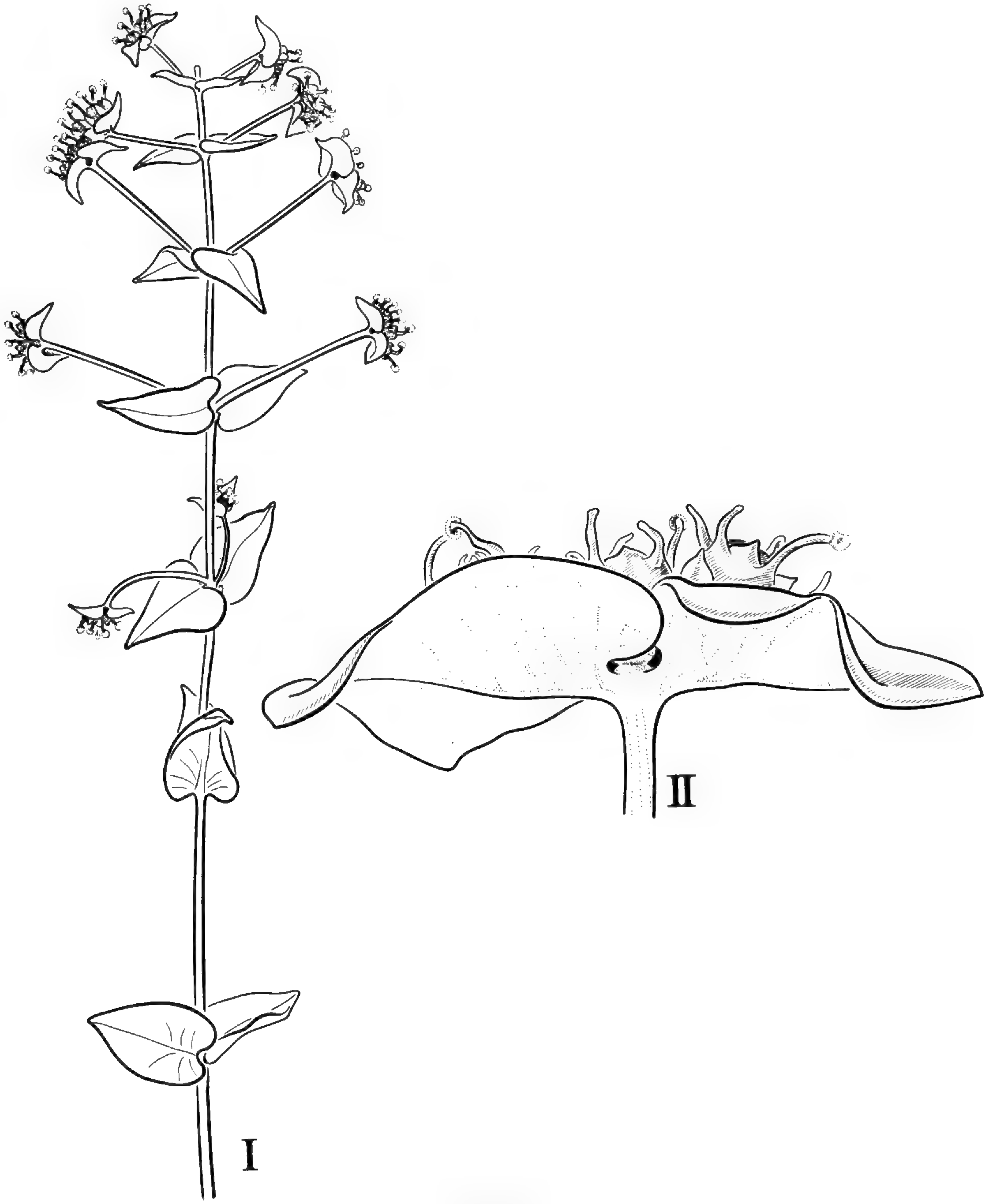


FIGURE 27. *Lythraceae.* Nesaea erecta.—*I. Flowering plant.—II. Cymose partial florescence. (Rhodesia: Mapanza,* E. A. Robinson 2839 *(M).)*

cences of these species, i.e., *Nesaea erecta* Guill. & Perr. (Fig. 27) or *N. cordata* Hiern, appear as botrytic systems composed of capitula.

In contrast to these species, the inflorescence of *Nesaea linearis* Hiern (sect. *Typonesaea* subsect. *Syntolypaea* Koehne) is described to form a terminal capitulum composed of "dichasia singula confertissima, sessilia, bracteolis superne dilatatis . . ." (Koehne, 1903: 223, 230, fig. 45C).

Likewise the lateral capitula of *Nesaea* *radicans* Guill. & Perr. (also subsect. *Tolypeuma*), which are of similar appearance to those in *N. erecta* and *N. cordata*, are described to have four or six enlarged "prophylls," each of them subtending a small "dichasium" (Koehne, 1903: 8, 231). Indeed, these capitula proved to have a thyrselike ramification and to be provided with a terminal flower as Koehne had affirmed already. He did not investigate *N. linearis* in this respect. At least for *N. radicans*, however, it seems to be evident that the inflorescences are monotelic, as Koehne (1903: 8) affirmed with the statement that the inflorescences of *N. radicans* seem to form a transition to those of *Woodfordia*, *Lagerstroemia*, and *Lawsonia*.

A remarkable condensation of florescences is typical for *Pleurophora polyandra* Hook. & Arn. also; here, however, the florescences are spikes (Fig. 28 I, II).

As the treatment of inflorescences in the Lythraceae has shown already, the disposition for proliferation of inflorescences is widespread within this family. Proliferation takes place especially in frondose florescences, for example in *Heimia*, *Nesaea crassicaulis* (Fig. 26 I), *N. sagittifolia* Koehne, or *Adenaria floribunda* (Fig. 25).

Another factor responsible for the high degree of growth-form diversity of inflorescences, especially in herbaceous and suffruticose taxa, is the variation of the proportions between the different zones of the flowering plant, i.e., in polytelic taxa the main florescence, the enrichment zone, the inhibition zone, and, in perennials, the innovation zone.

Thus, Troll (1970: 92) reported that in *Diplusodon thymifolius* DC. the main florescence remains very small in comparison with the paracladial zone. The same seems to apply to *D. virgatus* Pohl, whereas in other species, e.g., *D. villosissimus* Pohl and *D. villosus* Pohl, we found the main florescence to be predominant, although the paracladial zone can be well developed too. The distal paracladia of these species had no hypotagma.

Of course, to a certain degree such differences as the unfolding of a smaller or greater number of paracladia depend on the developmental stage of a plant and on environmental circumstances. The latter especially applies to annuals. Under severe environmental stresses such plants can be highly reduced and develop reduced inflorescences only, as Troll (1964: 363–364) described for *Ammannia coccinea* Rottb. The original plant depicted by Troll is presented here in a photograph (Fig. 28 IV). Probably the plant investigated and figured by Troll is not *Ammannia coccinea* but *A. latifolia* L.; the same then applies to Figure 28 IV. The hypotagma is reduced to two nodes. Only the uppermost of them bears paracladia, while the paracladia in the axils of the cotyledons remain undeveloped. The largest part of the plant is formed by the frondose proliferating florescence with many triadic partial florescences. In reduced plants of *Pleurophora polyandra* the inflorescence frequently only consists of a short headlike spike that is preceded by the cotyledons and two pairs of foliaceous leaves with paracladia absent from their axils (Fig. 28 I). In other individuals, more or less vigorous paracladia ending in a florescence can develop from the axils of the cotyledons and/or from the axils of the following leaf pairs (Fig. 28 II). In *P. pusilla* Hook. & Arn. the reduction of ramification seems to be a constituted character.

By dense sowing of *Lythrum hyssopifolia* L., plants without any paracladia were obtained by Troll (posthumous notices), whereas in normal plants the paracladial zone is well developed.

The frequent occurrence of accessory buds that develop as single flowers or vegetative or flower-bearing branches has been mentioned already. With the exception of *Cuphea* (Eichler, 1878b: 479), there is scarcely a genus of Lythraceae in which they are completely missing. Since Koehne (1873: 112) has given a survey of the various forms and their distribution within the family, we can confine ourselves to the treatment of the genus *Lythrum*, in which the occurrence of accessory flowers is very important for the appearance of the inflorescences.

In *Lythrum* the florescences of subgen. *Lythrum* (= *Salicaria* Koehne) and of sect. *Mesolythrum* Koehne of subgen. *Hyssopifolia* are spikes or botrya.

A flowering individual of *Lythrum salicaria* L. (Fig. 29 II, III) shows a clear zonation: the frondulose main florescence, a paracladial zone (enrichment zone) in which the paracladia are still unfolding, and an inhibition zone below the paracladial zone. Since *Lythrum salicaria* is a perennial, the inhibition zone is preceded by an innovation zone at the base of the plant. According to Troll (posthumous notices), *L. salicaria* is a subshrub rather than a perennial herb since the primary axis as well as the primary root shows intense lignification, as in *Hypericum perforatum*. In young plants (Fig. 29 I) a favored development of the axillary buds of the cotyledons (cotyledonary shoots) and of the next basal leaf pair can be seen. The cotyledonary shoots can develop branches from the axils of their prophylls at early stages, and a phylloscopic accessory bud can arise in the axils of the cotyledons. In vigorous plants the paracladial zone can be considerably expanded, and the paracladia can develop second-order paracladia. In the basal part of the flowering zone the phyllotaxis changes from decussate to alternate (Wydler, 1860: 238; for the phyllotaxis of *L. virgatum* and *L. hyssopifolia* see Wydler, 1872: 254). The florescences are thyrses, however exceedingly modified by the formation of phylloscopic accessory cymes or flowers (Roeper, 1826: 109).

Eichler (1878b: 479) observed that below the cymose partial florescence there are mostly two accessory three-flowered cymes (Fig. 30 IIa), the lower of which is often rudimentary. There is an additional accessory flower below each of the lateral (secondary) flowers of the primary partial florescence. These additional flowers bear prophylls as do the regular lateral (secondary) flowers of the cyme. Thus a transversal series of five flowers results, below which there is a three-flowered cyme still provided with prophylls of first order, and below this another one of rudimentary flowers without prophylls. *Lythrum purshianum* Steudel is reported to be similar in this respect (Fig. 30 IIb).

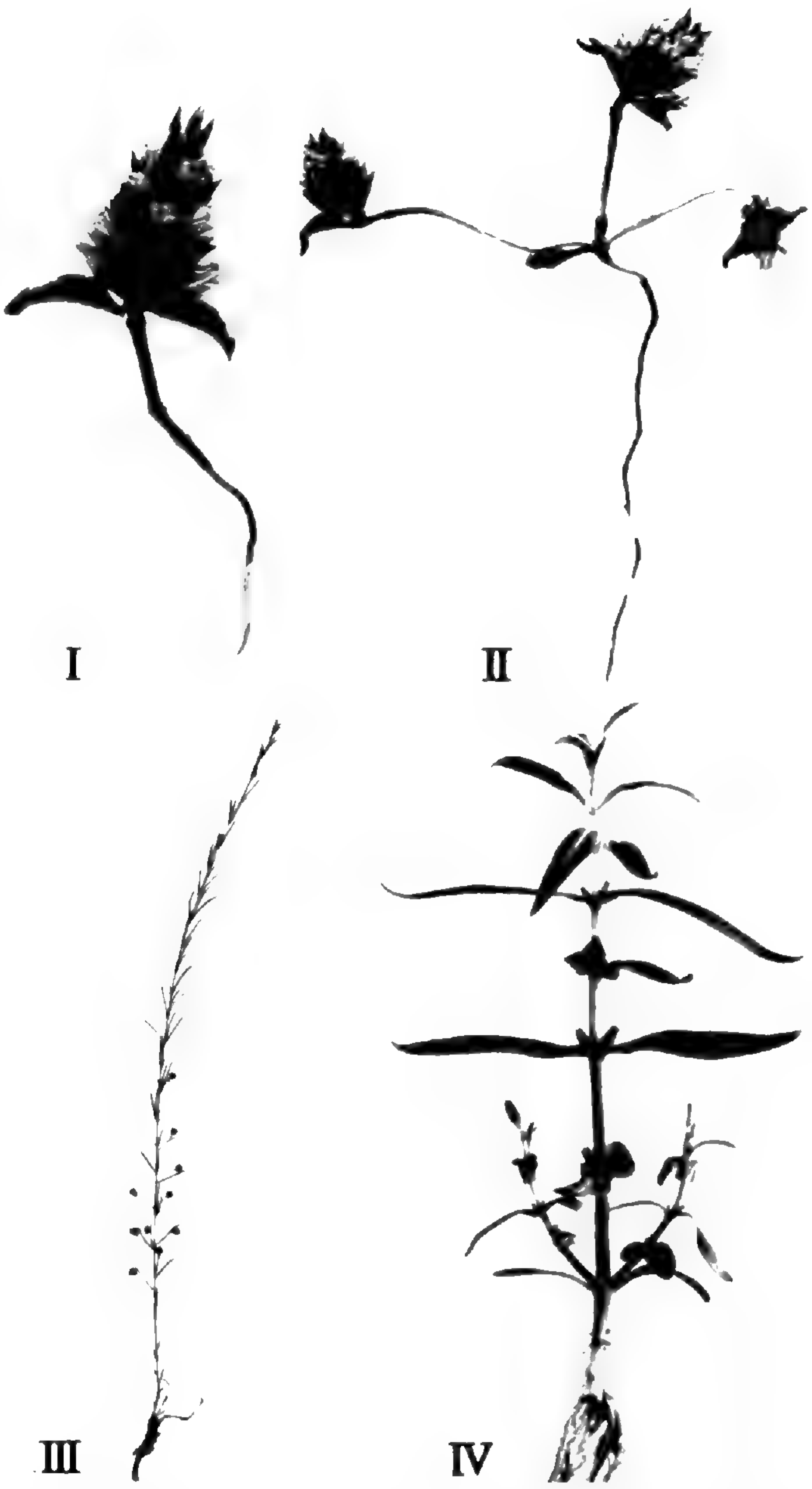


FIGURE 28. *Lythraceae.—I, II.* Pleurophora polyandra; *reduced form (I) and plant with well-developed basal paracladia (II).—III.* Nesaea linifolia; *flowering individual.—IV.* Ammannia coccinea; *reduced individual. (Photographs III and IV from Troll.)*

Troll (posthumous notices), however, found triadic flower groups in place of the singular accessory flowers that accompany the secondary flowers of the regular partial florescence (Fig. 30 Ia). He also noted that there may be one (as_1) or two (as_1, as_2) accessory cymes. In the latter case the as_1 bears single accessory flowers in the axils of its prophylls, and the as_2 likewise is provided with prophylls (Fig. 30 Ic).

In all partial florescences, anthesis of the primary flower takes place first, followed by the secondary flowers, then the primary flow-

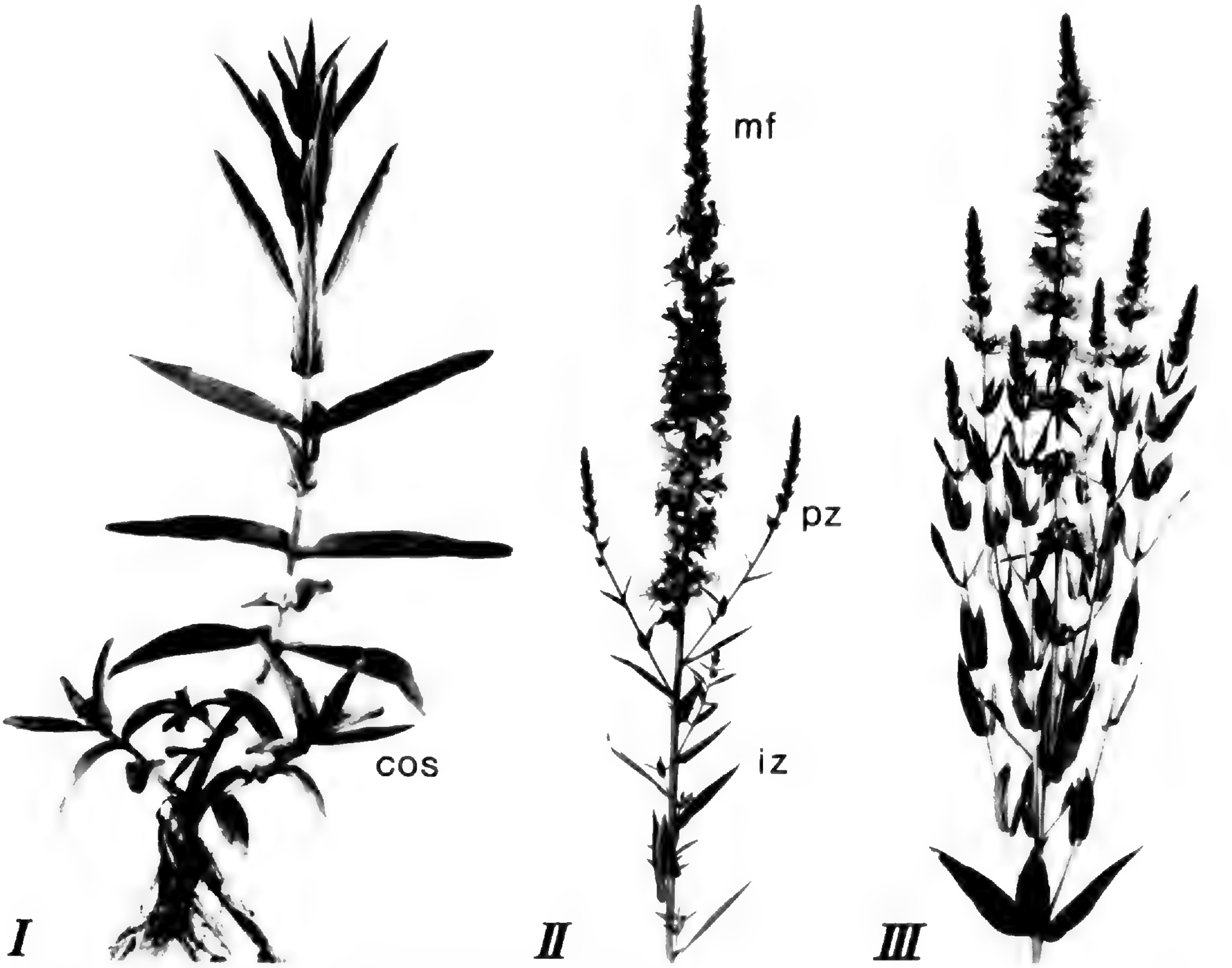


FIGURE 29. *Lythraceae.* Lythrum salicaria *L.—I. Young plant with favored development of the cotyledonary shoots (cos) and a second pair of basal branches.—II. Flowering individual with large main florescence (mf), enrichment zone (paracladial zone, pz), and inhibition zone (iz).—III. Plant with trimerous leaf whorls and expanded paracladial zone. (Photographs from Troll.)*

ers of the as_1, and so forth. As a consequence, the efflorescence of the whole florescence is progressing from base to top repeatedly "as in *Verbascum*" (Wydler, 1843: 184, 1851a: 370–371). According to Wydler (1860: 240), who referred to Koch, it is not rare to have a vegetative accessory bud below the single flowers of the spicate florescence.

Koehne (1903: 6) reported that in *Lythrum tribracteatum* Salzm. and some other species the accessory branch forms a short, dense botrytic florescence.

By *recaulescent* shifting, the place of attachment of the subtending leaves (pherophylls) can be relocated onto the pedicels of the flowers, which in reality originate from the axils of the pherophylls. Thus these can be situated just below the flower. Examples can be found in *Rotala* and *Decodon*.

In most species of *Cuphea*, the attachment of the flowers within the botrytic florescences is modified by the coalescence of their pedicels with the main axis up to the next node (Hochstetter, 1850: 182; Wydler, 1851a: 371, 1861; Eichler, 1878b: 478 ff.). This sort of concrescence is well known as *concaulescence*. In *C. nitidula* Kunth, *C. appendiculata* Benth., and some other species (cf. Koehne, 1883: 119), the flowers are mostly still in normal axillary position. In the case that both axils of the decussate leaves are fertile ("*Cupheae oppositiflorae*"), the pedicels of both flowers are attached to the main axis up to the next node (Fig. 31). Thus the flowers and prophylls attached between the insertion of the leaves (or somewhat below) really originate from the leaf axils of the preceding node. In "*C. oppositiflorae*" even the

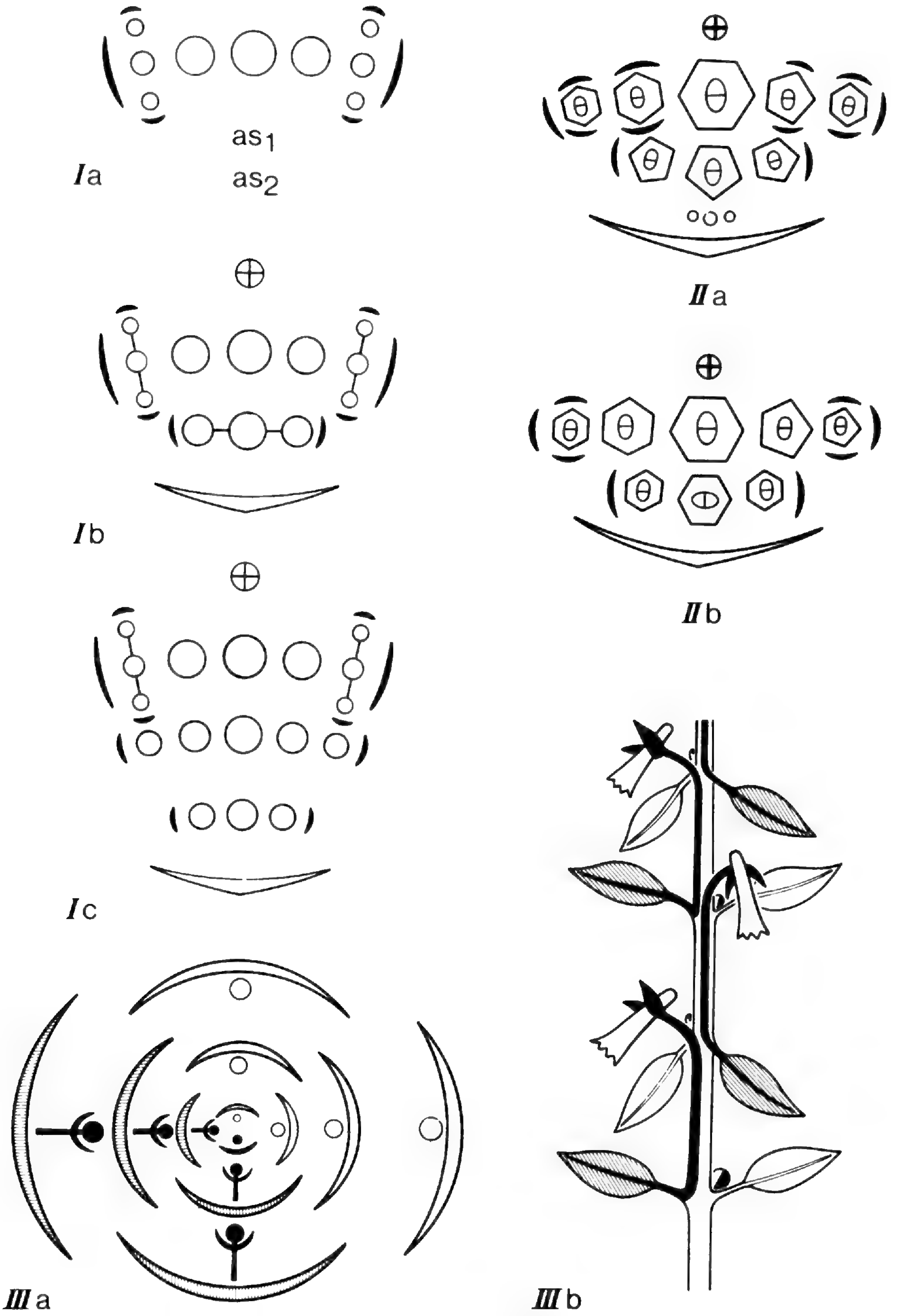


FIGURE 30. *Lythraceae.—I, II. Partial florescences and accessory flowering branches (as₁, as₂) of* Lythrum salicaria *in diagrams according to Troll (Ia–c) and Eichler, and of* L. purshianum *according to Eichler (IIb).—III. Horizontal (IIIa) and vertical (IIIb) projections of ramification in alternatiflorous* Cuphea latifolia *after Eichler (slightly modified).*

initially vegetative branches show a slight concaulescence (Koehne, 1873: 111). In the case that only one leaf axil of a node is fertile (*C. alterniflorae*), there is only one flower attached at the flanks of the next node. The bud situated in the second axil of the opposite leaves remains within the axil. Since the fertile axil of the third node always is placed above

FIGURE 31. *Lythraceae.—Top, left.* Cuphea latifolia; *plant at the beginning of flowering.—Top, right.* C. procumbens; *florescence.—Bottom.* C. micropetala; *florescence (left), and detail (right). (Photographs from Troll.)*

FIGURE 32. *Combretaceae.* Combretum coccineum; *flowering branches in anthesis (I) and before anthesis (II). (Photographs from Troll.)*

the fertile axil of the first, and the fourth always is superposed to the fertile axil of the second node (Fig. 30 IIIb), the result is two vertical rows of flowers diverging by 90° (just as two vertical rows of axillary buds, Fig. 30 IIIa).

The ligneous genus *Rhynchocalyx* Oliv., formerly included in Lythraceae and now regarded to represent a separate family, has monotelic inflorescences. In *R. lawsonioides* Oliv., the inflorescence forms a bracteose thyrso-paniculate system at the end of leafy shoots. At the bases of the paracladia uniflorous or triflorous accessory branches can be found.

The monotypic genus *Alzatea*, which is now regarded to form a separate family, has diplothyrsoidal inflorescences, probably of monotelic character. On the latter point some uncertainty remains because of the fragmentary state of the examined herbarium material of *A. verticillata* Ruiz & Pavón. The lowermost thyrsoidal paracladia are accompanied by accessory branches that form thyrsoids too.

In the monotelic character of their conical dithyrsoidal inflorescences, *Rhynchocalyx* and *Alzatea* at least do not join the progressed members of the Lythraceae.

COMBRETACEAE

The inflorescences of Combretaceae are polytelic throughout. Although there are prophylls present in *Laguncularia*, *Lumnitzera*, and *Macropteranthes*, the florescences are nearly always spikes or rarely botrya.

The central type of inflorescence architecture within the family may be represented by *Combretum coccineum* (Sonn.) Lam. (Fig. 32 I). The leafy shoots terminate in a synflorescence composed of a botrytic main florescence at the top of the whole ramification system, preceded by several pairs of paracladia. Phyllotaxis is often not strictly decussate

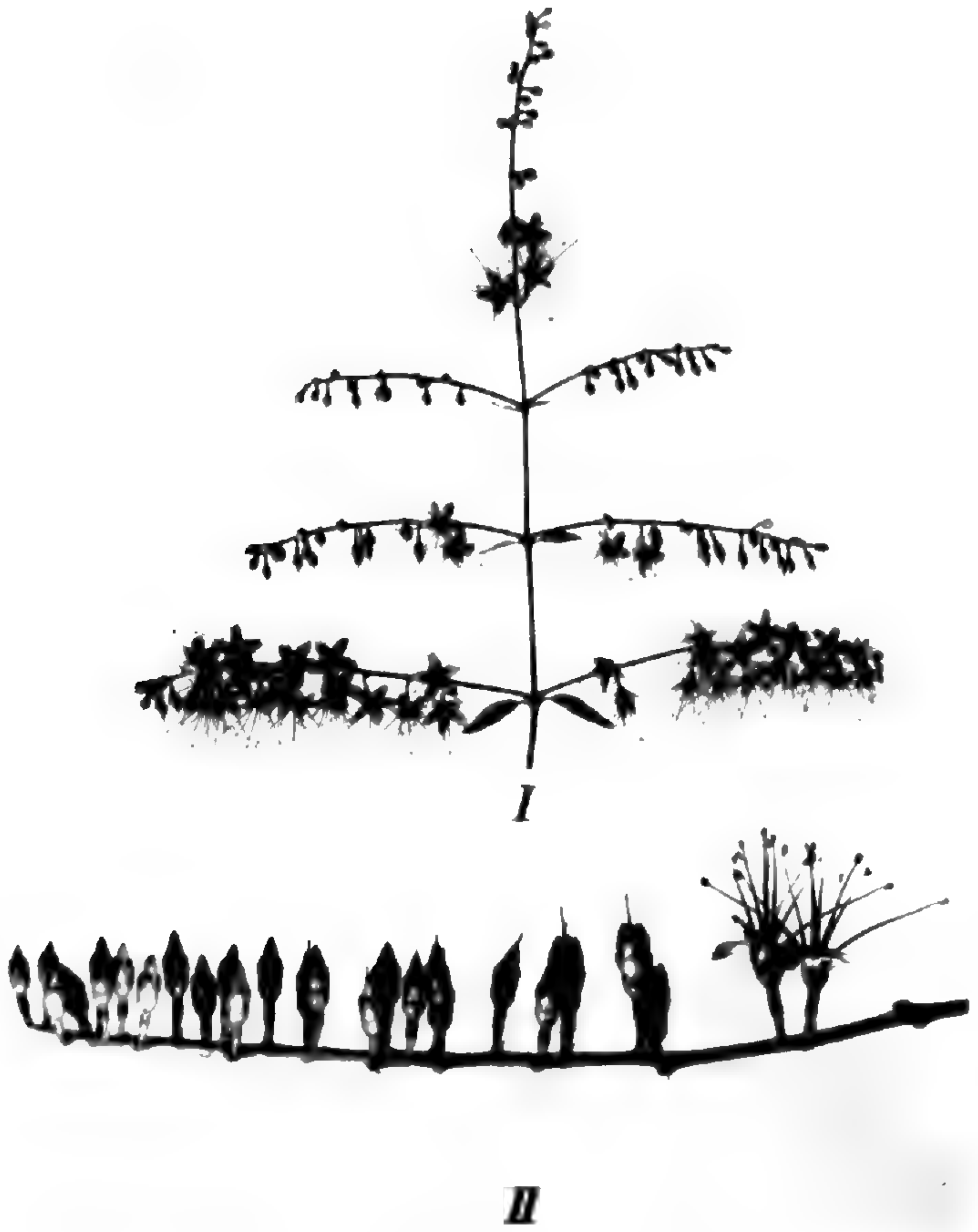


FIGURE 33. *Combretaceae*. Combretum coccineum.—*I. Mode of efforation.—II. Detail. (Photographs from Troll.)*

within the family. Besides *Terminalia*, seven genera are reported to have alternate leaves, though in many cases they are subdecussate. In many climbers only the distal branches show decussate leaves. In *Terminalia*, *Bucida*, *Buchenavia*, *Ramatuela*, *Anogeissus*, *Finetia*, *Conocarpus*, and *Lumnitzera*, the leaves are spiral. The four distal pairs of paracladia are confined to their (co-)florescences, whereas the two proximal pairs bear two or four pairs of second-order paracladia, which are likewise limited to their (co-)florescences. In descriptive terms the ramification can be classified as a heterothetic triplobotryum. The foliation in the proximal part of the main axis is frondose but quickly changes over to bracteose; the flower-bearing twigs only develop small bracts. As shown by Figure 33 I, II, the efflorescence progresses from base to top in the sequence of the paracladia (I) as well as in the paracladia themselves (II); in this course the main florescence gains a slight lead in comparison with the preceding paracladia. Figure 33 II also shows that all flowers of the florescences, even those of plagiotropic orientation, are turned upwards, a typical feature of many species, which has led to the popular name "cepillo de mono" (monkey's brush). This name especially applies to *C. fruticosum* (Loefl.) Stuntz (*C. secundum* Jacq., Fig. 34), in which the paracladia are poorly developed in favor of the vigorous development of the dense-flowered main florescence. In Figure 32 II, each of the first-order paracladia is accompanied by an accessory branch bearing a botrytic florescence. This is typical of many Combretaceae.

Synflorescences similar to those described here for *Combretum coccineum* can be found in various taxa of the family, such as *Laguncularia racemosa* (L.) Gaertner, *Thiloa glaucocarpa* (Martius) Eichler, *Calycopteris floribunda* (Roxb.) Lam., *Meiostemon tetrandrus* (Exell) Exell & Stace (cf. table I in Exell & Stace, 1966), *Campylogyne* Welw. ex Hemsley (the florescences with showy bracts), species of *Buchenavia* and *Terminalia* (*T. tomentosa* Bedd.; *T. paniculata* Roth, see also Sell, 1982, fig. 10a; *T. citrina* (Gaertner) Roxb. ex Fleming; *T. chebula* Retz., cf. Brandis, 1893, fig. 55), and in *Quisqualis*. In *Q. indica* L., the inflorescence can consist of a spicate main florescence terminating leafy twigs, contrasting with them by its bracteous foliation. The main florescence, however, can be accompanied by one or two pairs of paracladia originating from the axils of the foliaceous leaf pairs preceding the main florescence. These paracladia usually bear one or two more or less foliaceous leaf pairs at their bases. Likewise, the lowermost leaf pair of the main florescence may be somewhat foliaceous. *Cacoucia coccinea* Aublet (*Combretum cacoucia* (Ball.) Exell) seems to be characterized by developing only a long voluminous main florescence (Fig. 35). The same applies to some other species formerly included in this genus (*Cacoucia splendens* Hemsl. = *Combretum bracteatum* (Laws. pro parte) Engl. & Diels, *Cacoucia paniculata* Laws.).

Lumnitzera coccinea and *L. racemosa* differ considerably in the position of their spicate florescences (see also Brandis, 1893). In *L.*

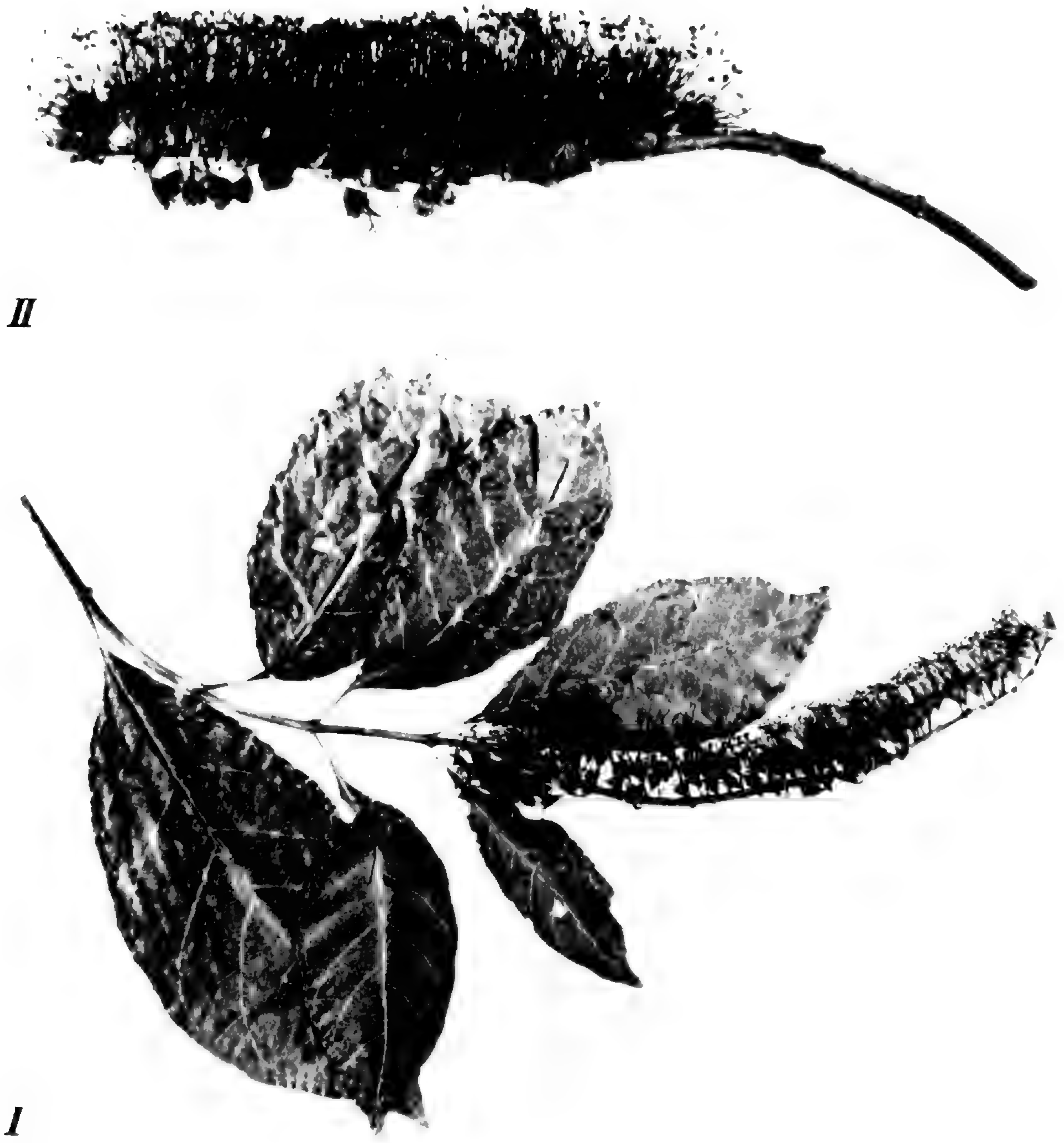


FIGURE 34. *Combretaceae.* Combretum fruticosum (= C. secundum); *flowering branch (I) and botrytic florescence (II). (El Salvador:* Weberling 164, 175.)

littorea (Jack) Voigt, normally a bracteose spicate main florescence terminates a leafy shoot, and paracladia are missing. In *L. racemosa* Willd., however, the synflorescence consists of paracladia only, which form 10–20-flowered, long-peduncled spikes originating in the axils of foliaceous leaves of a leafy shoot with indeterminate growth. In *L. coccinea*, however, the foliaceous shoots that end in a spicate main florescence are not very large and represent branches of a shoot with indeterminate vegetative growth, too.

Within *Terminalia*, a great number, perhaps the majority, of the species are characterized by leafy proliferating inflorescences. In some of these species the flowering branches grow with well-developed internodes, and after the production of several spicate paracladia which originate in the axils of foliaceous leaves, these branches return to vegetative growth. *Terminalia oblonga* (Ruiz & Pavón) Steudel serves as an example (see also *T. brownii* Fresen., Sell, 1982, fig. 10d). In other species the internodes of the main axis remain short within the flowering zone. Thus the leaves are "crowded at the ends of the

FIGURE 35. *Combretaceae.* Cacoucia coccinea *(from Aublet, J. B., Hist. Pl. Guiane Franç. III, pl. 179, 1775).*

branches," and the synflorescence has a rosettelike shape. This applies to *T. catappa* L. (Fig. 36; for the crown form and branching pattern of *T. catappa* and *T. latifolia* see Fisher & Hibbs, 1982), *T. bellirica* (Gaertner) Roxb., *T. zollingeri* Exell, *T. sumatrana* Miq., *T. trivialis* Slooten, and many other species, also to *Bucida* L. In *T. gigantea* Slooten, which shows a similar architecture, the spicate paracladia are very long, with many loosely arranged flowers. In *T. australis* Camb., on the other hand, the paracladia bear a smaller number of densely aggregated flowers that form a long-peduncled head. The flowering branches of this species are brachyblastlike proliferating twigs with well-developed internodes. They develop from axillary buds of an older shoot but also arise from its terminal bud and later continue its growth. In *T. triflora* (Griseb.) Lillo, the brachyblasts, which bear several bud scales at their bases, remain very short, at least during the anthesis of their four to six paracladia, which likewise form few-flowered, long-peduncled heads.

Formation of flowers is limited to brachyblasts in many species of other genera. Thus in the species of *Pteleopsis* Engl., the flowering branches are brachyblasts originating from older macroblasts. They bear a few bud scales at their bases, some pairs of foliaceous leaves, and an umbel-shaped to botrytic main florescence, which in its proximal part can bear small foliaceous pherophylls. We could, however, also observe heterothetic diplobotrytic inflorescences with somewhat umbellate florescences in some specimens of *P. myrtifolia* (Lawson) Engl. & Diels.

In *Combretum salicifolium* E. Meyer, and in *C. apiculatum* Sonder (Fig. 37 I) brachyblastlike branches situated on macroblasts of the previous year bear simple paracladia in the axils of the two or three lowermost pairs of foliaceous leaves; these brachyblasts proliferate at the end of the anthesis of the paracladia (see also Brandis, 1893, fig. 59). *Combretum bracteosum* (Hochst.) Brandis is similar.

The florescences of *Combretum salicifolium* are contracted to 15–20-flowered headlike aggregations (see Brandis, 1893: 122, fig. 59A). The same applies to *C. erythrophyllum* (Burch.) Sonder (Fig. 37 II), in which the proliferating brachyblasts bear several pairs of long-peduncled globose umbels arising from the axils of foliaceous leaves. Capituliform florescences are also reported, for example in *C. punctatum* Bl. (van Slooten, 1922), whereas in *C. apiculatum* Sonder the axillary florescences are spicate (Fig. 37 I).

Capitulate and very densely flowered, long-peduncled florescences can also be found in *Guiera senegalensis* Lam. and in species of *Buchenavia*, *Finetia*, and *Anogeissus*. In *Buchenavia capitata* (Vahl) Eichl. and *B. ochroprumna* Eichl., the paracladia bearing globose, ca. 20-flowered heads were observed on terminal rosette-shaped proliferating brachyblasts. They were inserted here at the base of the brachyblasts, thus preceding the leaf rosette. In contrast to these species, the floral zone of the brachyblasts in *B. kleinii* Exell succeeds the leaf rosette, and the inflorescences are ovoid. In some other species the paracladia bear loosely flowered spikes and are inserted at the top of the brachyblasts

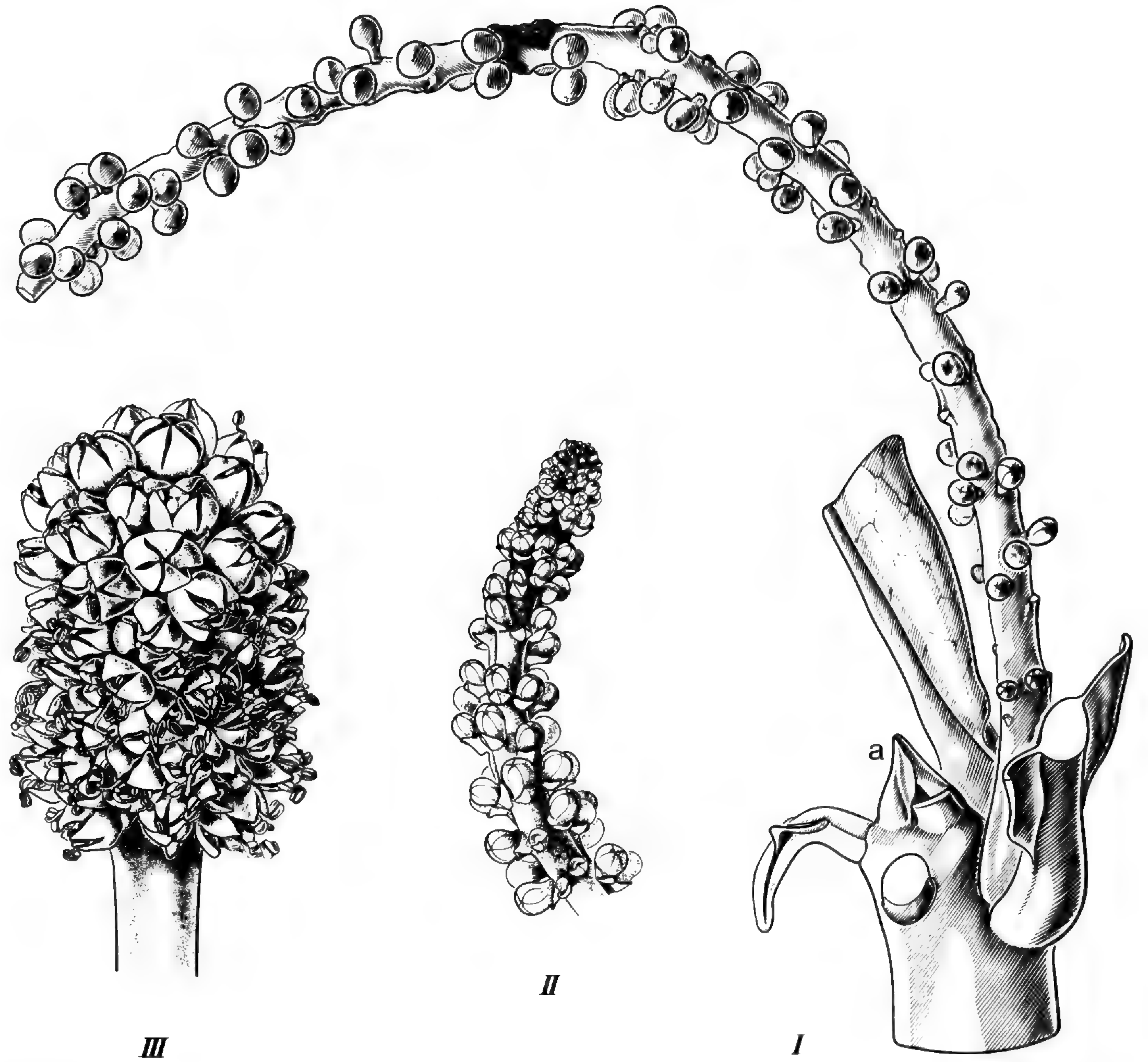


FIGURE 36. *Combretaceae. I, II.* Terminalia catappa.—*I. Proliferating inflorescence with one spikelike paracladium, the leaves partly removed; apex (a) of the main axis.—II. Distal part of a paracladium.—III.* Conocarpus erecta; *capitulate paracladium.*

more or less following the leafy zone (*B. macrophylla* Eichl., *B. suaveolens* Eichl.) or at the base of the brachyblasts, preceding the rosette (*B. oxycarpa* (Martius) Eichl.).

In *Anogeissus acuminata* (Roxb. ex DC.) Wall. ex Bedd. and *A. latifolia* (Roxb. ex DC.) Wall. ex Bedd., the synflorescences consist of a globose main florescence and an enrichment zone comprising several paracladia, each originating in the axil of a foliaceous leaf and bearing a globose co-florescence on a long peduncle. The paracladia can be accompanied by similar-shaped accessory branches.

In *Conocarpus erecta* L. (Fig. 38) the inflorescence terminating a leafy shoot is composed of one terminal and many lateral, short-peduncled, ovoid capitula, which together form a heterothetic botrytic or diplobotrytic system. The basal leaves within this system are foliaceous, diminishing distally, and ultimately convert to small bracts. At least in the distal part of the inflorescence the paracladia are accompanied by accessory branches forming particular peduncled capitula.

In general the tendency to form condensed inflorescences is not very strong within the Combretaceae. Exell (1962), however, saw some evolutionary consequences resulting from a conflict between pollination strategies and the development of winged fruits of "massed flowers" that might cause "space

FIGURE 37. *Combretaceae. Brachyblasts.—I.* Combretum apiculatum. *(SW Africa, Windhoek,* R. Seydel 3666 *(M).)—II.* C. erythrophyllum. *(South Africa, Cape Prov.: King Williams Town,* D. M. Comens 1715 *(M).)*

problems." The problem, however, seems to be more complex and needs empirical treatment with regard to flower biology as well as to carpology and chorology.

PENAEACEAE

The inflorescences of Penaeaceae were carefully investigated in the monographic work of Dahlgren (1967a–c, 1968, 1971). The basic type of ramification is a thyrsoid (a thyrse with a terminal flower) as in *Sonderothamnus petraeus* (Barker) Dahlgren (Fig. 39 II) and *S. speciosus* (Sonder) Dahlgren. In the majority of taxa the cymose (triadic) paracladia are reduced to their primary flower. The thyrsoid thus is converted to a stachyoid as presented by *Saltera sarcocolla* (L.) Bullock (Figs. 39 I, 41 II, 42 I).

A peculiarity of the *Saltera* inflorescence is that the terminal flower is preceded by two pairs of pale membranaceous bracts. The lower bracts are narrow but broaden distally to an emarginate end; the next pair is much narrower, nearly linear, but also broadens to a truncate or slightly emarginate end. Two or three of the preceding leaf pairs bear single flowers in their axils, each of them with a pair of linear-spathulate prophylls. Since these prophylls are similar in shape to the upper pair of bracteoles preceding the flower that terminates the whole inflorescence, one could wonder if this flower is terminal or lateral. Dahlgren (1968), however, reported that the inflorescence can be reduced so far that the terminal flower is the only one remaining (Fig. 43 II). This, together with the comparison with the structure of inflorescences in some related taxa, particularly that of *Stylapterus fruticulosus* (L. f.) A. Juss. (Figs. 40 II, 41 IV), confirms that there is a true terminal flower.

In some other taxa the terminal flower is sometimes facultatively lacking or missing in all specimens. Thus in *Glischrocolla formosa* (Thunb.) R. Dahlgren the "inflorescence apex generally bears a terminal flower, but this may drop in an early stage" (Dahlgren, 1967b).

The inflorescences of *Brachysiphon rupestris* Sonder and *B. mundii* Sonder still have a terminal flower, whereas *B. fucatus* (L.) Gilg and *B. acutus* (Thunb.) A. Juss. have indeterminate spikes. In such cases the "apex ends in some scalelike leaves" (*B. fucatus*) or "as a dry tip" (Dahlgren, 1968). In *B. fucatus* (Fig. 39 IV), however, all the paracladia end in a terminal flower, and this refers not only to paracladia that are provided with the pair of prophylls only (and therefore otherwise could be interpreted as partial florescences of a polytelic thyrse), but also to the lower paracladia with three or more leaf pairs. With some alterations the same applies to *Brachysiphon acutus*. Consequently we have to interpret these inflorescences as truncate monotelic systems.

In *Stylapterus* the inflorescence is "generally indeterminate, the apical tip being degenerated and dry, but in *S. fruticulosus* and *S. ericifolius* it often ends with a terminal flower" (Dahlgren, 1967a). The semidiagrammatic figures of "selected rich-flowered inflorescences" of both species (Fig. 40) show that there is a strong tendency to reduce the number of flowers in the paracladia to their terminal flower. Particularly in *S. fruticulosus* the result of this reduction is that the terminal flower of the whole ramification system as well as the terminal flower of the paracladia are preceded by two or three pairs of sterile leaves (see also Fig. 41 IV). This is in good concordance with the occurrence of two pairs of sterile bracts below the terminal flower of the *Saltera* inflorescence (Fig. 39 I). We also should note that the flowering system of *Stylapterus fruticulosus* has a secondary inhibition zone below the terminal flower in addition to the primary inhibition zone that commonly precedes the paracladial zone.

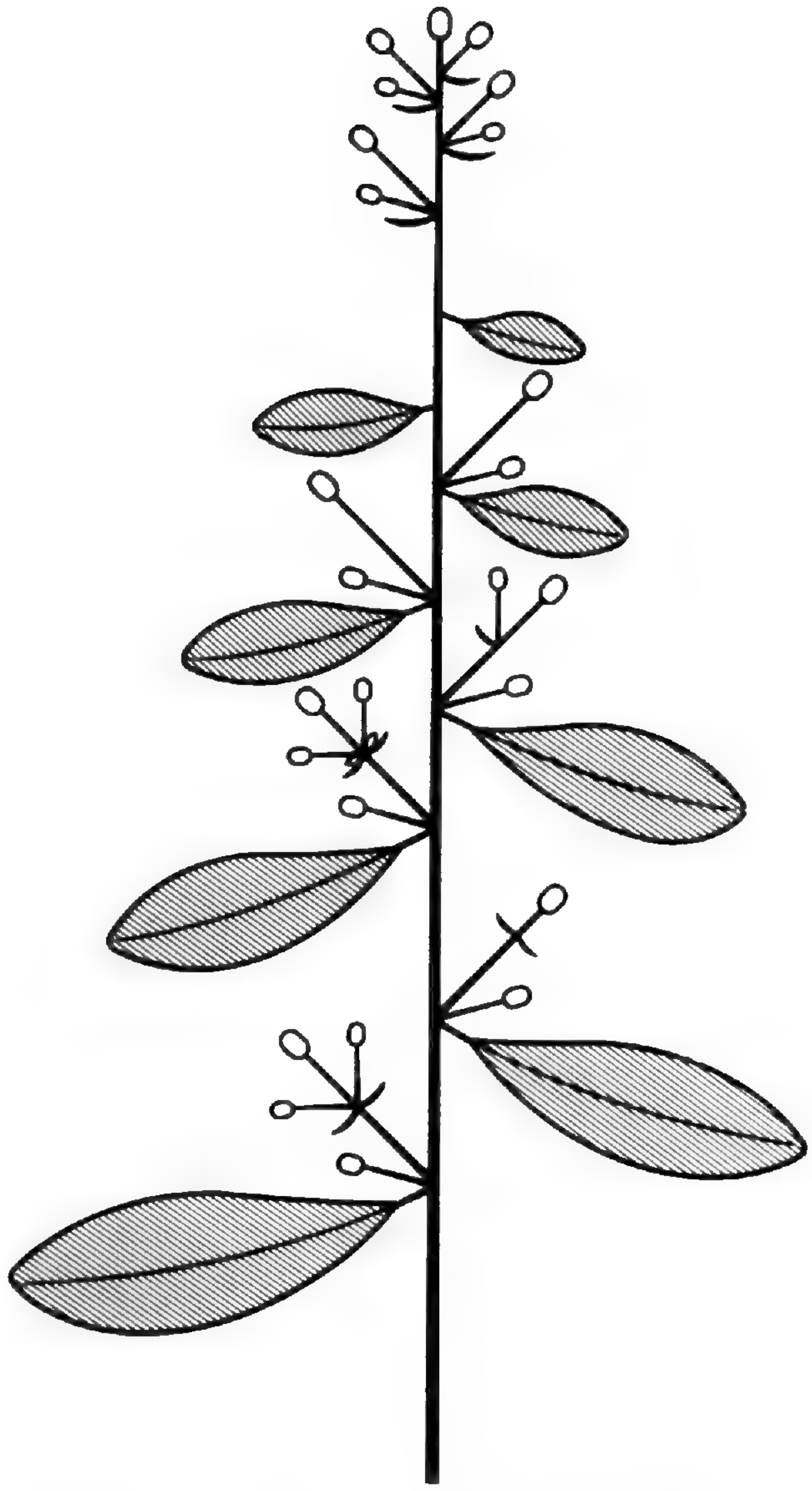
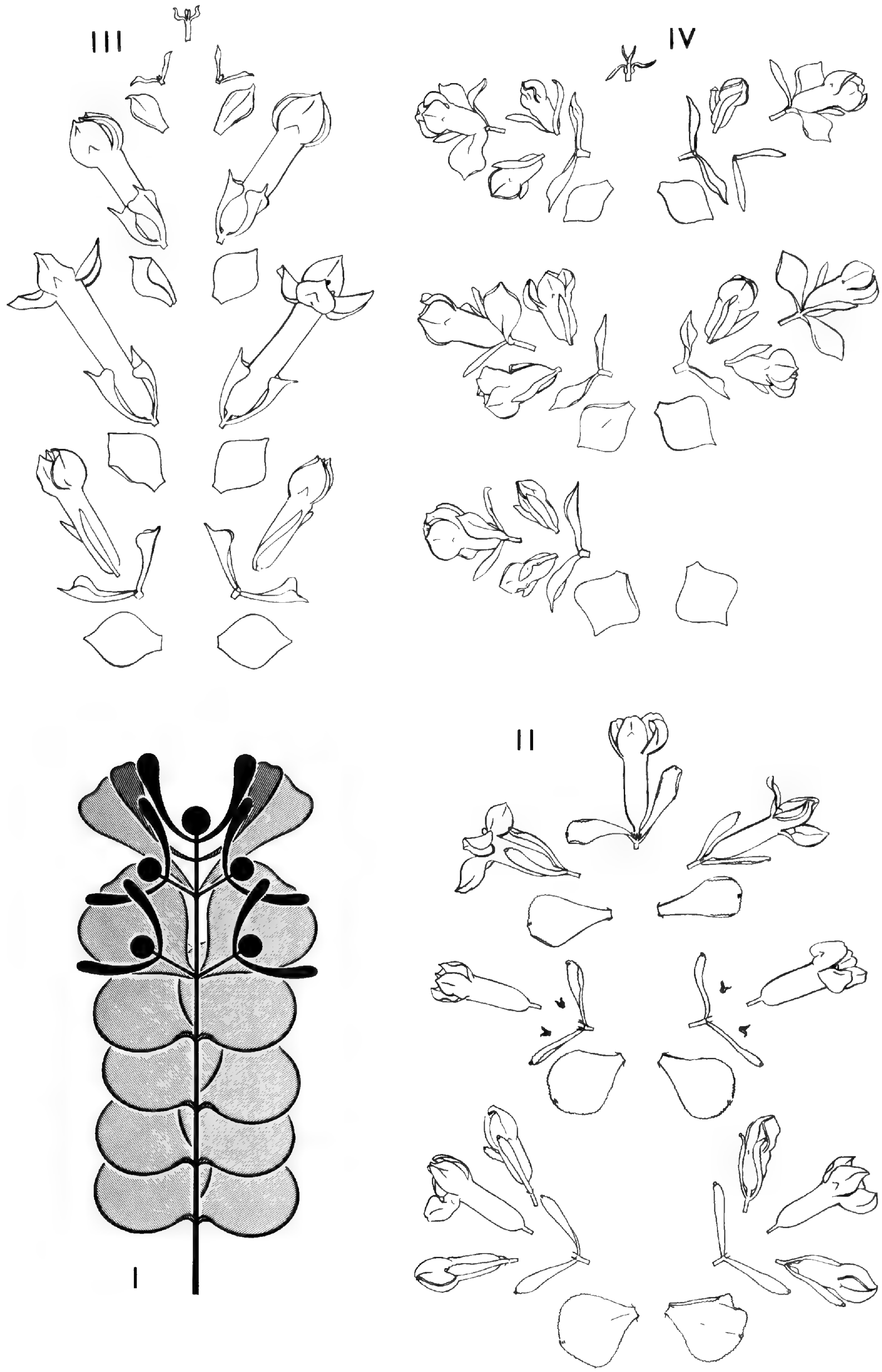


FIGURE 38. *Combretaceae.* Conocarpus erecta; *diagram of a flowering branch.*

Dahlgren (1971) described the inflorescence of *Penaea acutifolia* A. Juss. as "generally with a terminal flower," whereas *P. mucronata* L. was reported as "with or without terminal flower," and *P. cneorum* Meerb. as "without or sometimes with a terminal flower, when well developed with 6–14 flowers." In our own investigations based on very restricted material only, we could only once find a terminal flower. An indeterminate (anauxotelic) inflorescence of *P. mucronata* is shown in Figure 42 II, a terminal flower in Figure 41 III. Dahlgren (1971: 8) stated that in general the "flowering sequence is acropetal, but when a terminal flower is present, this develops in head of the upper neighboring flowers." This feature is very typical for terminal flowers.

In all genera, innovation, i.e., the production of vegetative shoots continuing the ramification system and perhaps later producing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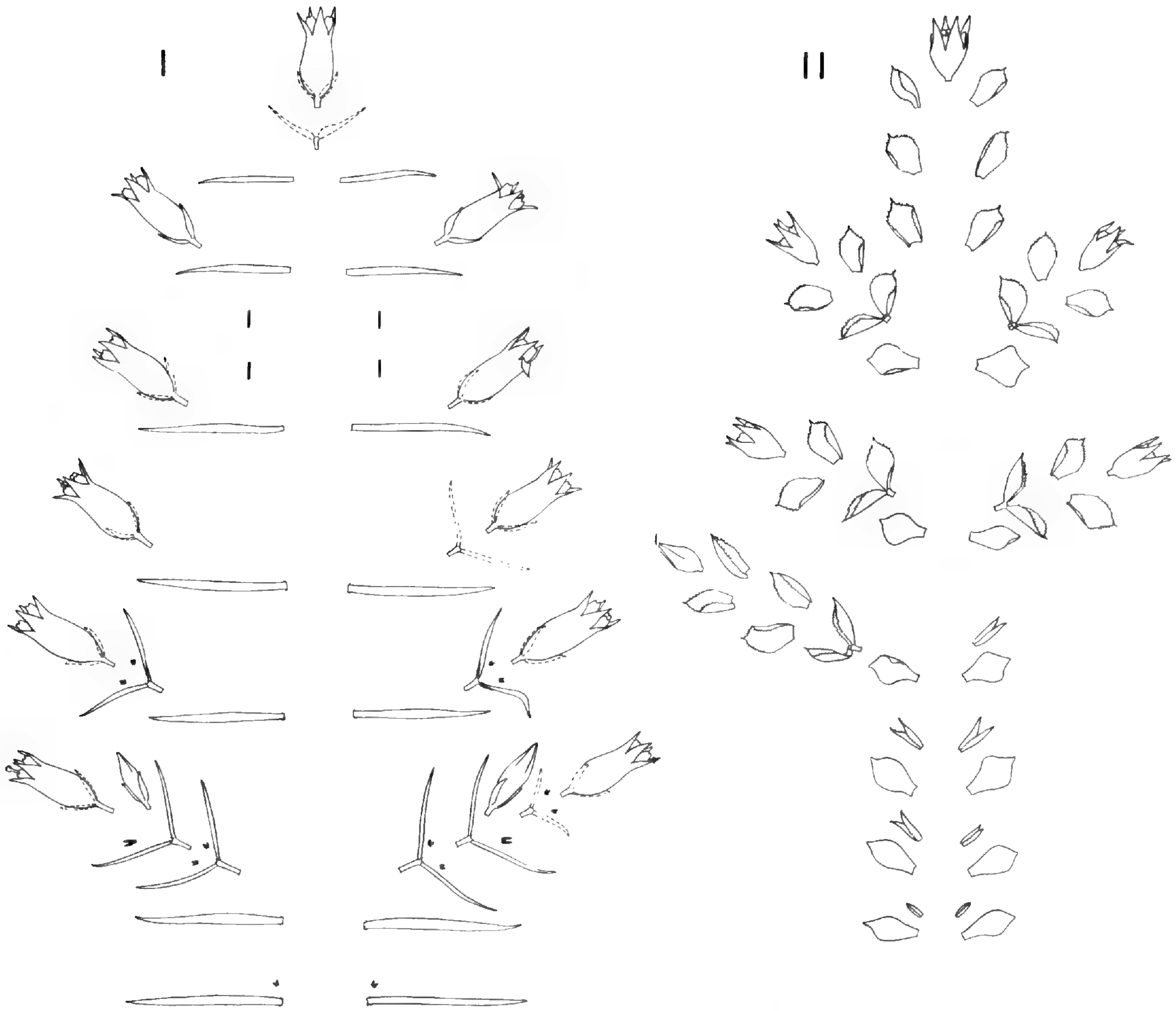

FIGURE 40. *Penaeaceae. Semidiagrammatic representation of selected rich-flowered inflorescences.—I.* Stylapterus ericoides *(shed bracteoles with broken lines).—II.* S. fruticulosus. *(All from Dahlgren.)*

terminal inflorescences, takes place from the axils of foliage leaves somewhat below the flower-bearing zone.

Inasmuch as the spikelike inflorescences actually no longer develop a terminal flower, they could be interpreted as a botrytic polytelic main florescence. We hesitate, however, to classify them in this way, not only because terminal flowers are reported for some cases, but particularly because of the lack of paracladia terminating in co-florescences. If such paracladia could be found in well-developed inflorescences, this would prove that the strong evolutionary tendency from the formation of monotelic inflorescences to the development of polytelic systems that appears independently in various branches of the family has really arrived at the polytelic stage. Without this proof we prefer to classify the indeterminate inflorescences as truncate monotelic systems.

A special case within the family is the inflorescence of *Endonema*. In both species, *E. lateriflora* (L. f.) Gilg and *E. retzioides* Sonder (Fig. 43 I), two or more single flowers are situated in the axils of leafy pherophylls

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FIGURE 39. *Penaeaceae. Semidiagrammatic representations of richly developed inflorescences.—I.* Saltera sarcocolla. *(South Africa. Cape Prov.:* Forstmeier s.n.*)* —*II.* Sonderothamnus petraeus.—*III.* Brachysiphon acutus.—*IV.* B. fucatus. *(II–IV from Dahlgren.)*

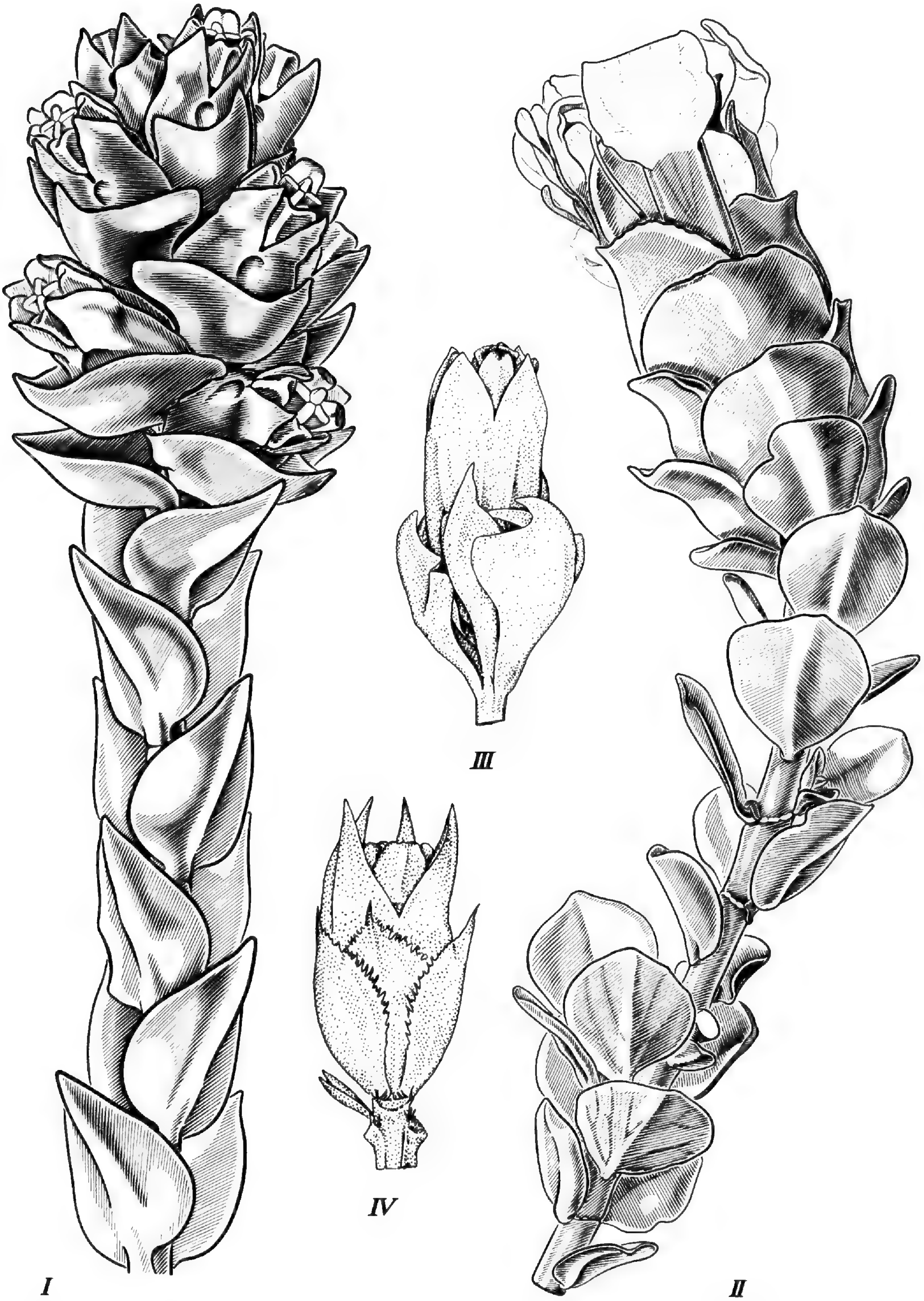

FIGURE 41. *Penaeaceae. I, II. Flowering branches.—I.* Penaea mucronata. *(South Africa. Cape Prov.: near Elim,* Weberling 7819.*)—II.* Saltera sarcocolla. *(South Africa. Cape Prov.: Fernkloof, Hermanus,* Weberling 7862a.*)—III, IV.* Penaea mucronata *and* Stylapterus fruticulosus; *terminal flowers subtended by three decussate pairs of bracteolate leaves or bracts. In IV the lowest pair is shed. (III, IV from Dahlgren.)*

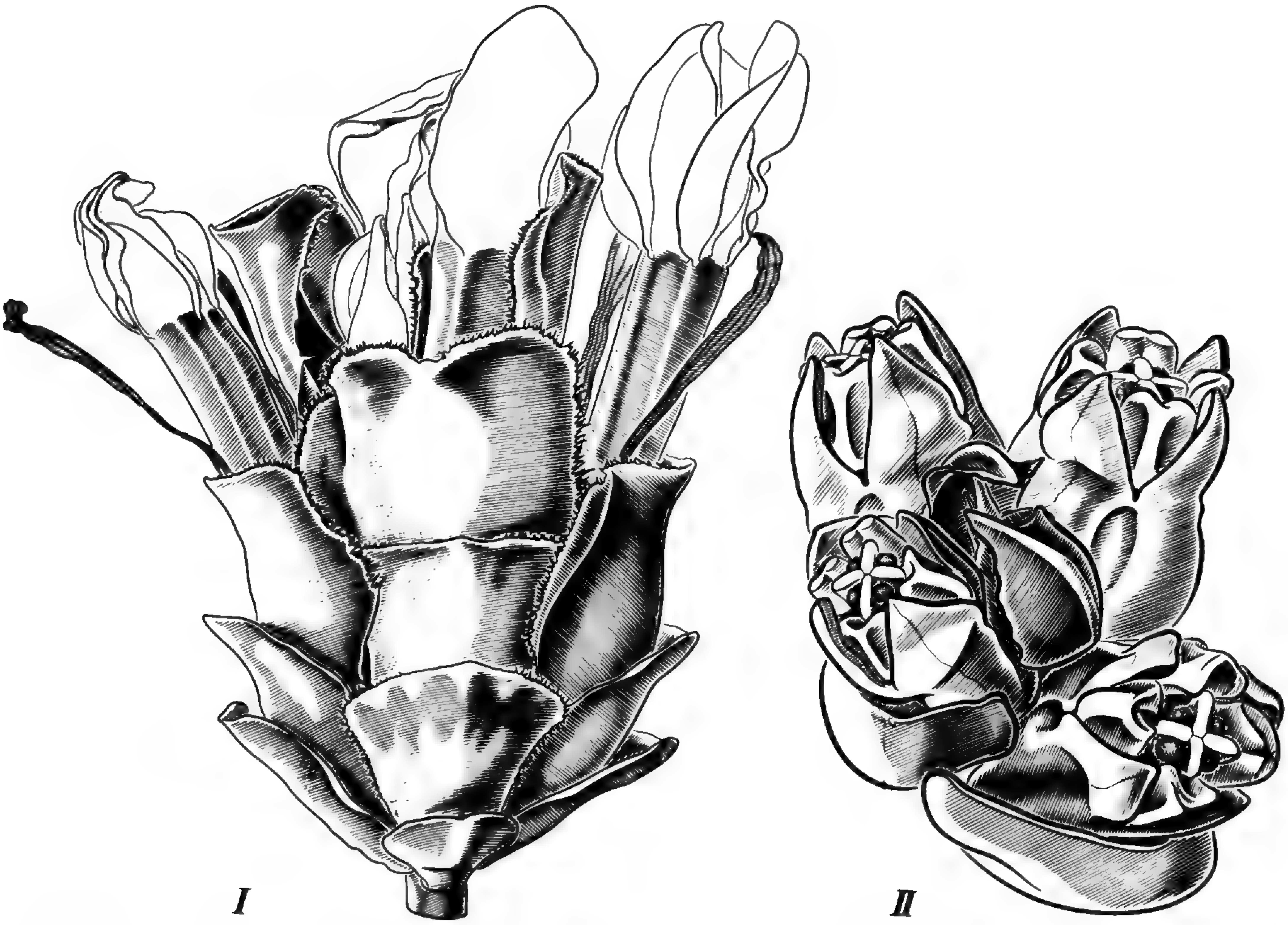

FIGURE 42. *Penaeaceae.—I.* Saltera sarcocolla; *inflorescence. (South Africa. Cape Prov.:* Weberling 7862a.*)—II.* Penaea mucronata; *inflorescence apex ending in a sterile bud. (South Africa. Cape Prov.:* Weberling 7819.*)*

on a young branch, which continues vegetative growth. Each of these lateral flowers bears two (*E. retzioides*) or three (*E. lateriflora*) pairs of bracts. Dahlgren (1967c) reported that suppressed buds are sometimes found in the axils of the lowest pair of "bracteoles." Thus the whole branchlet in Figure 43 I may be explained as a proliferating monotelic inflorescence with highly reduced paracladia.

MELASTOMATACEAE

Variety of inflorescences in Melastomataceae corresponds to the size of the family but shows less diversity than Myrtaceae.

The inflorescences are monotelic throughout. Cases of complete transition to polytelic structures were not found. Even truncation seems to be rare. A single case noted by Troll (posthumous manuscript) is that of *Medinilla magnifica* Lindley, in which the inflorescence sometimes ceases development before the ultimate lateral cymes and the terminal flower of the distal thyrsic zone have completed their formation. Thus the whole end of the inflorescence atrophies (Fig. 64 III). Cremers (1983/1986) reported that the thyrse of *Desmoscelis villosa* (Aublet) Naudin remains indefinite. This, however, may only happen facultatively; in several plants investigated terminal flowers of the thyrsoids were well developed (Fig. 45). On the other hand, proliferation is not infrequent.

The basic form of ramification is a pleiothyrsoid terminating in a leafy shoot, as in *Miconia argentea* (Sw.) DC. (Fig. 44). Such bracteose or frondo-bracteose pleiothyrsoids, diplothyrsoids, or even monothyrsoids (haplothyrsoids) can be found in a terminal position in nearly all the 1,000 species of the genus *Miconia* as well as in many other ligneous genera such as *Conostegia*, most species of *Tococa*, and the large genera *Leandra* and *Clidemia*. Elongate conical thyrsoids or diplothyrsoids are also typical of many species

FIGURE 43. *Penaeaceae.—I.* Endonema retzioides; *part of a branchlet with two uniflorous inflorescences.— II.* Saltera sarcocolla; *branchlet with terminal uniflorous inflorescence. (Both after Dahlgren, 1967c, 1968: I.* Hohenacker s.n.; *II. South Africa: S. Cape Peninsula,* Dahlgren & Peterson 652.*)*

of *Tibouchina.* In some species of *Tibouchina* and of *Heterocentron,* the thyrsoids get a somewhat botrytic appearance since the hypopodia of the paracladia of first order are long compared with the other internodes ("thyrsus racemiformis"). Many examples have been analyzed and figured by Cremers (1983/1986), who published a thorough study on inflorescence structures of Guianese Melastomataceae. His investigations also include interesting studies on growth forms. While the manuscript of the present article was in press, W. S. Judd (1986) published the results of studies on variation in inflorescence position in Miconieae.

The cymose ramification of the partial inflorescences usually remains limited, and the mode of ramification is different. Eichler (1878c: 483) observed a formation of a helicoid cyme (bostryx) by preferential ramification from the axils of the β-prophylls in *Tibouchina* (cited by Eichler as *Lasiandra*). A bostryx also is reported for *Centradenia floribunda* Planchon by Wydler (1878: 349), who supposed that ramification continued from the axils of the β-prophylls as in *Tibouchina.* Ziegler (1925: 410), however, observed a preferential ramification from the axils of the larger α-prophylls. The statement of Eichler (1878c: 483) that in the helicoids of *Centradenia* only the fertile prophylls are developed proved to be wrong (Troll, posthumous manuscript). Krasser (1893) reported helicoid cymes for *Miconia secundiflora* Cogn. Simple or double helicoids also occur in *M. hookeriana* Triana (Fig. 46 I) and *Fordiophyton.*

FIGURE 44. *Melastomataceae.* Miconia argentea; *monotelic pleiothyrsoid inflorescence. (El Salvador:* Weberling 2024.*)*

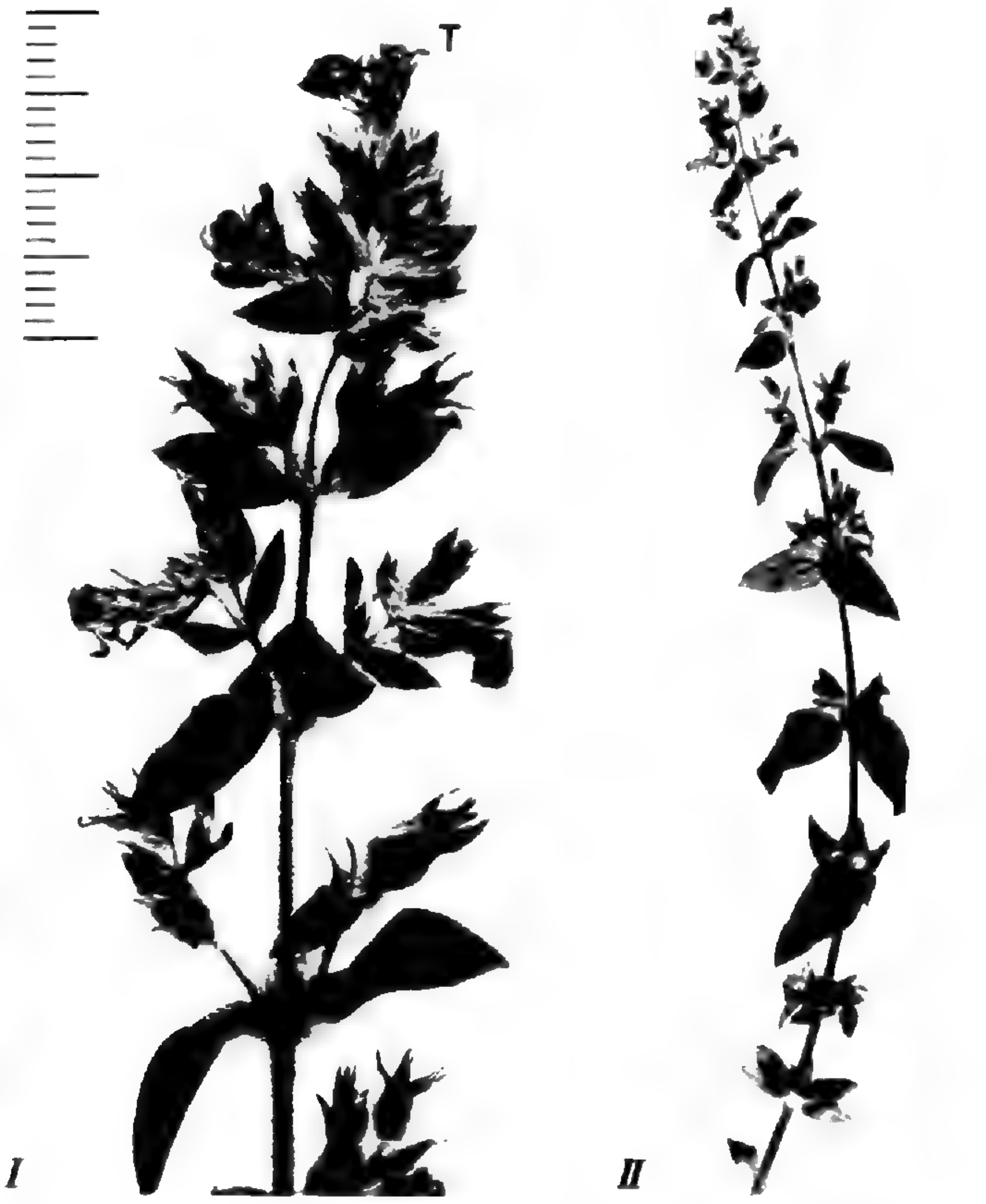

FIGURE 45. *Melastomataceae.* Desmoscelis villosa. *(N. Brazil:* Ph. v. Luetzelburg 22181 *(M).)—I. Distal part of II. T, terminal flower.*

The formation of scorpioid cymes (cincinni) by preference of the ramification from the axils of the α-prophylls was reported by Eichler (1878c: 483) for *Salpinga* and *Clidemia.* Scorpioid ramification of the cymose partial inflorescences is also known for *Rhynchanthera* (Wydler, 1851a: 370), the Bertolonieae and Sonerileae (see Krasser, 1893, and p. 278), *Arthrostema, Centradenia inaequilateralis* (Schldl. & Cham.) G. Don (see p. 282), *Amphiblemma cymosum* (Schrader & Wendl.) Naudin (see p. 272), *Appendicularia thymifolia* (Bonpl.) DC., and *Aciotis acuminifolia* (DC.) Triana, *A. acutiflora* (Martius) Triana, *A. longifolia* Triana, and others.

The cymose paracladia in the mono-thyrsoid inflorescence of *Miconia hookeriana* Triana are simple helicoid cymes in the distal part, and double helicoid cymes in the proximal part (Fig. 46 I). The inflorescence, which has only caducuous bracts, is preceded by several pairs of foliage leaves bearing vegetative buds in their axils. From the axils of older leaves sylleptic branches with several foliaceous leaves and a terminal thyrsoid can develop (Fig. 46 II).

In most of the ligneous Melastomataceae, the axillary buds of the leaf pairs preceding the terminal inflorescence develop innovation shoots some time after anthesis, as is shown here for *Miconia guatemalensis* Cogn. (Fig. 47 II). The order of precedence in this development can be indicated already by the size of the buds (Fig. 47 I).

On the other hand, there are ligneous members of the family with proliferating inflorescences. A favorable disposition for proliferation seems to be given with the occurrence of leafy pherophylls, as in *Huilea macrocarpa* Uribe (Fig. 47 III). After the production of long-peduncled axillary thyrsoids or cymes the apex of the inflorescence axis returns to vegetative growth, producing axillary buds that develop vegetative branches instead of flower-bearing paracladia (Mora Osejo, 1966). Among the numerous species of *Clidemia,* which mostly have terminal bracteose thyrsoid or diplothyrsoid inflorescences, there is *C. rubra* (Aublet) Martius

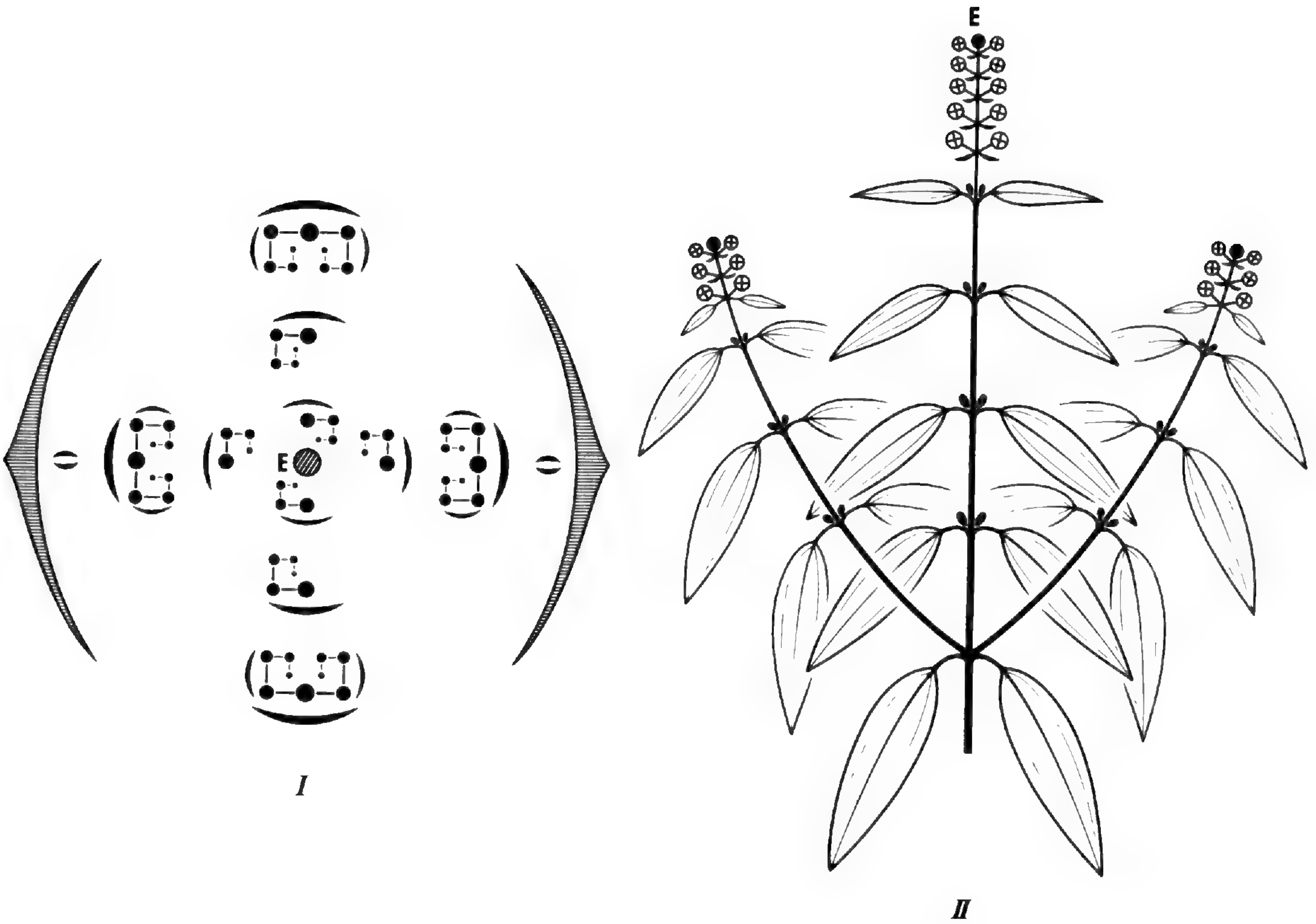

FIGURE 46. *Melastomataceae.* Miconia hookeriana.—*I. Horizontal projection of the ramification of a thyrsoid.—II. Vertical projection of a flowering branch system. (From Troll.)*

with leafy proliferating inflorescences (Fig. 48 I). In contrast to *Huilea macrocarpa*, however, the paracladia in *C. rubra* are reduced to sessile densely flowered cymes.

Proliferation also can be observed within the genus *Comolia*, which also comprises some herbaceous species with proliferating inflorescences (Cremers, 1983/1986). Proliferating inflorescences are characteristic of many or all species of many additional genera, including *Amplectrum* (*homoeandrum* Stapf), *Blastus, Bellucia, Cambessedesia, Ernestia, Maieta, Marumia, Mecranium, Meriania, Microlicia* (*M. pseudo-scoparia* Cogn.), *Microphysca, Myriaspora* (*M. egensis* DC.), *Myrmidone, Ochthocharis, Opisthocentra, Ossaea, Plethiandra, Tococa, Trembleya*, and others. In *Acanthella*, the paracladia of the proliferating inflorescence are reduced to single flowers; the same applies to species of *Blakea* (*B. spruceana* Cogn., see fig. 80 in Krasser, 1893), *Kibessia, Pyxidanthus*, and *Topobea*. *Topobea* and *Blakea* are placed in the Blakeae, which is characterized by the flowers bearing an involucrum of two or more pairs of bracts. This may be interpreted as the remnant of a formerly richer ramification. In addition, in many species of *Blakea* and *Topobea*, we found one to three accessory single flowers below the original one.

Delayed anthesis of the paracladia of proliferating inflorescences in such ligneous plants results in a more or less pronounced cauliflory. Thus in contrast to *Clidemia rubra*, which was mentioned above for its proliferating inflorescences, *C. septuplinervia* Cogn. is cauliflorous (Cremers, 1983/1986). The same applies to many Memecyloideae. Nearly all species of this subfamily are characterized by auxotelic (or sometimes anauxotelic) inflorescences or by more or less cauliflorous partial inflorescences. Transitional forms may be found even in the same plant. Only in *Memecylon cumingianum* Presl we found axillary and terminal thyrsoids. The latter, however, were terminating an older ligneous stem

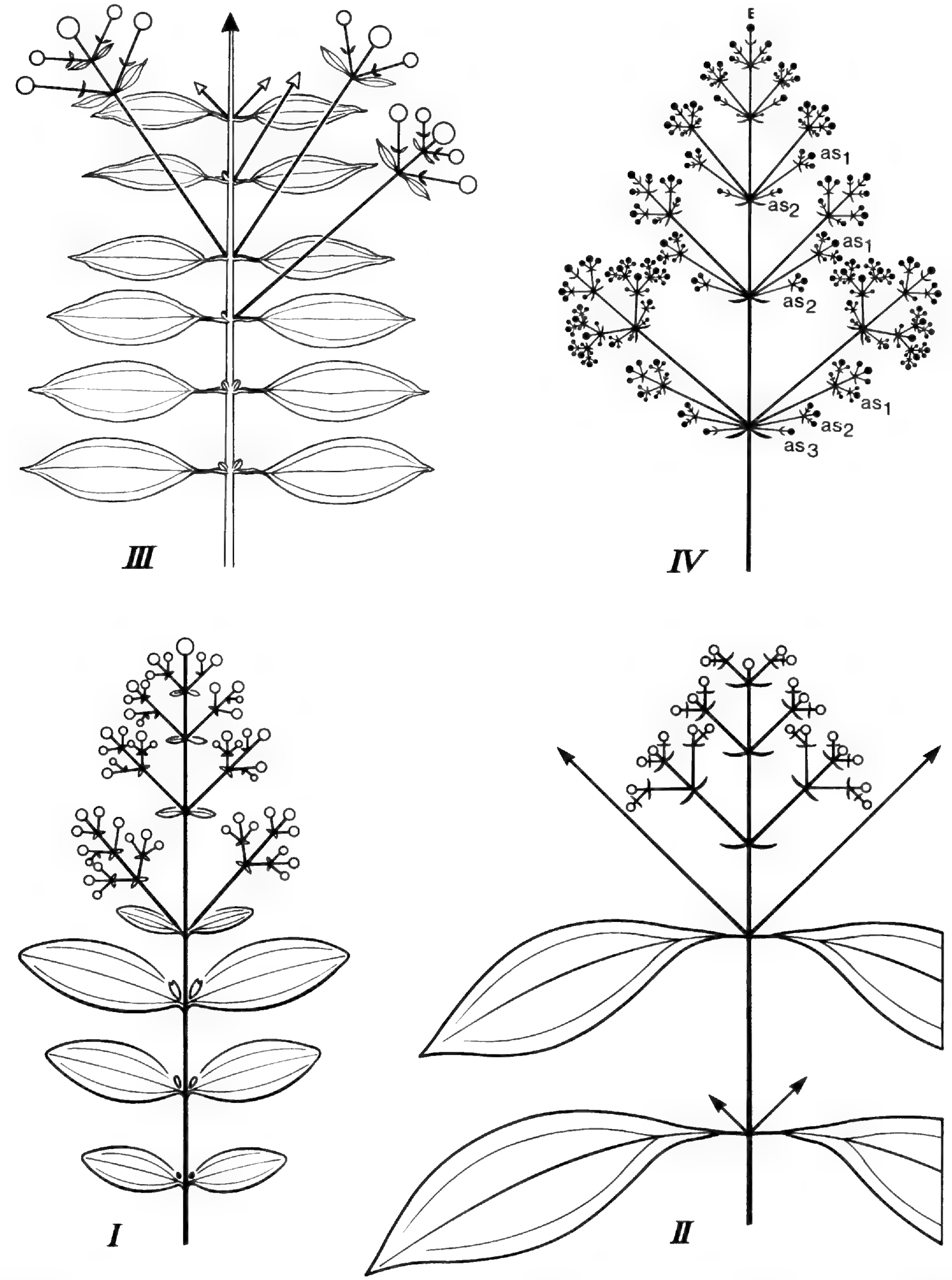

FIGURE 47. *Melastomataceae. Vertical diagrams of flowering shoots and inflorescences.—I.* Miconia squamulosa *(from Mora).—II.* M. guatemalensis. *(El Salvador:* Weberling 2299.*)—III.* Huilea macrocarpa; *with a proliferating inflorescence axis (from Mora.)—IV.* Tococa symphyandra; *synflorescence with accessory flower-bearing branches of first to third order* (as_1–as_3). *(All from Troll.)*

FIGURE 48. *Melastomataceae.—I.* Clidemia rubra; *proliferating flowering shoot. (El Salvador: La Palma,* Weberling 732.*)—II.* Tococa spadiciflora; *spadixlike inflorescence (from Troll).—III.* Henriettella macfadyenii; *cauliflorous branch (from Troll.)*

that was still bearing its foliage leaves. Cauliflory is also well known for the genera *Loreya, Henriettea, Henriettella* (e.g., *H. macfadyenii* (Triana) Alain (Fig. 48 III), and *H. glazioviana* Cogn., see fig. 79B in Krasser, 1893), *Bellucia* (e.g., *B. imperialis* Sald. & Cogn.), and *Myriaspora.* All of these genera belong to the Miconieae, which also includes *Clidemia.*

The contours and forms of terminal inflorescences can be modified by different features. Thus the conical thyrsoid, as mentioned already for *Conostegia* or *Miconia* (Figs. 44, 47 I), can be transformed into a corymboid by more or less effective suppression of the internodal growth of the inflorescence axis, combined with pronounced basitonic development of the paracladia and especially prolongation of their hypopodia. Two shrubs, *Fordiophyton fordii* (Oliv.) Krasser and *Dichaetanthera cormybosa* (Cogn.) Jacques-Félix (see Krasser, 1893: 156), may be mentioned as examples.

In *Amphiblemma cymosum* (Schrad. & Wendl.) Naudin (Fig. 49), a corymboid of pleiochasial structure is formed. The internodes in the distal part of the inflorescence axis, with the exception of the final internode, remain very short. As a result the insertions of the paracladia are crowded together (Fig. 49 I). The arrangement of these paracladia is not decussate as might be expected, but alternate, since phyllotaxis changes above the uppermost pair of foliaceous leaves, which is usually somewhat smaller. The bracteose pherophylls of the paracladia are shifted on their axillary paracladia by recaulescence. Usually there are five paracladia (maximum

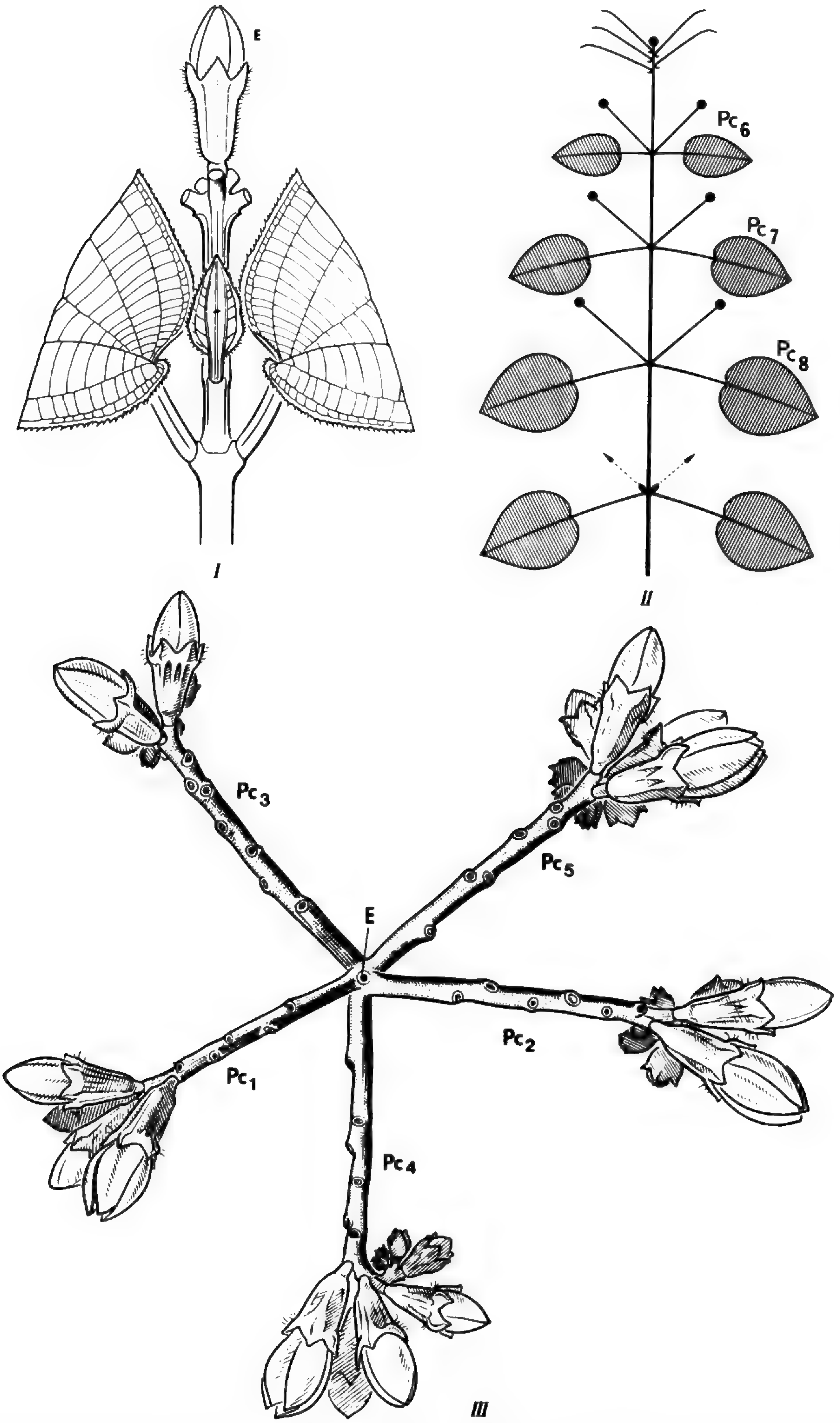

FIGURE 49. *Melastomataceae.* Amphiblemma cymosum.—*I. Inflorescence apex, the paracladia have been cut off.—II. Vertical projection at the beginning of anthesis of a flowering shoot.—III. Pleiochasial corymboid at the end of anthesis from above. Pc$_1$–Pc$_5$, paracladia of first to fifth order; E, terminal flower. (All from Troll.)*

eight) forming helicoid cymes. If there are more than five paracladia, the lower ones can form "paired" or "double helicoids," because in these more vigorous paracladia both first-order prophylls are fertile. Since the paracladia elongate considerably by the formation of many flowers, the position of the terminal flower finally is at the deepest point of the whole pleiochasium (Fig. 49 III). In older and vigorous plants more paracladia, mostly double-helicoid, can develop from the axils of the foliaceous leaf pairs in the lower part of the stem (Fig. 49 II, pc_6–pc_8).

The monotelic (pleio-)thyrsoid as the basic form of inflorescences in Melastomataceae can also be modified by reduction of 1) the ramification of the paracladia and 2) the number of paracladia.

1) Reduction of cymose ramification of the paracladia ultimately results in the formation of dibotryoids, as shown for *Leandra sylvatica* Cogn. or *Miconia sarmentosa* Cogn. by Cremers (1983/1986, figs. 25/3, 27/2; see also *Tibouchina frigidula* (DC.) Cogn., fig. 30/2), or in the formation of simple botryoids. A transitional stage on the way to formation of botryoids is exemplified by *Tococa guianensis* Aublet (Fig. 50 II). Compared with other elongate thyrsoids like that of *Tococa formicaria* Martius (Fig. 50 III) or *Allomorphia magnifica* Guill. (Fig. 50 I), its ramification appears to be much reduced, although the proximal paracladia are still three-flowered. If these paracladia are reduced to uniflorous elements, the inflorescence forms a simple botryoid, as occurs facultatively in *Tibouchina canescens* (D. Don) Cogn. (Cremers, 1983/1986, fig. 30/5), *Clidemia capitellata* (Bonpl.) DC. (Fig. 51 III), and *C. minutiflora* (Triana) Cogn. (Cremers, 1983/1986, fig. 32/7), or generally in *Adelobotrys spruceana* Cogn. (Cremers, 1983/1986, fig. 19/9) or *Castratella piloselloides* (Bonpl.) Naudin (Cremers, 1983/1986, fig. 19/9).

In another way the dense spikelike or nearly spadix-formed inflorescence of *Tococa spadiciflora* Triana (Fig. 48 II) can be derived from an elongate monothyrsoid: as indicated in Figure 50 III, the hypopodia of first and second orders (dotted lines) remain undeveloped. If this is combined with a shortening of the main axis, a capitulate inflorescence like that of *T. capitata* Cogn. (= *Sagraea capitata* Triana) results. According to Troll (posthumous manuscript), the inflorescence apex of *T. spadiciflora* probably remains indefinite.

If in contrast to the previous examples all internodes of the inflorescence are prolonged, a loosely branched thyrsoid results, as in *Nepsera aquatica* (Aublet) Naudin (Fig. 57 I).

As already mentioned for ligneous members of the family, foliaceous proliferating botrytic inflorescences are not rare (see also *Tibouchina axillaris* Cogn., Fig. 51 I). *Comolia purpurea* Miq. (Cremers, 1983/1986, fig. 22/1) and *Tibouchina petroniana* Cogn. (Cremers, 1983/1986, fig. 30/8), with its diplobotrytic inflorescences, are herbaceous examples.

2) This reduction of cymose ramification of the paracladia resulting in the formation of botryoids can be combined with diminution of the number of paracladia. Thus the botryoids of *Castratella piloselloides* mentioned above (Fig. 50 IV) bear two or three pairs of paracladia only. Reduction can go further, as in *Clidemia involucrata* DC., with sometimes only two uniflorous paracladia below the terminal flower (Cremers, 1983/1986, fig. 21/11). Ultimately a solitary terminal flower remains, as in the fruticose *Tibouchina sellowiana* (Cham.) Cogn. and *T. petroniana* Cogn. (Fig. 51 II; Cremers, 1983/1986, figs. 30/6, 7). Cogniaux (1888: 598) described the flowering system of the latter as "floribus ad apices ramulorum solitariis; bracteis saepius 6." Indeed, the main axis and a series of

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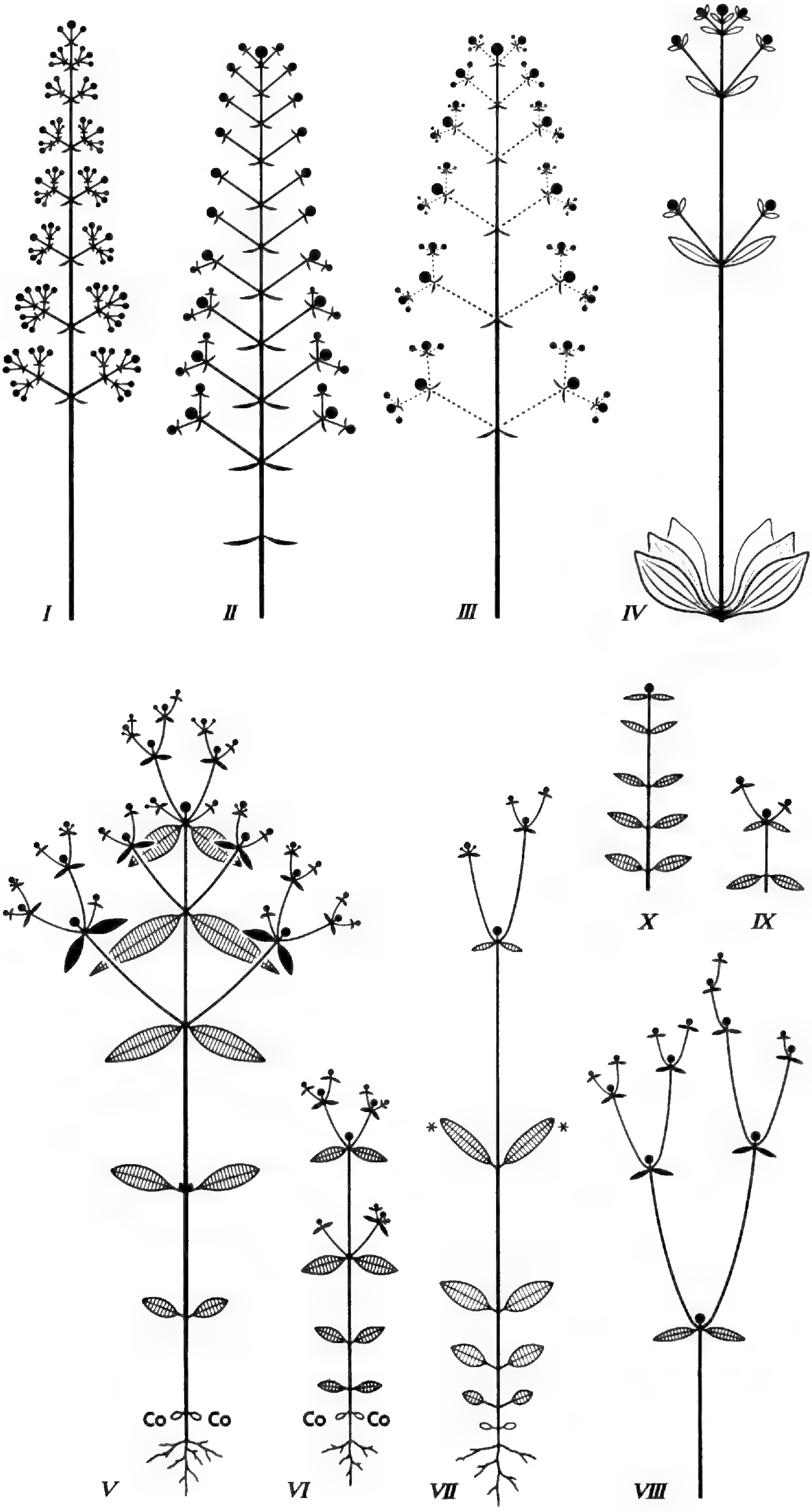
FIGURE 50. *Melastomataceae. Vertical diagrams of inflorescences and flowering plants.—I.* Allomorphia magnifica.—*II.* Tococa guianensis.—*III.* T. formicaria; *the hypopodia (dotted lines) remain completely undeveloped in* T. spadiciflora.—*IV.* Castratella piloselloides. *V–X. Rich- and poor-flowered plants of* Pterolepis trichotoma *(V, VI)*; P. repanda *(VII, VIII); and* P. pauciflora *(IX, X). (All from Troll.)*



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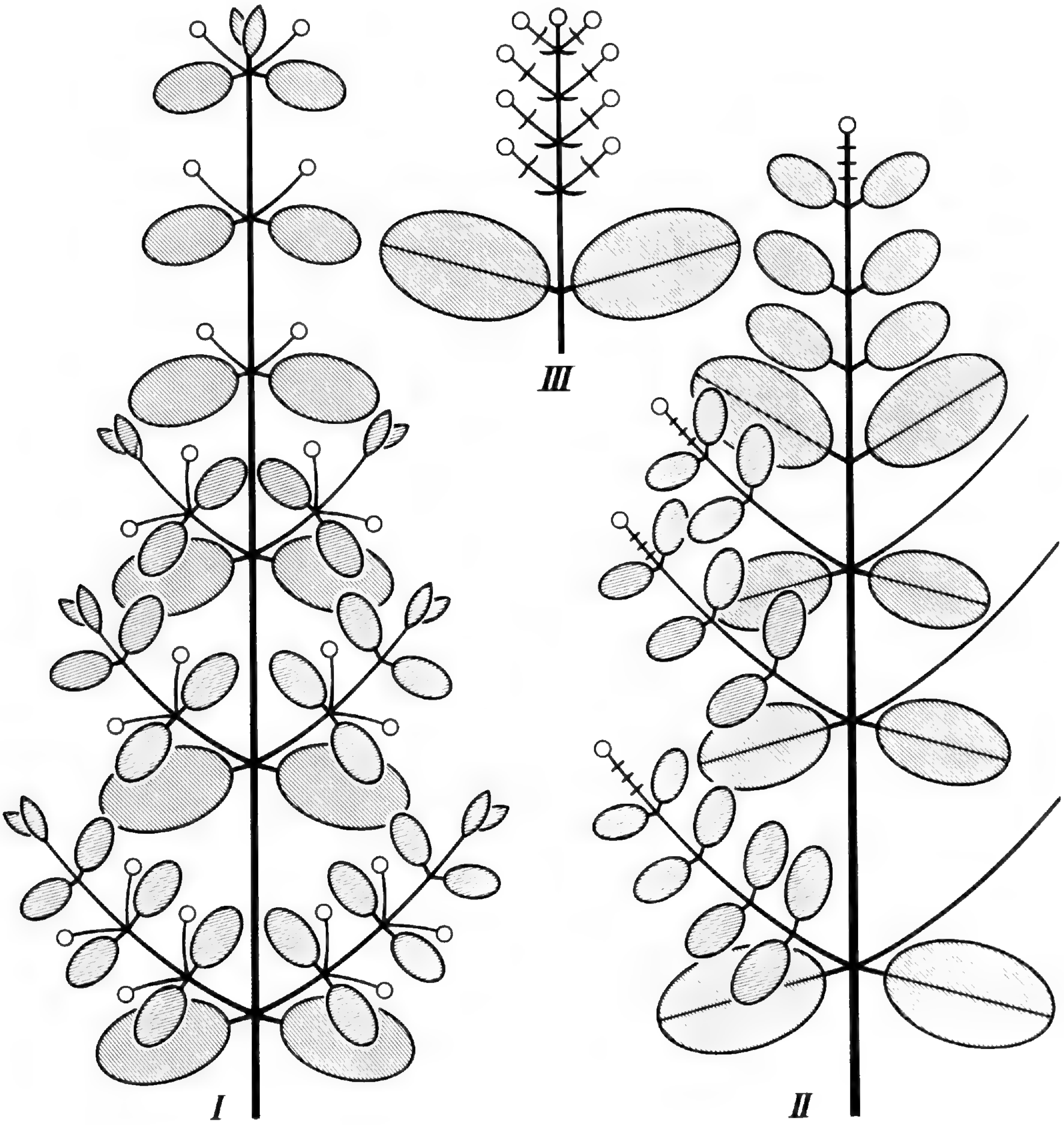

FIGURE 51. *Melastomataceae. Vertical diagrams of inflorescences.—I.* Tibouchina axillaris.—*II.* T. petroniana.—*III.* Clidemia capitellata. *(I, II diagrams according to Martius,* Flora Brazil. *XIV/3, pl. 92, XIV/4, pl. 128; III after Cremers, modified.)*

foliaceous paracladia originating from the axils of foliaceous leaf pairs in the proximal part of the main axis bear a single terminal flower only. Each of these flowers is preceded by three pairs of sterile bracts—a remnant of the thyrsoid ramification system.

In the prevalently herbaceous genus *Salpinga* were found two-flowered inflorescences in *S. pusillum* (Gleason) Wurd. (= *Macrocentrum pusillum*) and uniflorous inflorescences in *S. glandulosum* (Gleason) Wurd., whereas within the related genus *Macrocentrum, M. cristatum* (L. C. Rich.) Triana apparently has cymoids with scorpioid paracladia (Krasser, 1893, fig. 75C); the same applies to *M. latifolium* Wurd. (Cremers, 1983/1986: 69). According to Cremers (1983/1986, fig. 25/5, 5'), *M. vestitum* Sandw. normally develops the terminal flower only, but in some exceptional cases this can be accompanied by two lateral flowers.

In such cases uniflory is obviously facultative. This especially applies to individuals of herbaceous annual species grown under unfavorable conditions. In such plants the ramification is more or less reduced, sometimes with the result that only the terminal flower is developed. According to Troll (posthumous manuscript), examples can be found within the genus *Pterolepis*, which is closely related to *Tibouchina*. Figure 50 shows vigorous (V) and reduced (VI) plants of *P. trichotoma* Cogn., which differ in the number and the vigor of their cymose paracladia. In Figure 50 V the lowest pair of paracladia has the longest hypopodia of first and second orders and is the most copiously branched. The uppermost pair of paracladia, however, is also vigorous and bears more flowers than the preceding one. This indicates a certain tendency of an acrotonic support of ramification. Therefore it is not surprising that in the reduced plant (Fig. 50 VI) the distal pair of paracladia is the only one fully developed. In *P. repanda* (DC.) Triana (Fig. 50 VII, VIII) the acrotonic support of ramification becomes so effective that only the distal pair of paracladia is developed and a more (VIII) or less (VII) copiously branched cymoid is formed. In *P. pauciflora* (Naud.) Triana pauperization of the inflorescence finally progresses to the formation of a three-flowered (Fig. 50 IX) or uniflorous (X) inflorescence. Some other examples have been given by Cremers (1983/1986), who analyzed species of *Acisanthera* and *Appendicularia* and found uniflorous individuals in *Acisanthera bivalvis* (Aublet) Cogn. (Cremers, 1983/1986, fig. 18/8); a similar diversity of inflorescence forms occurs in *Appendicularia thymifolia* (Bonpl.) DC. Altogether the inflorescences of the mostly or exclusively annual species of *Acisanthera*, *Appendicularia*, *Aciotis* (e.g., *A. amazonica*, *A. aequilaterialis*, *A. dichotoma* Cogn.), and probably also *Pterogastra* are very variable: plants with extremely acrotonic ramification forming "dichotomic" inflorescences (cymoids) can be found beside plants with extremely reduced, sometimes even uniflorous inflorescences. The herbaceous *Catacoryne linnaeoides* Hook. f. probably also can develop uniflorous inflorescences.

Obligatorily uniflorous inflorescences are known for some fruticose taxa, especially the genus *Chaetostoma* and some species of the genera *Marcetia*, *Lavoisiera*, and *Microlicia*.

A flower-bearing shoot system of *Marcetia sertularia* DC. (Fig. 52 III) shows the branches more vigorously developed in the distal zone, i.e., an acrotonic ramification system. Most of the densely foliate branches as well as their relative main axes end in a terminal flower (Fig. 52 II). Lateral flowers or even vestiges of lateral flowers inserted below the terminal flowers cannot be found, in contradistinction to some other species of the genus. The whole system, however, cannot be regarded as an entire inflorescence but must be interpreted as a ramification system comprising numerous uniflorous inflorescences.

Accessory buds or branches are very common within the family (see also Wagner, 1907). They form single flowers or dyads in the inflorescence of *Pterolepis trichotoma* (Rottb.) Cogn. (Fig. 50 V) and occur in the leaf axils of the main axis as well as of the paracladia and can even form triadic or many-flowered cymes, as in *Adelobotrys ciliata* (Naudin) Triana, *A. permixta* Wurd., *Leandra polyadena* Ule, and *L. rufescens* (DC.) Cogn. (Cremers, 1983/1986, figs. 19/2, 6, 24/1, 4), or even thyrsoid flowering systems, as in *Miconia kappleri* Naudin and *M. tillettii* Wurd. (Cremers, 1983/1986, figs. 26/1, 2). If there are two or more buds, they are always arranged in a phylloscopic sequence, as in *Topobea guianensis* Aublet (Cremers, 1983/1986, fig. 31/6) or *Creochiton* Bl. (see Wagner, 1907). Sometimes differentiation between the buds of the same axillary series can take place. In *Ernestia confertiflora* Wurd. the upper of two buds develops into a vegetative branch and the lower forms a flowering system, whereas in *Maieta guianensis* Aublet the reverse situation occurs (see Cremers, 1983/1986, figs. 23/5, 25/6). Troll (posthumous manuscript) found in an inflorescence of *Tococa symphyandra* (Triana) Cogn. that 92 of a total 220 flowers belonged to accessory branches (Fig. 47 IV).

The formation of cymoids has been mentioned already in the context of the reduction

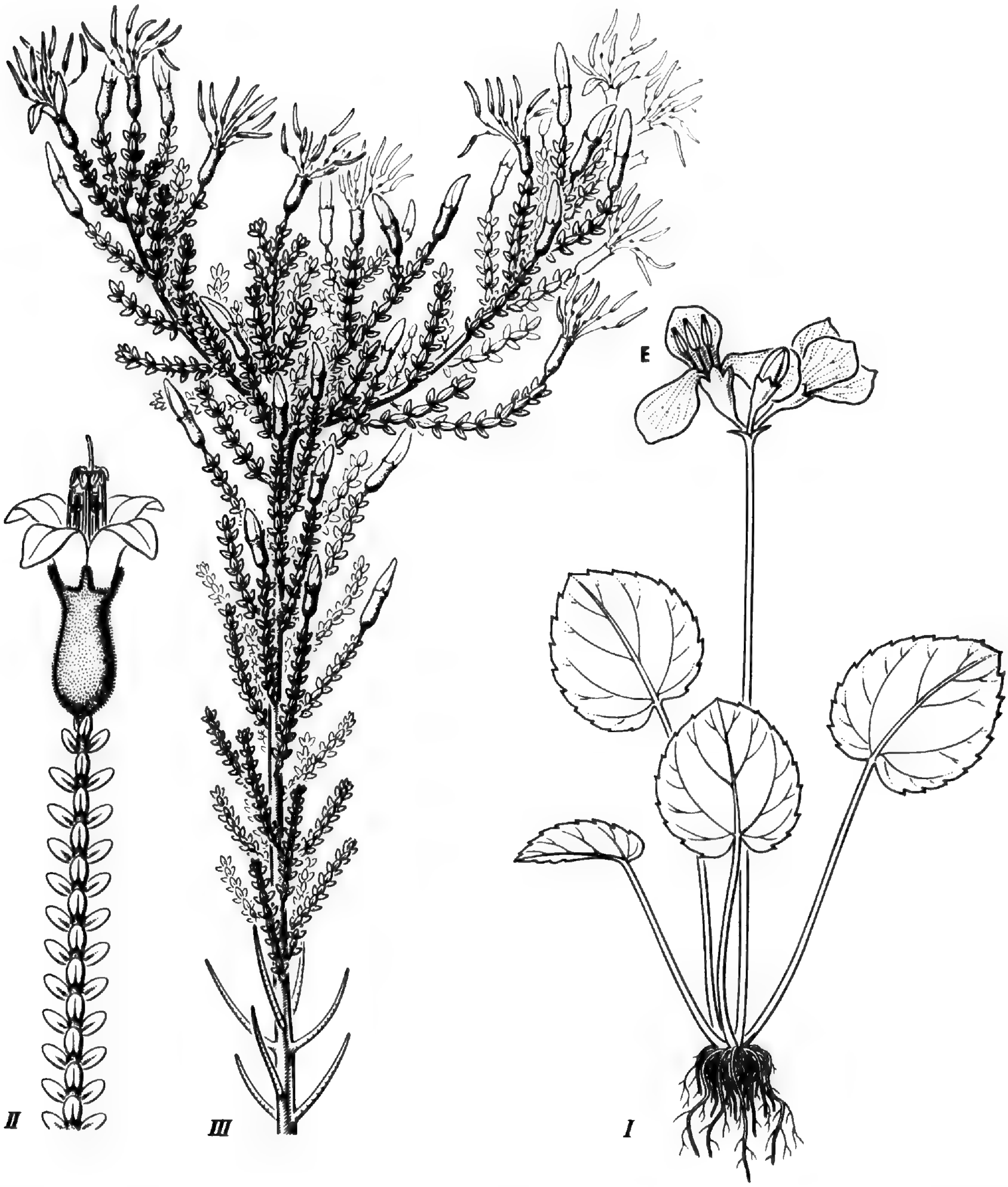

FIGURE 52. *Melastomataceae.—I.* Sonerila rotundifolia; *flowering plant (after Beddome). E, terminal flower. II, III.* Marcetia sertularia.*—II. Single branch with terminal flower (after De Candolle).—III. Flowering branching system.*

of inflorescences in reduced individuals of *Pterolepis* species (p. 277). Cymoids occur especially within the mostly herbaceous Sonerileae and Bertolonieae. Only a few examples are needed here.

In *Calvoa sessiliflora* Cogn. (Sonerileae) the cymoids are very conspicuous, especially in fruiting plants (Fig. 53 II). In this plant the leaves of the main axis are already lost. The foliation of the main stem is leafy and only the distal pair of leaves is bracteose (Fig. 54 I). These bracts are inconspicuous and by recaulescence united with their axillary branches, the uppermost paracladia, which form simple scorpioids. Between these two scorpioids the main axis ends with the terminal flower that is sessile because the final internode remains undeveloped. The same applies to the flowers of the scorpioid paracladia. The internode preceding the insertion of the

FIGURE 53. *Melastomataceae.—I.* Sonerila margaritacea.—*II.* Calvoa sessiliflora; *flowering plant. (From Troll.)*

scorpioid paracladia is very thin in proportion to the other internodes of the main stem. The same difference appears between the scorpioids and the preceding paracladia, which in thickness attain about double the size. These paracladia, which originate from the axils of foliage leaves, repeat the architecture of the main stem: they end in a cymoid and their foliation is leafy, with the exception of the pherophylls bearing the scorpioids. However, there is one important difference: the leaf pairs, especially that in the median position are anisophyllous, and the leaf pointing outwards by far exceeds the size and differentiation of its partner (Fig. 54 II). The trans-

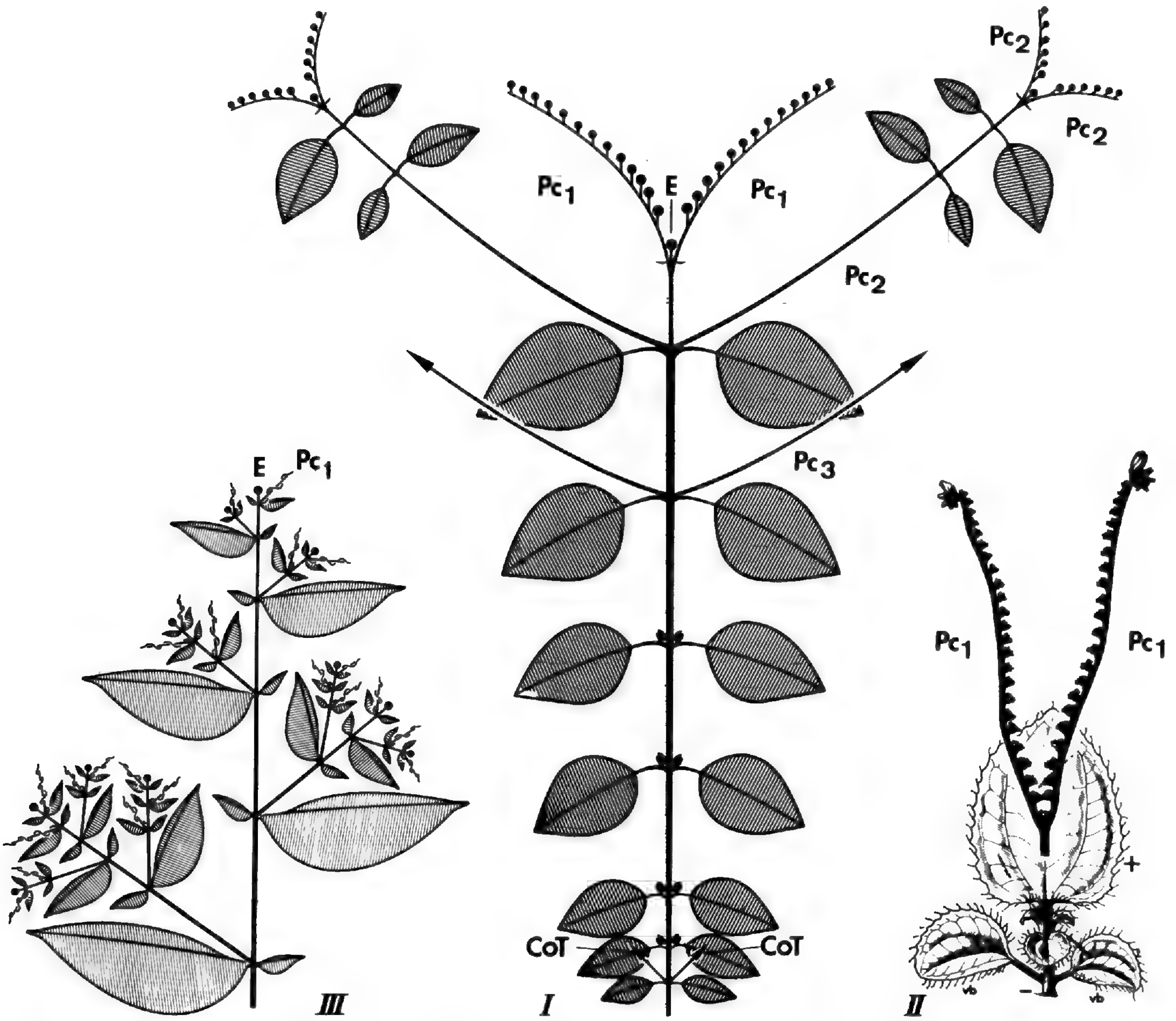

FIGURE 54. *Melastomataceae. I, II.* Calvoa sessiliflora.—*I. Vertical diagram of a flowering individual; E, terminal flower; CoT, cotyledonary branches.—II. Paracladium (Pc_2 from I), view from the ventral (upper) side; vb, prophylls; +, the larger leaf of the anisophyllous second leaf pair.—III.* Centradenia grandifolia; *analytical vertical diagram of a flowering branch. (II, III from Troll.)*

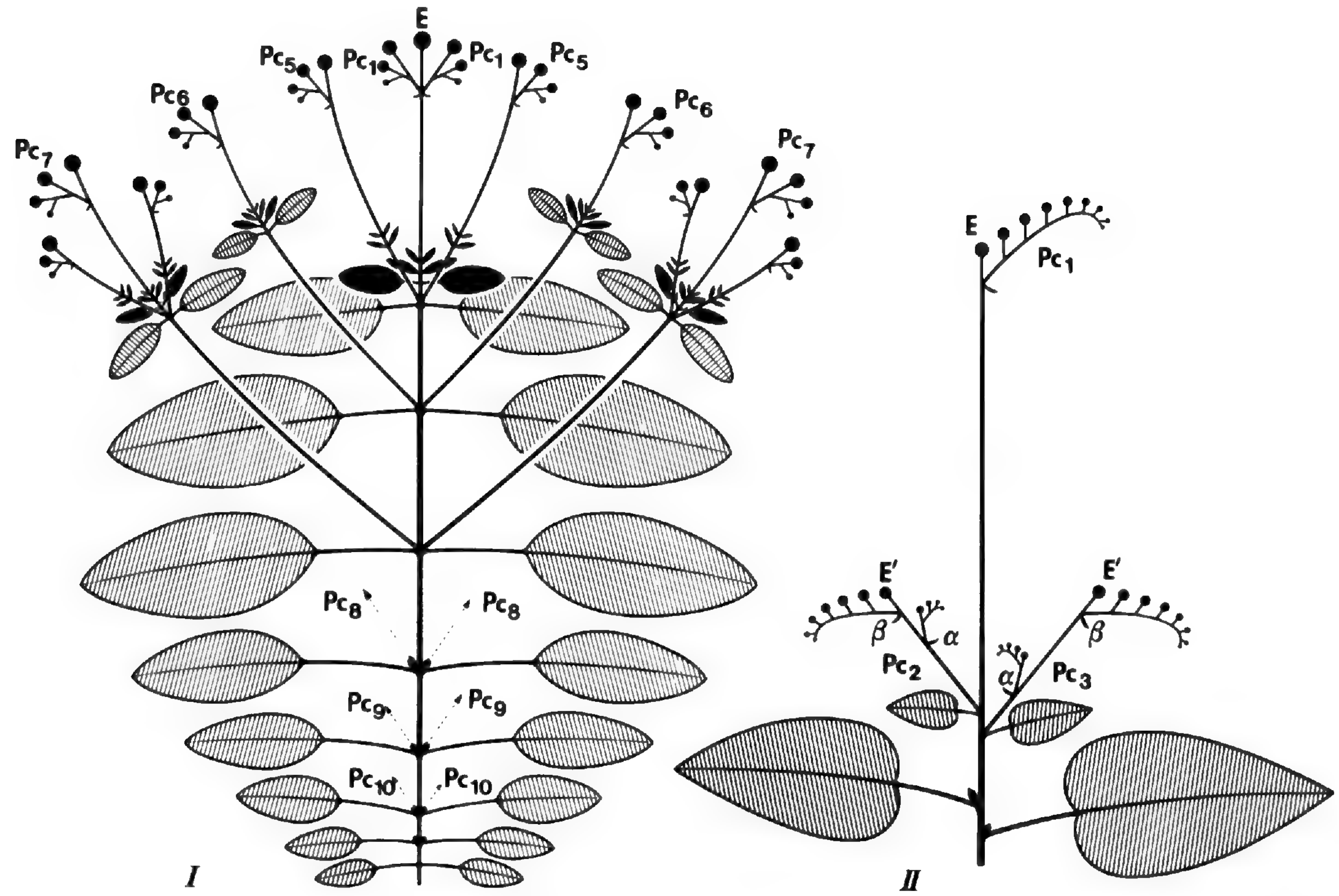

FIGURE 55. *Melastomataceae. Vertical inflorescence diagrams of* Sonerila margaritacea *(I) and* Bertolonia marmorata *(II). (From Troll.)* Pc_1–Pc_{10}, *first through tenth order paracladia; E, terminal flower; E′, secondary terminal flower; α, β = prophylls.*

versely arranged prophylls are asymmetric, the side pointing outwards (downwards) being larger. The whole paracladial zone comprises two or three pairs of paracladia and is preceded by an inhibition zone, within which only the cotyledonary branches show a slight tendency to unfold. In some way the species resembles *Amphiblemma cymosum* (Fig. 49), which belongs to the same tribe. In *A. cymosum*, however, the flower-bearing system that terminates the shoot comprises about five alternately arranged paracladia. The flowering system of *Sonerila margaritacea* Lindley (Fig. 53 I) is also similar to that of *Calvoa sessiliflora* inasmuch as there are two scorpioid paracladia originating from the axils of a pair of bracts below the terminal flower. The whole "double-scorpioid" is separated from the basal part of the plant by a long and comparatively thin internode. This scape is preceded by three pairs of frondulose to bracteose sterile leaves that form a transition between the preceding foliaceous leaf pairs and the uppermost pair of minute bracts. Since the preceding pairs of foliage leaves bear paracladia in their axils, the three pairs of sterile leaves form an intercalary inhibition zone within the flowering system. Each of the paracladia pc_5–pc_7 (pc_2–pc_4 are missing) in Figure 55 I nearly gives a complete copy of that part of the main stem that follows the point of its insertion, apart from the fact that all of them bear simple scorpioids. In *S. pilosula* Thwaites this also applies to the main axis.

Unlike previous species, *Sonerila rotundifolia* Bedd. (Fig. 52 I) is a rosette plant. The basal part of the main axis bearing the foliaceous rosette leaves is short and vigorous; only the distal part tapers and forms a flower-bearing scape. Since the plant is hapaxanthic, however, the vigorous basal part cannot be termed a rhizome. The umbellike inflorescence that is elevated above the rosette leaves by a long internode consists of two scorpioid paracladia that are inserted below the terminal flower. In *S. scapigera* Dalz. there are more long-peduncled umbellike flowering systems arising from the rosette. The morphol-

FIGURE 56. *Melastomataceae.* Bertolonia marmorata.—*I. Flowering plant.—II. Same, with most of the rosette leaves removed. (From Troll.)*

ogy of this plant has not been clearly elucidated, but we only can confirm that each of the flowering shoots bears its own basal rosette of foliage leaves.

A transitional form that connects *Calvoa sessiliflora* and *Sonerila margaritacea* on the one hand with *Sonerila rotundifolia* and similar species on the other hand is *Bertolonia marmorata* Naudin (Bertolonieae). In this semirosulate plant (Figs. 55 II, 56) the basal leaves are decussate, whereas the cauline leaves change over to alternate arrangement. In the distal part of the main axis there is only one scorpioid paracladium inserted below the terminal flower. Some more paracladia arise from the axils of the frondulose leaves in the lower part of the stem. These paracladia, however, can bear more than one scorpioid. The axillary buds of the upper rosette leaves can also produce paracladia, but most of them remain vegetative. The lowermost axillary buds ordinarily do not develop, nor do they function as innovation buds. Thus the plant is hapaxanthic. Since the scorpioid is formed gradually during anthesis and turns to the direction of the main axis, it can appear as a spike later on.

Eriocnema acaulis Triana, also in the Bertolonieae, seems to resemble *Bertolonia* in its growth form, but has long-peduncled umbel-like cymoids similar to those in *Sonerila rotundifolia.* On the other hand, *Cincinnobotrys oreophila* Gilg (1898, pl. VI), which belongs to the Sonerileae (Jacques-Félix, 1976), bears only one scorpioid paracladium below the terminal flower, which is elevated above the basal rosette by a long internode of the main axis (Fig. 57 II).

Finally *Monolena primulaeflora* Hook. f. may be mentioned here for its very peculiar architecture, which Troll investigated (posthumous manuscript). With regard to the architecture of the primary axis, this plant is similar to *Sonerila rotundifolia.* The main axis is short and vigorous in its basal part, which bears the rosulate foliage leaves. In its distal part the axis tapers and forms a long scape that bears the terminal inflorescence consisting of the terminal flower and one or two scorpioid paracladia. The latter originate in the axils of two broad bracts that fit very well to protect the young flowers. Below these broader bracts there is a pair of smaller bracts that remains sterile. The significant feature of this plant is that it develops plagiotropic paracladia from the axils of the basal foliage leaves. These paracladia are equal to the main axis especially in their vigor. Together with

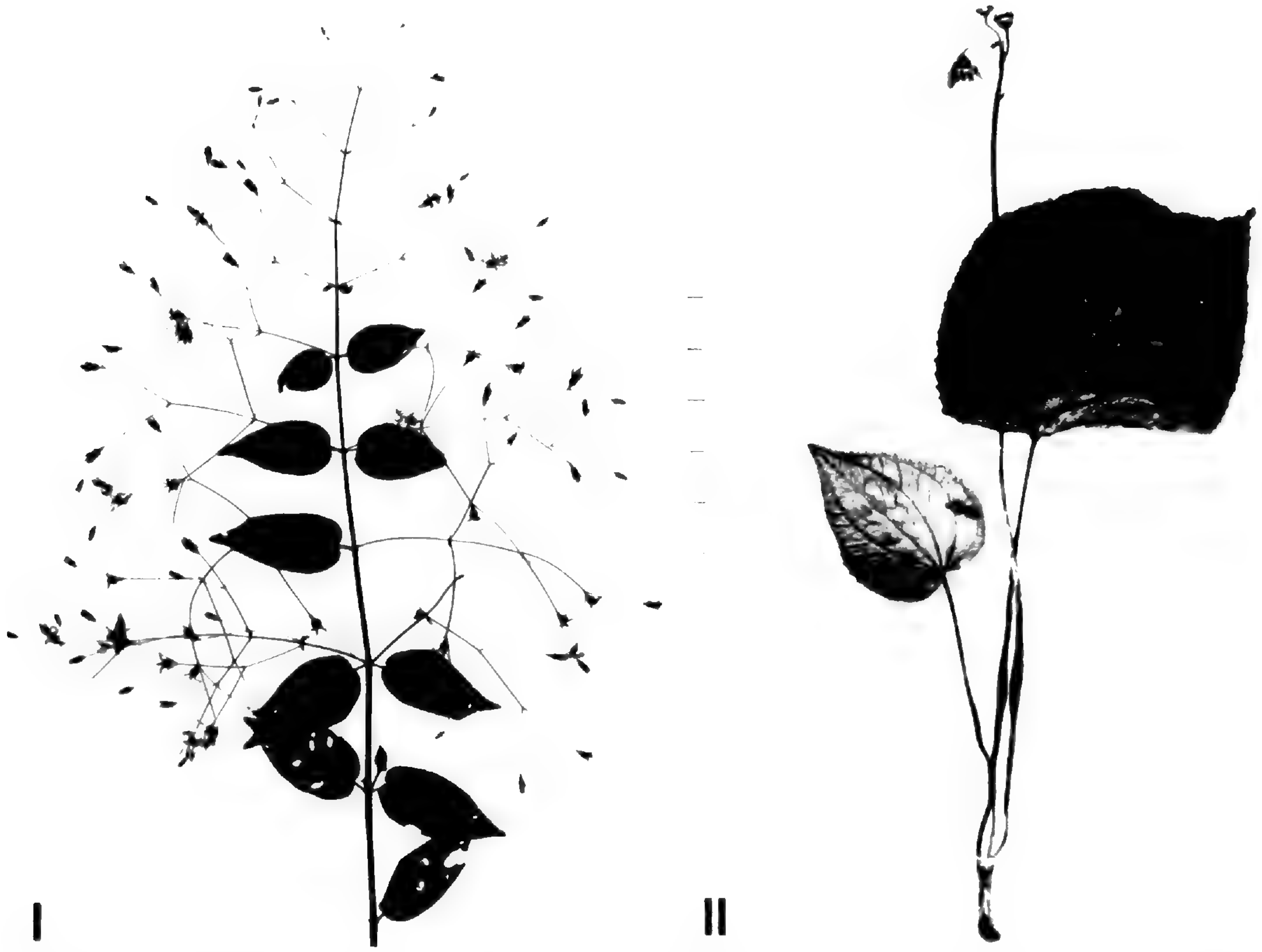

FIGURE 57. *Melastomataceae.—I.* Nepsera aquatica*; inflorescence. (Brazil. Amazonas: vicinity of Manaus,* Prance et al. *11645 (M).) —II.* Cincinnobotrys oreophila*; flowering plant. (Tanganjika Territory, distr. Morogoro, Ulugura Mts.,* Schlieben 2824 *(M).)*

the bulbous base of the primary axis they form a knobby lump. They remain short, and after the development of foliage leaves, finally taper into a scape bearing an inflorescence. The vigorous basal region of the paracladia can ramify repeatedly and form monochasial or dichasial sympodia. Thus the older plant gives the impression of a multiplicity of foliage leaves and inflorescences that extend and unfold in a centrifugal manner. The character of the plant becomes still more complex because of the anisophylly of the leaf pairs. One may suppose that the vigorous basal paracladia ought to be explained as proleptical innovation shoots.

A difference in size and/or form of paired leaves—commonly called anisophylly (Fig. 58)—already has been mentioned for some taxa. It is typical for a considerable number of species. It ensues from the dorsiventrality of the plagiotropic axis and is consequently often connected with the the development of the axillary shoots (see Troll, 1937: 608). This usually means that the leaves inserted at the underside of the axis are the larger ones (+ leaves), as shown here for *Centradenia grandifolia* (Schldl.) Endl. (Fig. 59 I and the diagram in Fig. 59 II). In *C. inaequilateralis* (Schldl. & Cham.) G. Don and *C. grandifolia*, which have very pronounced anisophylly, only the axils of the (+) leaves subtend axillary shoots. Thus there appear two rows of branches inserted on the underside of the mother axis. This is shown for *C. inaequilateralis* by Figure 59 III, IV. The flowering shoot ends in a terminal flower, which is accompanied by a scorpioid or rarely helicoid paracladium. This arises from the axil of the larger leaf of the small and scarcely anisophyllous leaf pair below the terminal flower (Fig. 59 V). The paracladia of the preceding leaf pairs differ from this uppermost paracladium by their leafy and more extended hypotagma. They repeat the architecture of their mother shoot by ending in a terminal flower (E′) and bearing one scorpioid paracladium (pc′) in one of the axils of the distal leaf pair. The effloration of the paracladia proceeds from base to top (Fig. 59 IV). In contradistinction to *C. inaequilateralis*, the paracladia (pc) of *C. grandifolia* (Fig. 54 III) develop flowering second-order paracladia (pc′) from the axils of all leaf pairs, and even third-order paracladia (pc″), which are all helicoids.

Generally in anisophyllous species the axillary shoot may be favored or inhibited in the same way as the subtending leaf, or rarely the favored (+) leaf bears a small (−) branch in its axil and the small (−) leaf a vigorous (+) branch. The latter case was described for *Dissotis rotundifolia* (Sm.) Triana by Troll (posthumous manuscript; see Fig. 64 I for explanation).

For the Blakeae (*Topobea* and *Blakea* including *Pyxidanthus*), it was mentioned already that their single flowers are enclosed by an involucrum formed by several pairs of bracts. The same applies to some species of *Dissotis* (e.g., *D. rotundifolia*) and many species of *Osbeckia*. In other species of this latter genus the involucrum is composed of large pherophylls of some paracladia that are crowded at the ends of the shoots, forming small heads. Often, as in *O. brachystemon* Naudin, *O. chinensis* L., and *O. capitata* Benth. ex Walp., we found the involucrum consisting of two leaf pairs which sometimes (in *O. capitata*) included only the terminal flower and one pair of uniflorous paracladia or even only the terminal flower. Many-flowered heads were observed in *O. chinensis*. The dense heads of *Dissotis capitata* (Vahl) Hook. f. (Fig. 60) consist of the terminal flower and one many-flowered monochasial-helicoid paracladium (Troll, posthumous manuscript). In the annual *Nerophila gentianoides* Naudin the involucrum is formed by foliaceous leaves.

FIGURE 58. *Melastomataceae.* Maieta guianensis *Aubl.; anisophyllous branch. (Brazil: vicinity of Pará,* Baker 91 *(M).)*

Well known for its large and showy pink bracts is *Medinilla magnifica* Lindley. This evergreen plant must be regarded as a shrub since it has a basitonic mode of ramification that is conspicuous even when young (Fig. 61 I). The inflorescences contrast sharply with the vegetative parts by the abrupt change of the leaf character and its pendulous position (Fig. 61 II). This position is produced primarily by an active incurvation of the lowermost pedunclelike internode (segregation internode); later it is the weight of the many-flowered inflorescence that keeps it in a hanging position, since the pink-colored segregation internode is very thin. The proximal part of the diplothyrsoid inflorescence bears mostly two pairs of thyrsoid paracladia; in vigorous inflorescences there may be three or even four or five pairs. Sometimes the lowermost pair of bracts remains sterile. The bracts of the lowermost pairs commonly form false tetramerous verticils by an abbreviation of the internode between two dimerous verticils. In the distal and thyrsoid part of the inflores-

FIGURE 59. *Melastomataceae. I, II.* Centradenia grandifolia.—*I. Anisophyllous branch.—II. Horizontal diagram; L (as in I), the larger, fertile leaves; l, the smaller, sterile leaves.—III–V.* C. inaequilateralis; *distal part of main shoots with terminal flower (E) and the distal paracladium at the beginning of effloration (E′ its terminal flower); the small (−) and large (+) leaves.—V. Distal paracladium (pc_1) with its terminal flower (E) and scorpioid pc. 1–4 = sequence of effloration. (From Troll.)*

cence the phyllotaxis changes to the formation of proper tetramerous verticils. Sometimes trimerous or hexamerous verticils occur; this also applies to *M. sieboldiana* Planchon. In the distal region of the thyrsoid part of the inflorescence the bracts become smaller and inconspicuous.

The ramification of the paracladia within the thyrsoid region decreases gradually from the formation of maximally seven-flowered cymes in the proximal part to uniflorous paracladia in the distal part. The inflorescence can be closed by a terminal flower but often remains indefinite, and the ultimate lateral flowers atrophy (Fig. 64 III). In this case the result is a truncate monotelic synflorescence. If the terminal flower is present, its development is slightly precurrent in relation to the neighboring lateral flowers. Generally the effloration of the whole synflorescence is acropetal.

The thyrsoid paracladia at the base of the

FIGURE 60. *Melastomataceae.* Dissotis capitata.—*I. Shoot with terminal inflorescence.—II. Headlike inflorescence from above. (From Troll.)*

inflorescence more or less repeat the structure of the distal part with some alterations due to their lateral position and consequently their dorsiventrality. Their foliation starts with dimerous verticils of large bracts, especially the prophylls, that in their axils can bear thyrsoid paracladia of second order. The whole inflorescence is then a triple thyrsoid.

In the distal part of the thyrsoid paracladia the bracts become smaller. The conformity of the paracladia with the distal thyrsoid part of the inflorescence also refers to the possibility that the apex can atrophy without the formation of a terminal flower.

The inflorescences of *Medinilla sieboldiana* are also pendulous (Fig. 62 I) but differ from those of *M. magnifica* by their very inconspicuous bracts and by the lack of thyrsoid paracladia. The inflorescence thus is a monothyrsoid. It resembles *M. magnifica* in having tetramerous verticils of bracts. In the proximal part the cymose paracladia can comprise 15 flowers, but distally they are gradually reduced to triads. The development of the terminal flower is conspicuously precurrent to the neighboring lateral flowers. *Medinilla pendula* Merr. is another species with long-peduncled hanging diplothyrsoid inflorescences. There are, however, also species of *Medinilla* with upright inflorescences, as in *M. javanensis* Bl. (Fig. 62 II) and *M. venosa* Bl. (Fig. 63 I). In the latter species and in *M. magnifica* there sometimes occur cauliflorous inflorescences from the axils of leaves that have fallen off already (Fig. 63 II).

Species with proliferating inflorescences are not rare, and some of them show a more or less pronounced tendency to cauliflory. *Medinilla myrtiformis* Triana bears few-flowered botryoids and triadic accessory branches (perhaps even botryoids) in the axils of foliage leaves of proliferating axes. *Medinilla parviflora* Baker and *M. papillosa* Baker are

FIGURE 61. *Melastomataceae.* Medinilla magnifica.—*I. Basitonic ramification of a young plant.—II. Inflorescence, thyrsoid paracladia. (From Troll.)*

similar, the latter showing a slight tendency to cauliflory. In *M. monantha* Merr. the axillary flowering systems are reduced to their terminal flower, which, however, is preceded by two pairs of small bracts. On the other hand, the axillary partial inflorescences of *M. ericarum* Jum. & Perrier are long-peduncled diplothyrsoids.

In *Medinilla ramiflora* Merr., the axillary glomerate thyrsoid flowering systems effloresce when their foliaceous pherophylls have fallen off, and *M. tawaensis* Merr. with likewise thyrsoid partial inflorescences is evidently cauliflorous. The same probably applies to *M. clarkei* King.

Medinilla sedifolia Jum. & Perrier, an epiphytic plant with succulent foliage leaves, is another example with proliferating inflorescences. A zone with a few single flowers in the axils of foliaceous leaves is followed by a zone with vegetative axillary shoots (Troll, 1973: 105, who partly refers to W. Rauh). Probably after a while the main axis can return to the production of lateral flowers again. The foliation of the uniflorous paracladia normally consists only of the scalelike prophylls. Sometimes, however, the prophylls are foliaceous and are followed by two pairs of scales, which in all cases investigated remain altogether sterile.

There is also one case of "epiphyllous inflorescences" reported for the family: *Phyllagathis scortechinii* King, which was investigated by Weber (1982). Among the ca. 35 species of *Phyllagathis* Bl. with essentially terminal "umbel-shaped" or "headlike" inflorescences, *P. scortechinii* is an exception. Its foliage leaves "are posed terminal on woody, axis-like structures ('carriers'), from which they fall off after their life span. Additionally the 'carrier' bears several inflorescences and/or vegetative buds along its upper side" (Fig. 64 II). Weber showed "that this structure is no axis, but a basal, anatomically

FIGURE 62. *Melastomataceae.—I.* Medinilla sieboldiana; *shoot with pendulous terminal inflorescence.—II.* M. javanensis; *terminal inflorescence. (From Troll.)*

distinctly differentiated part of the leaf, onto which the axillary shoots (multiplied by accessory shoot formation) are displaced."

PSILOXYLACEAE

Psiloxylon mauritianum Baillon, now recognized to represent a separate family Psiloxylaceae, "has small axillary racemiform inflorescences; these are perhaps anthotelic (botryoids?), but the limited available material (all dried) is insufficient to determine whether the apparently terminal flower is indeed truly so. Disperse phyllotaxy in the inflorescence (as well as in vegetative regions) and general recaulescence of the bracts increase the difficulty of interpretation." We cannot add much to this statement given by Briggs & Johnson (1979: 181) for the same reason: scantiness of material. It does appear, however, that there is no terminal flower. In this case the inflorescence could be termed a botrytic florescence. According to our observations, the flowers are subtended by bracteous pherophylls and bear bracteous prophylls. In the material investigated (Fig. 65) the flower-bearing systems are brachyblasts reduced to their florescence and inserted on older axes. Thus the plant might be called cauliflorous.

MYRTACEAE

In Myrtaceae, the "central type" and perhaps the phylogenetically primitive form of inflorescence is a monotelic thyrsoid (i.e., a thyrsic inflorescence with terminal flower) or panicle terminating a leafy shoot. Inflorescences of this type can be found among the Myrtoideae (species of *Syzygium* and *Eugenia*) and the Leptospermoideae (species of *Metrosideros*, *Eucalyptus*, and *Angophora*), and they are characteristic of the Heteropyxidoideae (*Heteropyxis natalensis* Harvey, Fig. 66; see also Weberling, 1963). A

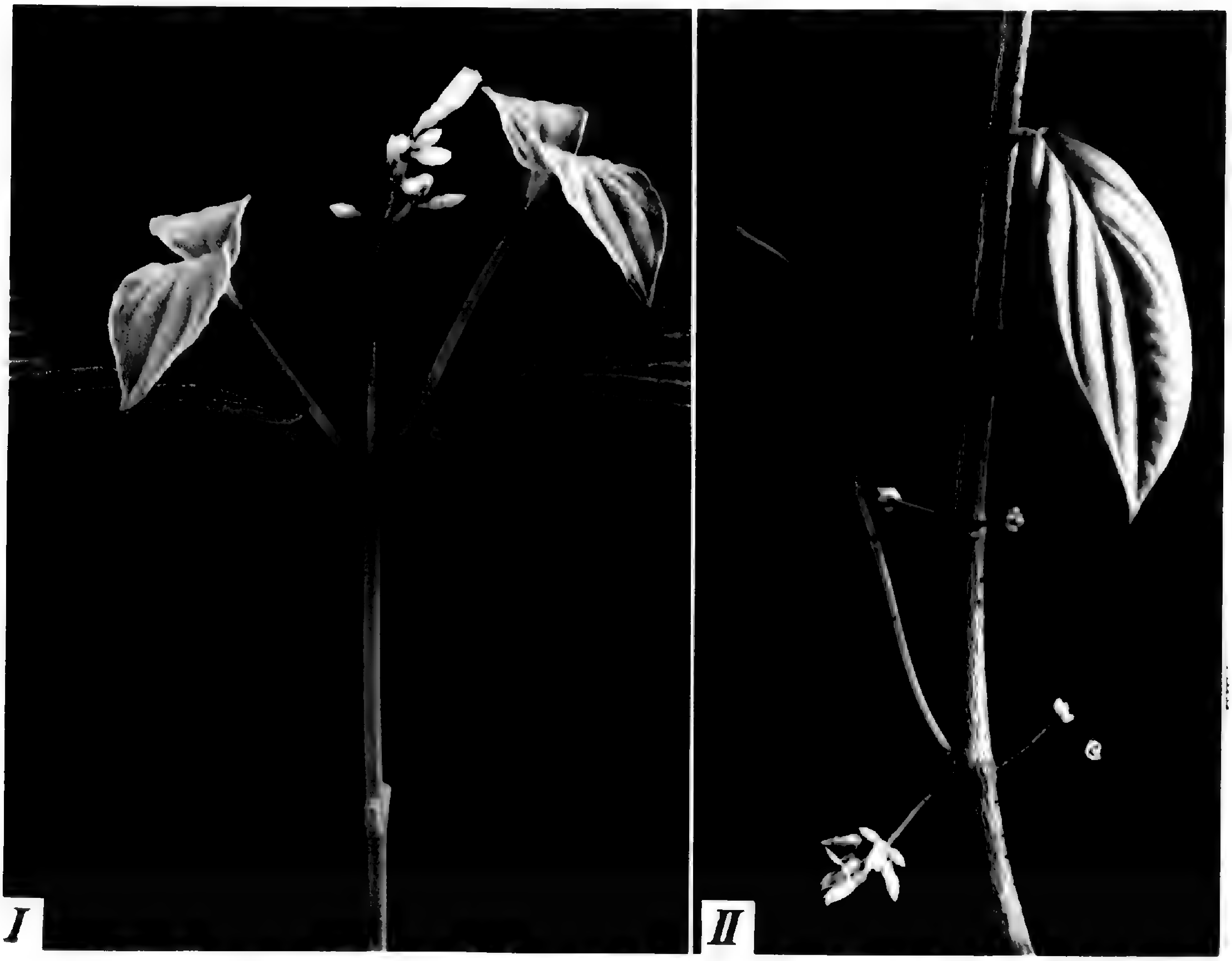

FIGURE 63. *Melastomataceae.* Medinilla venosa.—*I. Terminal inflorescence.—II. Cauliflorous inflorescences. (From Troll.)*

typical monotelic inflorescence is exemplified by *Syzygium aromaticum* (L.) Merr. (Figs. 67, 68 I). The inflorescence axis ends with a terminal flower. This also applies to all floral branches below the terminal flower. All these branches, whether branched or not, are homologous and all are referred to by the term paracladia. Accordingly the ramifications of these paracladia are called paracladia of second to n^{th} order (pc′, pc″, . . .).

As is well known, the complexity of such an inflorescence, that is, the degree of ramification of the paracladia and the extension of the enrichment zone, may be modified to a certain extent in the same species. On the other hand, the differences in complexity may be a distinguishing character between different taxa. Thus in contrast to *Syzygium aromaticum,* in *S. paniculatum* Banks & Gaertner (Fig. 67) the paracladia of first order are uniflorous throughout (Troll, 1969: 258). This results in the formation of a botryoid. In this species, reduction may even go further until only the terminal flower remains.

In *Syzygium aromaticum,* frequently in *S. paniculatum,* as well as in many other Myrtaceae, a pair of sterile bracts (metaxyphylls, Zwischenblätter) preceding the terminal flower can be observed. In *S. paniculatum* they may be replaced by more foliaceous leaves that bear single-flowered (monadic) paracladia in their axils (Troll, 1969: 258–259).

In *Eugenia lanceolaria* Roxb. (now *Syzygium lanceolarium*) and *E. macrocarpa* Roxb. (*Syzygium macrocarpum*) the usual form of the inflorescence seems also to be a botryoid, whereas in *S. thumra* (Roxb.) Merr. & Perry the ramification of the floral branches is increased (Fig. 69). To a certain extent

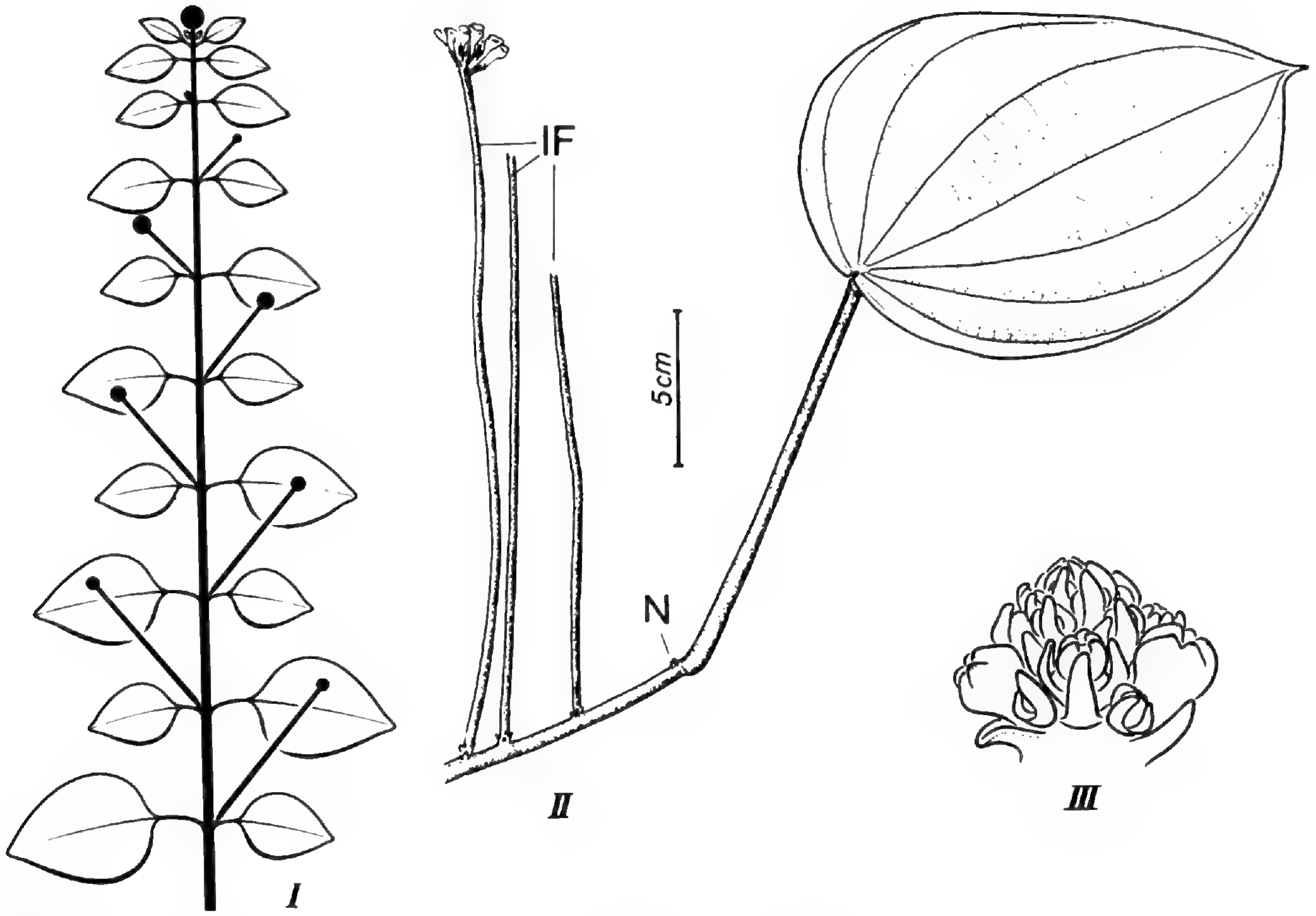

FIGURE 64. *Melastomataceae.—I.* Dissotis rotundifolia; *vertical diagram of an anisophyllous flowering shoot.—II.* Phyllagathis scortechinii; *"carrier" with foliage leaf and some (partly incomplete) inflorescences/infrutescences (IF) and leaf scar (N).—III.* Medinilla magnifica; *inflorescence apex in state of truncation. (I, III from Troll; II from Weber, 1982.)*

this is due to a high degree of cymose branching, which means a consecutive ramification from the axils of the prophylls. An inflorescence with the main axis bearing lateral cymes is defined as a thyrsoid; in this sense the inflorescence of *S. thumra* as well as of *Heteropyxis* (Fig. 66) is a pleiothyrsoid.

As already shown by the few species mentioned here, the foliation of the flower-bearing system may consist of bracts only (bracteose), or there may be a transition from foliage leaves at the base to distal bracts (frondo-bracteose), or the foliation may be leafy throughout (foliose, frondose). The latter applies to the inflorescence of *Syzygium acuminatum* (Roxb.) Miq. (Fig. 70). This inflorescence also presents another feature that is significant for many Myrtaceae: the main axis of the inflorescence is not closed by a terminal flower but ends in a bud (*blastotelic* in the sense of Briggs & Johnson, 1979: 176). Nevertheless, all of the paracladia, including those with more than one pair of flower-bearing branches, are provided with terminal flowers, thus demonstrating the monotelic character of the inflorescence (Troll, 1969: 255; Radlkofer, 1890: 184).

The close morphological relations between these different forms of monotelic inflorescences becomes evident by the comparison of closely related taxa, as among the various species of *Metrosideros* sensu lato that Dawson (1968) investigated. Among these, *M. albiflora* Sol. ex Gaertner (Fig. 71 I) has a bracteose (thyrso-paniculate) inflorescence, and *M. carminea* W. Oliver (Fig. 71 II) a frondose diplobotryoidal inflorescence; both still terminate in an apical flower. As a result of further reduction, the inflorescence of *M. diffusa* Sm. (Fig. 71 III) consists of several densely contracted pairs of triadic paracladia only but still ends in a terminal flower. In the similar inflorescence of *M. perforata* A. Rich. (= *scandens* Sol. ex Gaertner?), the terminal flower is replaced by a vegetative bud (Fig. 71 IV). Moreover, in the loose inflorescences

FIGURE 65. *Psiloxylaceae.* Psiloxylon mauritanicum. *(Mauritius: 1825,* Sieber s.n.; *Fl. Maurit. II, No. 123; G.)*

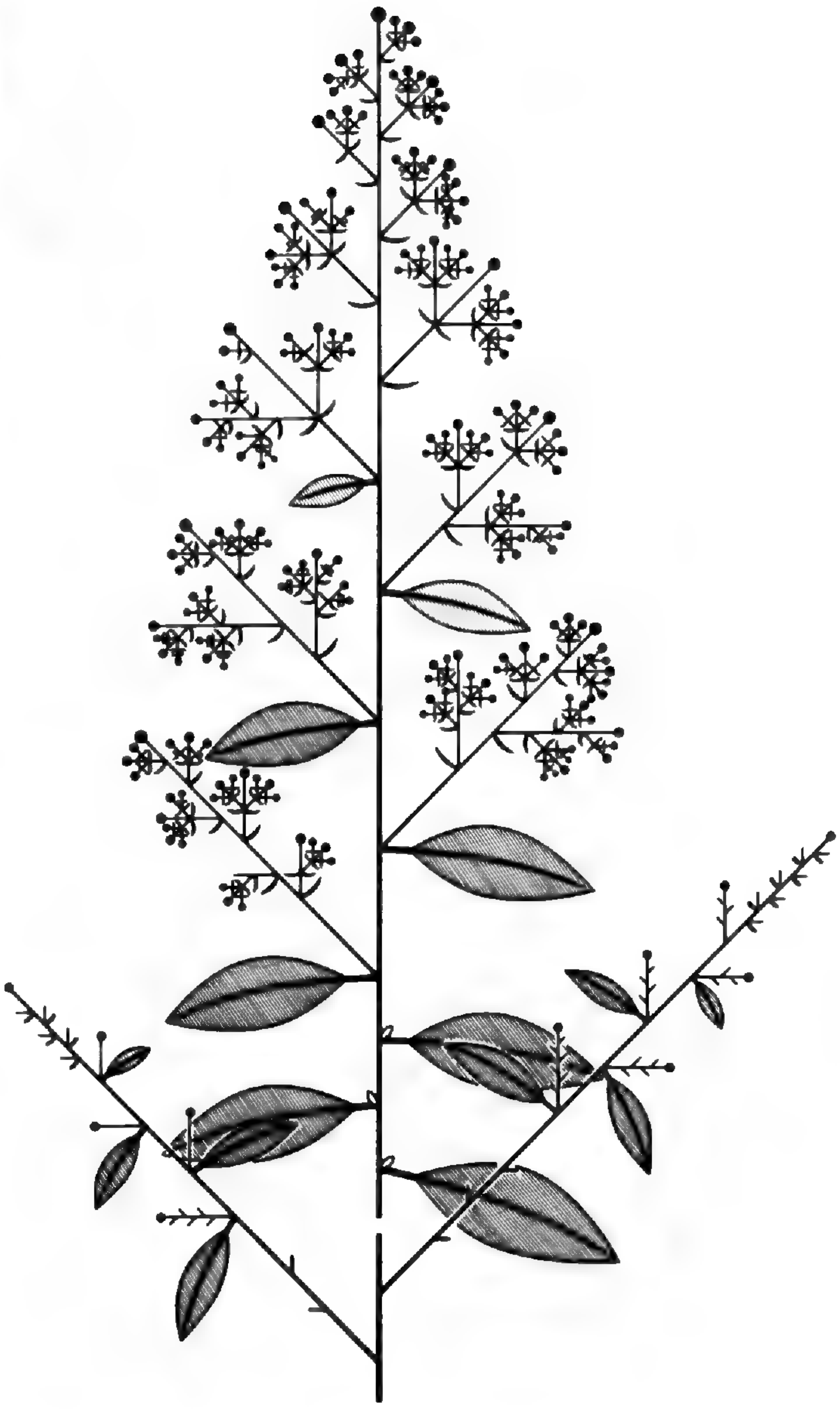

FIGURE 66. *Heteropyxidaceae.* Heteropxyis natalensis; *diagram of a flowering shoot. At the interruption of the main axis three foliaceous leaves and their internodes have been omitted, and the ramification of the vigorous basal branches was not carried out in detail. (South Africa: koppie in the area of the University of N. Transvaal,* Weberling 7644.*)*

of *M. kermadecensis* W. Oliver (= *M. polymorpha* Hook.?), not only the terminal flower closing the inflorescence axis, but also those of the paracladia of first order are replaced by buds (Fig. 71 V). The same applies to *M. umbellata* Cav. (= *M. lucida* A. Rich.?) with more contracted (Fig. 71 VI) or reduced inflorescences (Fig. 71 VII).

Similar differences can be found among species of *Angophora.* While in *A. hispida* (Sm.) Blaxell, *A. floribunda* (Sm.) Sweet, *A. costata* (Gaertner) Britt., *A. melanoxylon* Bak., and *A. subvelutina* F. Muell. the main axis of the (thyrso-)paniculate inflorescences is closed by a terminal flower, the thyrsopanicula of other species end in a bud.

These terminal buds, which appear "to consist of vegetative rather than floral organs," become abortive in many cases (the inflorescence being *anauxotelic* in the sense of Briggs & Johnson, 1979: 176). In many other cases sooner or later the terminal bud continues growth beyond the flowering region, producing a vegetative shoot (for inflorescences of this kind the term *auxotelic* is used by Briggs & Johnson, 1979). In *Angophora costata,* Briggs & Johnson (1979, fig. 6b, c) observed inflorescences closed by a terminal flower ("anthotelic" inflorescences) as well as those ending in a terminal bud, which sometimes aborted and sometimes continued growth. The inflorescence of *A. subvelutina* was found with a terminal flower (Briggs & Johnson, 1979), while Troll (unpubl. data) found a terminal bud continuing growth in the same species. Thus especially within *An-*

FIGURE 67. *Myrtaceae. Inflorescences.—Left.* Syzygium aromaticum *(from Köhler, 1923).—Right.* S. paniculatum. *(From Troll.)*

gophora (and in some other taxa of the *Eucalyptus* alliance) a high degree of flexibility in the formation of terminal flowers is revealed.

Dawson (1968: 48) pointed out that in those species of *Metrosideros* that bear terminal buds, the "bud is inactive during flowering, but may later develop into a leafy branch." As will be shown later, however, the moment in which the apical vegetative bud turns to continue growth may be sooner or later.

The reversion of the inflorescence apex to vegetative growth, commonly called *proliferation* (Troll, 1959a: 116), is characteristic for many Myrtaceae, perhaps even for the majority of species.

Parkin (1914: 556) regarded proliferating inflorescences as a separate type of inflorescence, which he called "intercalary inflorescences," because "the flower-bearing part of the axis is . . . intercalated between two foliage-bearing portions." In using this term he especially referred to the Australian (or prevalent Australian) genera *Callistemon*, *Melaleuca*, and *Metrosideros*. Indeed the appearance of the flowering shoots of *Melaleuca* (Fig. 72) and *Callistemon* (Fig. 72) suggest this term, all the more as the process of the formation of a terminal inflorescence and proliferation can recur in regular intervals of development, mostly in connection with climatic factors.

We must emphasize, however, that there are many taxa (e.g., *Veronica, Lysimachia,* several ligneous Melastomataceae or Rubiaceae) that include species with terminal bracteose and terminal foliose inflorescences as well as species with proliferating leafy inflorescences. Often these forms are connected by continuous series of intermediate forms. Thus the so-called "intercalary inflores-

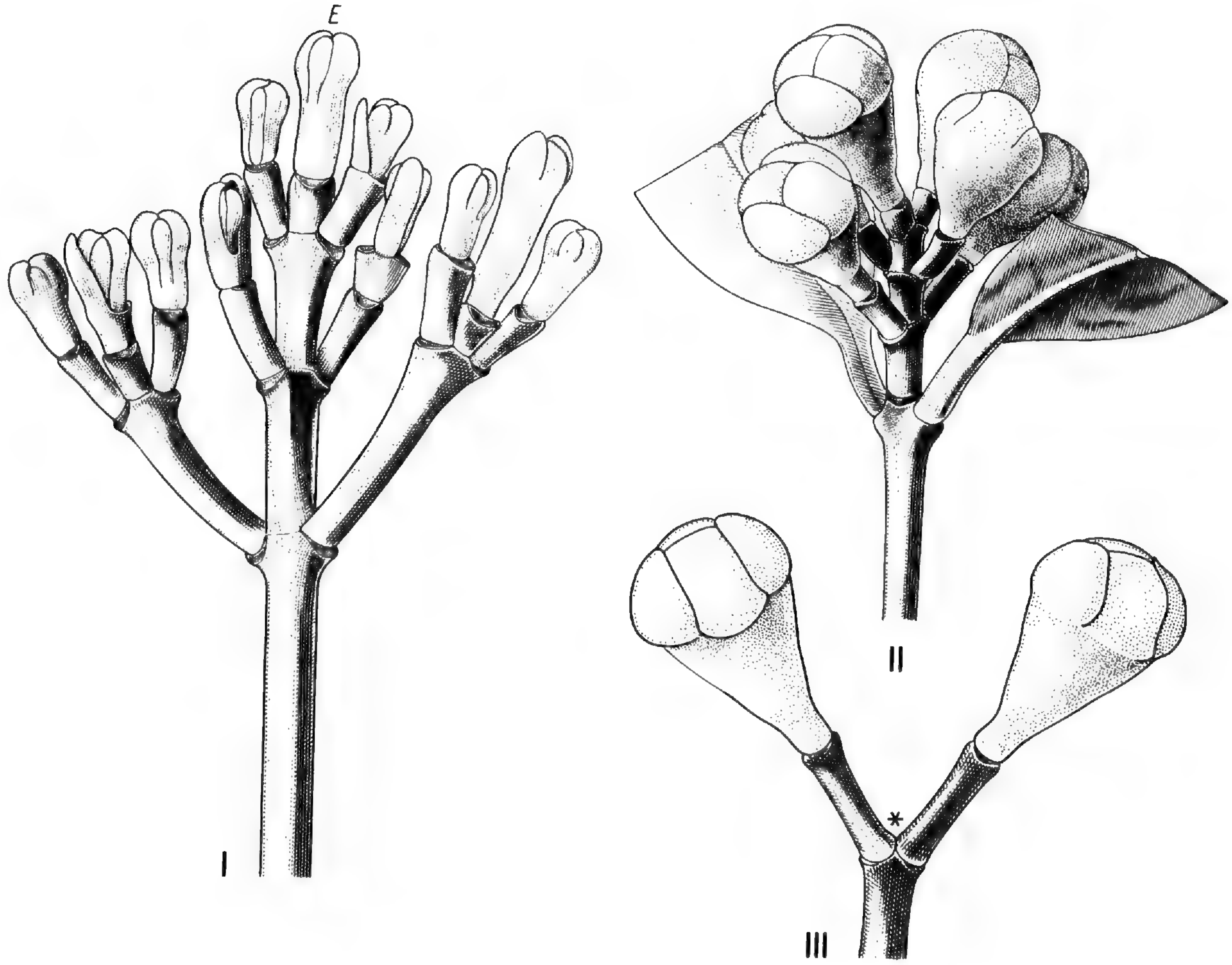

FIGURE 68. *Myrtaceae.—I.* Syzygium aromaticum; *few-flowered inflorescence, the bracts fallen off. II, III.* S. jambos.*—II. Inflorescence, the terminal flower aborted (truncate monotelic synflorescence).—III. Distal part of the inflorescence in detail. Asterisk indicates place of the aborted terminal flower. (From Troll.)*

cences" are regarded as derived from the terminal ones.

The fact that the development of flower-bearing systems and vegetative zones occurs successively in the same shoot, which continues growing over a long time, may prove to be favorable under certain conditions, especially for plants with enduring leaves.

In the examples mentioned above, the proliferation takes place after or during the efloration of the inflorescence. The efloration, however, may be delayed somewhat more while the shoot apex reverts to vegetative growth and may even form branches, as in *Beaufortia decussata* R. Br. (Fig. 73 II).

In such cases the normal zonation in the flowering systems of monotelic as well as of polytelic character (Fig. 3) seems to be reversed, since the continuation of the vegetative ramification system takes place above the flower-bearing zone. On the other hand, the extreme retardation of formation and anthesis of the flowers may result in different manifestations of cauliflory. Thus in *Calothamnus rupestris* Schau. and *C. villosus* Ait., anthesis can be delayed so long that the resting flower buds are occluded by peridermal tissue.

The degree of ramification of the flower-bearing systems can be very different, and this applies to proliferating inflorescences as well as to nonproliferating inflorescences. Thus in the proliferating inflorescence of *Pimenta dioica* (L.) Merr. (Fig. 74), *Gomidesia hookeriana* Berg, *Krugia ferruginea* (DC.) Urban, or *Calyptranthes chytraculia* (L.) Swartz, the partial inflorescences that originate from the axils of foliage leaves are highly ramified and present themselves as thyrsoid-paniculate systems. In contrast to the leafy

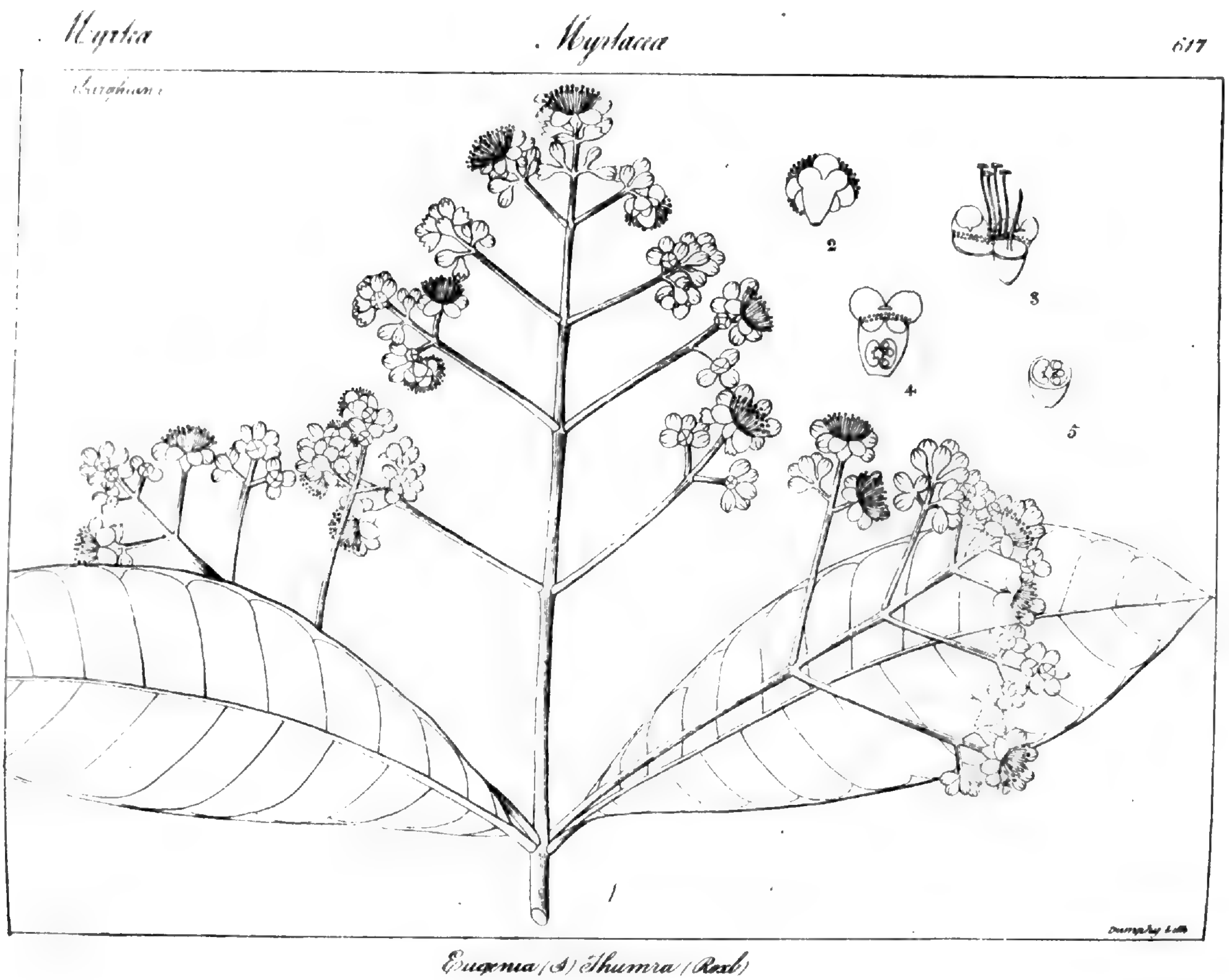

FIGURE 69. *Myrtaceae.* Syzygium thumra; *flowering branch. (From Wight, 1843.)*

main axis, they end in a terminal flower, thus revealing the monotelic character of the whole inflorescence. The same applies to some species of *Marlierea* and *Myrcia,* which produce more or less ample ramified thyrsoid-paniculate paracladia, whereas other species of these genera, as well as *Mitranthes eggersii* and *Myrrhinium loranthoides* (Cabrera, 1978: 78), only bear simple thyrsoids in the axils of foliage leaves.

A high degree of flexibility in the alternative formation of terminal flowers or terminal auxotelic or anauxotelic buds is represented by *Decaspermum paniculatum* Lindley. As reported by Briggs & Johnson (1979: 187) "the second-order and higher-order axes may produce: a) both terminal and lateral paniculate shoots . . . or b) lateral paniculate shoots only, the apical bud retaining the capacity for continued growth." Figure 75 I, which illustrates the results of Briggs & Johnson, resembles Figure 75 II, reporting our own results. The somewhat contradictory examples of inflorescence structure, however, can be elucidated in an acceptable way as being derived from a monotelic thyrsoid-paniculate base type. In *D. parviflorum* Kurz, we observed an indeterminate main axis bearing axillary loosely branched monothyrsoids with slightly disperse phyllotaxy.

Figure 75 I and II also represents examples of the development of *accessory branches.* Within the Myrtaceae these accessory branches are mostly phylloscopic. They occur as single accessory flowers (Fig. 75 I, II), triadic branches (Fig. 75 I), or even as botryoids (Fig. 75 I) and perhaps also as thyrsoids. Sometimes several accessory axes in a

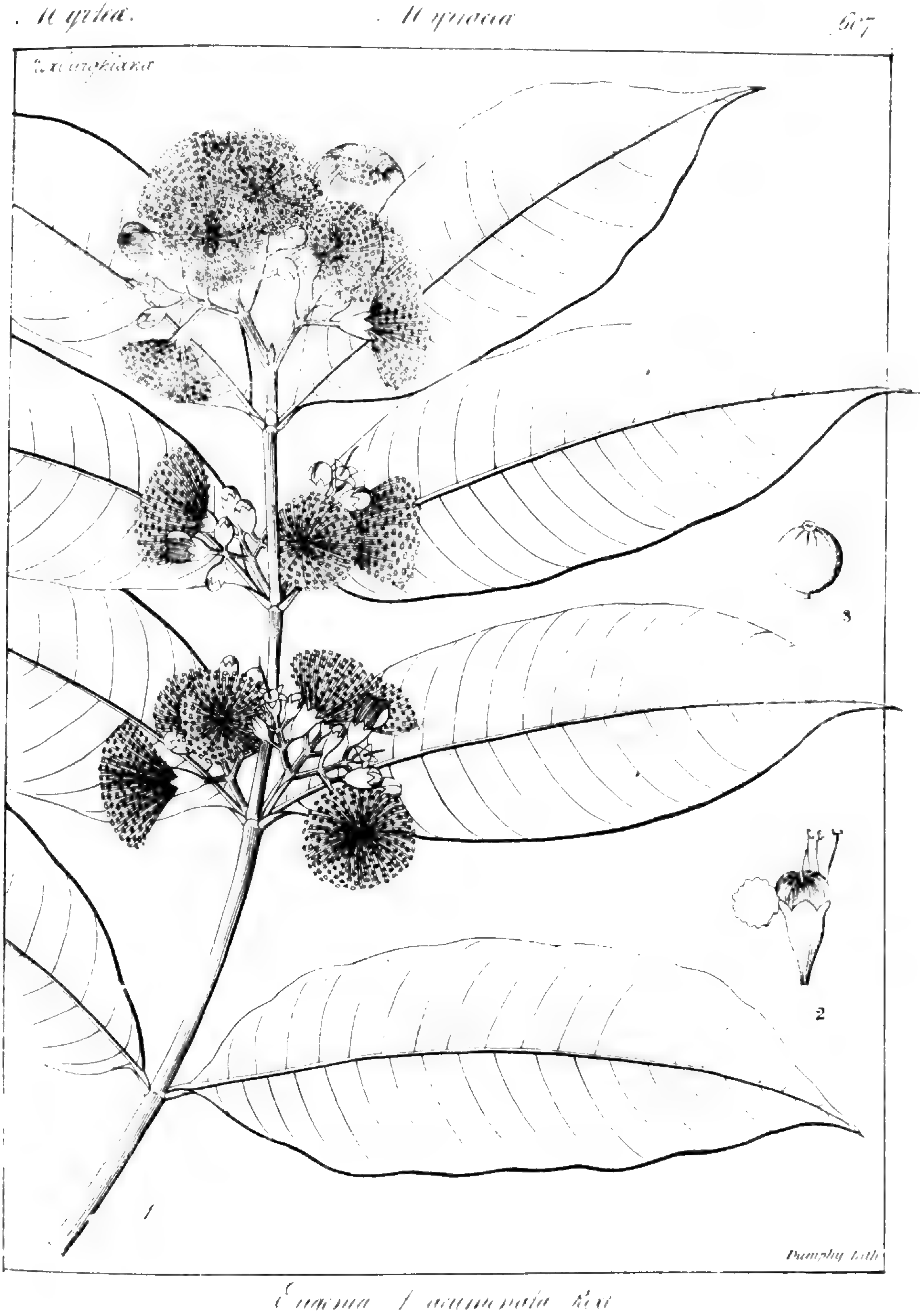

FIGURE 70. *Myrtaceae.* Syzygium acuminatum; *flowering branch. (From Wight, 1843.)*

vertical series are developed in the same axils. In this case they may be different in their degree of ramification or not, both demonstrated in *Myrceugenia exsucca* (DC.) Berg (Fig. 80 IX).

Within the large genus *Eucalyptus,* terminal thyrsoid-paniculate inflorescences ending in a terminal flower as well as proliferating inflorescences can be observed. Although some sections of the genus may exclusively follow

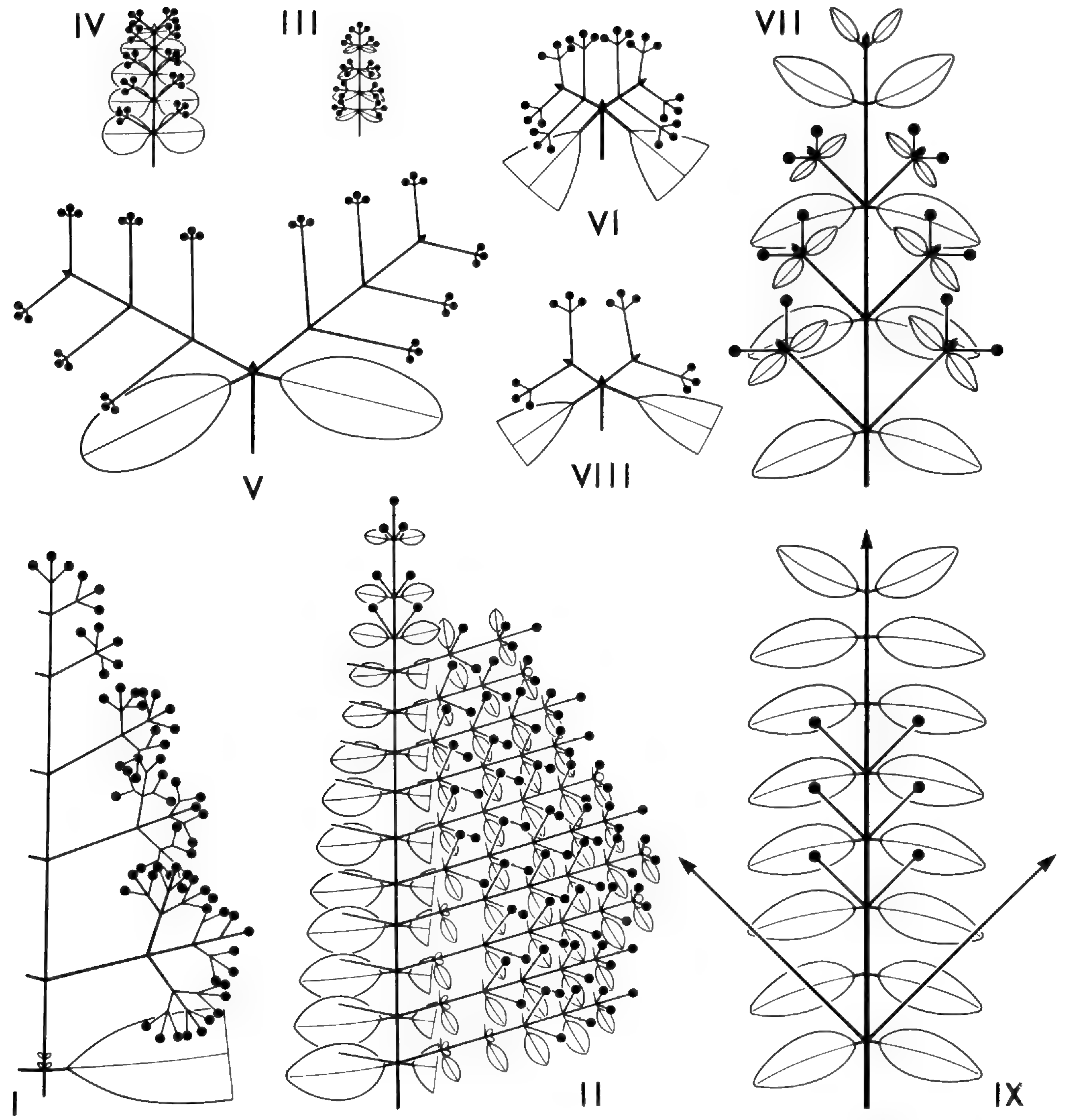

FIGURE 71. *Myrtaceae. Inflorescence diagrams.—I.* Metrosideros albiflora.—*II.* M. carminea.—*III.* M. diffusa.—*IV.* M. perforata.—*V.* M. kermadecensis.—*VI, VII.* M. umbellata.—*VIII.* Rhodomyrtus tomentosa.—*IX.* Acca sellowiana. *(I–VII from Dawson (1968) with some graphical alterations; bracts were ommited by Dawson.)*

one or the other mode, even closely related species can be different in this respect. Thus in many species of sect. *Adnataria* of subg. *Symphyomyrtus* (Pryor & Johnson, 1971), the main axes of the inflorescences were found to have terminal flowers (*E. melliodora* A. Cunn., *E. paniculata* Sm. (Fig. 76 I), *E. polycarpa* F. Muell., *E. polyanthemos* Schau., *E. populnea* F. Muell., *E. pruinosa* Schau. (Fig. 76 II), while others (e.g., *E. sideroxylon* A. Cunn.) have a proliferating main axis. In still others (e.g., *E. intertexta* R. T. Baker) inflorescences with terminal flowers and proliferating inflorescences were even found on the same herbarium sheet (Penfold & Willis, 1961, pl. 38, fig. 6). According to Johnson (1972: 23, fig. 5) this form "has adaptive significance" and is derived from forms without a terminal flower (the reverse seems more probable).

The partial inflorescences are condensed cymes (Fig. 75 III, IV), which often are described as umbels but more correctly should be called umbellasters (Johnson, 1972; Briggs

FIGURE 72. *Myrtaceae. I, II.* Melaleuca decora; *inflorescence before (left) and after (center) proliferation.—Right.* Callistemon rigidus; *proliferating shoot after anthesis, with fruits of preceding flowering phase. (From Troll.)*

& Johnson, 1979) or sciadioids (Troll, 1964: 53).

The number of flowers in such umbellasters can be seven or more, but often their number is reduced, and they are not rarely uniflorous (*Eucalyptus globulus* Labill., *E. tetraptera* Turcz.). They can show significant characters, such as concrescence of their gynoecia in *E. lehmannii* (Schau.) Benth. or broadening of the hypopods, especially in *E. platypus* Hook. (Fig. 77). In *E. cinerea* F. Muell. (Fig. 73), *E. macrorhyncha* F. Muell., and other species with proliferating inflorescences, a strong delay of anthesis as already noted for *Beaufortia decussata* takes place. As a consequence the top of the inflorescence axis may produce vegetative branches while the partial inflorescences at its base are still in flower. The connection of these conditions with the formation of cataleptic (Müller-Doblies & Weberling, 1984) flower-bearing short shoots and with cauliflory seems to be obvious here.

Frequently the flower-bearing branches are reduced to botryoids, as in *Myrciaria floribunda* (Willd.) Berg (Cremers, 1983/1986, fig. 42/7) or *Eugenia guatemalensis* Cogn. In species of *Blepharocalyx* (*B. tweedii* Hook. & Arn., *B. gigantea* Lillo, cf. Cabrera, 1978, fig. 143; Digilio & Legname, 1966, fig. 82) or *Backhousia myrtifolia* Hook. & Harvey, the paracladia are long-stalked and loosely branched, seven- to five-flowered cymes. This reduction of the paracladia goes even further to form long-stalked, loosely branched triads, as in *Myrcianthes cisplatensis* (Camb.) Berg, *Myrceugenella apiculata* (DC.) Kausel, or *Eugenia pseudo-mato* Legr. (Digilio & Legname, 1966, figs. 84, 87) or to long-stalked, biflorous or uniflorous (monadic or dyadic) paracladia still with prophylls (*Eugenia pungens* Berg; Digilio &

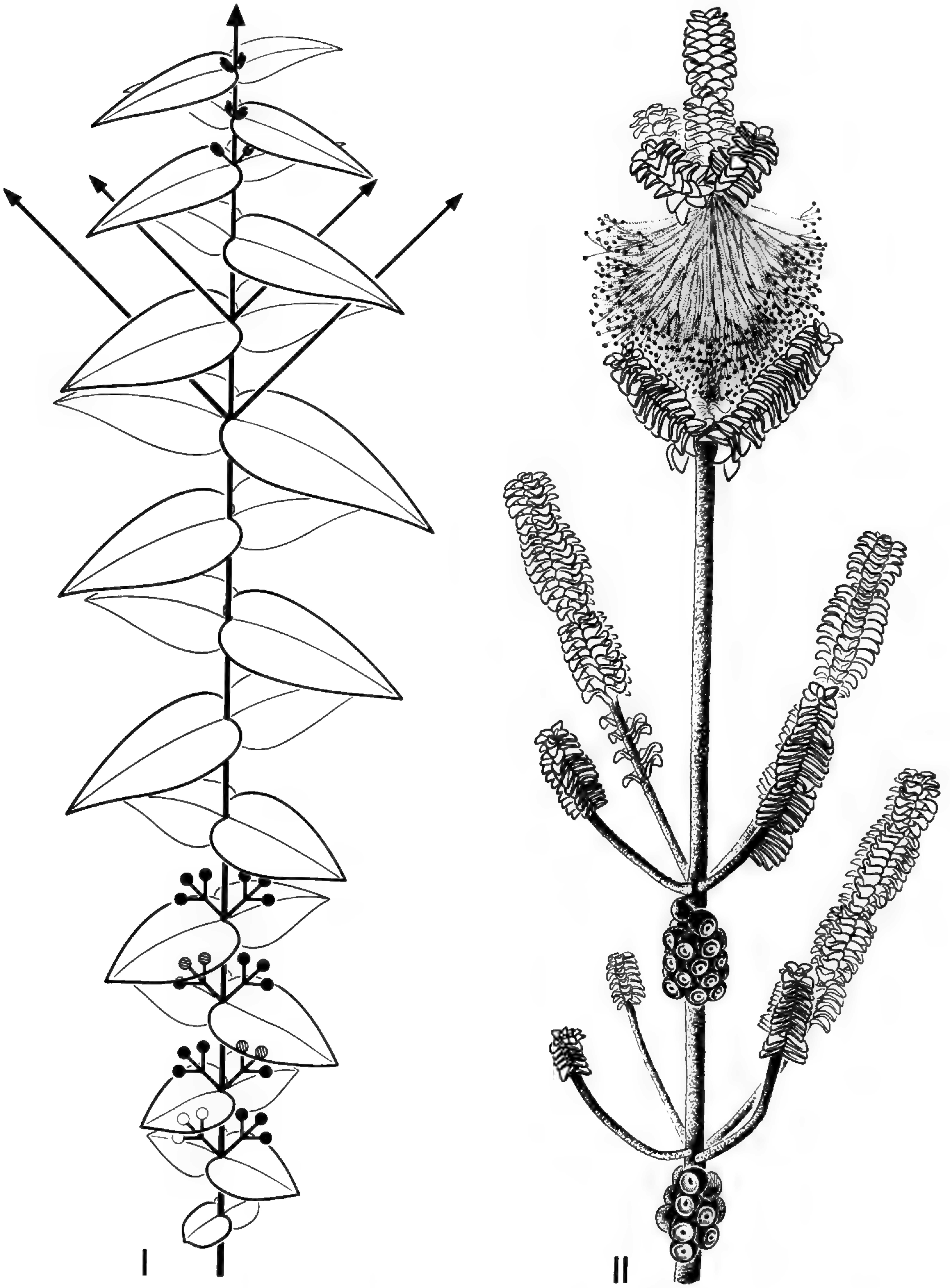

FIGURE 73. *Myrtaceae.—I.* Eucalyptus cinerea; *diagram of a flowering shoot. The proliferating inflorescence axis already had developed branches when anthesis had started (*Weberling 7413*).—II.* Beaufortia decussata; *flowering shoot with fruits of preceding flowering phases.*

FIGURE 74. *Myrtaceae.* Pimenta dioica; *inflorescences.—Left. Proliferation has taken place already.—Right. The inflorescence axis still ends in a bud. (From Troll.)*

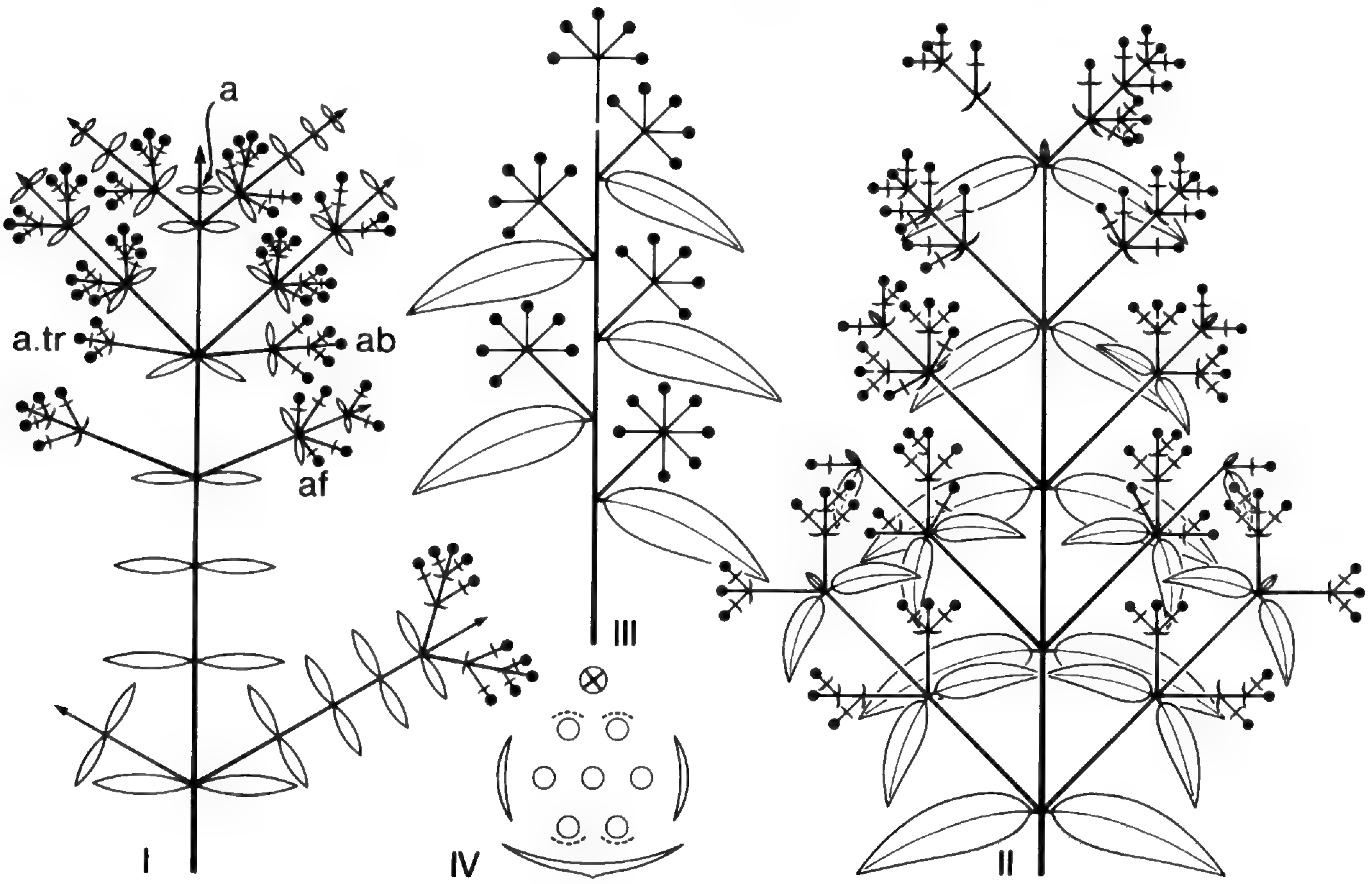

FIGURE 76. *Myrtaceae.—I.* Eucalyptus paniculata.*—II.* E. pruinosa; *flowering branches. (From F. Mueller.)*

Legname, 1966, fig. 85). Condensed and sessile triadic or uniflorous paracladia compose the spikelike proliferating inflorescences so characteristic of many species of *Calothamnus, Callistemon* (triadic pc in *C. suberosum* only; Dawson, 1978a, fig. 3), *Melaleuca* (Fig. 72), and *Beaufortia* (Fig. 73 II).

Leafy proliferating botrya are characteristic for all or many species of the myrtoid genera *Ugni, Myrtus, Fenzlia, Psidium, Myrceugenia, Luma, Acca* (Fig. 71 IX), and others and of the leptospermoid genera *Eremaea, Baeckea, Balaustion, Calythrix, Wehlia, Pileanthus, Thryptomene, Micromyrtus* (Fig. 78 III, IV), *Verticordia* (Fig. 78 I, II), *Regelia* (also triadic pc?, cf. Briggs & Johnson, 1979), and others.

In many species of *Kunzea* (e.g., *K. capitata* Reichb. and *K. ericifolia* Reichb., Fig. 79 I), the botrytic or spikelike inflorescences are capitate, as in species of *Agonis* (Fig. 80 II) and *Sinoga.*

The agglomeration of flowers into showy heads decidedly supports the attraction of pollinators. This is especially true for the pseudanthial inflorescences of *Darwinia* and *Actinodium.* In both, the dense heads are botrya that can proliferate after flowering (especially in *Darwinia,* Fig. 81). In *Darwinia* the subtending leaves of the flowers are inconspic-

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FIGURE 75. *Myrtaceae. I, II.* Decaspermum paniculatum.*—I. Flexibility of inflorescence development (from Briggs & Johnson; showing the actual branching of a herbarium specimen:* Castlewood. *Johore, Malaysia;* NSW 13876).*—II. Diagram of the inflorescence of another herbarium specimen (Khasia:* Hooker s.n. *(M)). III, IV.* Eucalyptus intertexta.*—III. Inflorescence drawn from herbarium specimen (Australia. New South Wales: Byrock, Oct. 1903,* J. L. Boorman s.n. *(M)). In another inflorescence represented on the same sheet, the apex was proliferating.—IV. Diagram of a partial inflorescence ("umbellaster"). a, apex of blastotelic main axis; a.tr, accessory triadic branch; ab, accessory botryoid; af, accessory flower. (IV From Troll.)*

FIGURE 77. *Myrtaceae.* Eucalyptus platypus.—*Left. Herbarium specimen.—Right. Detail. (Algeria: Oran à Santa Cruz, 9.5.1918,* A. Faure s.n. *(M).)*

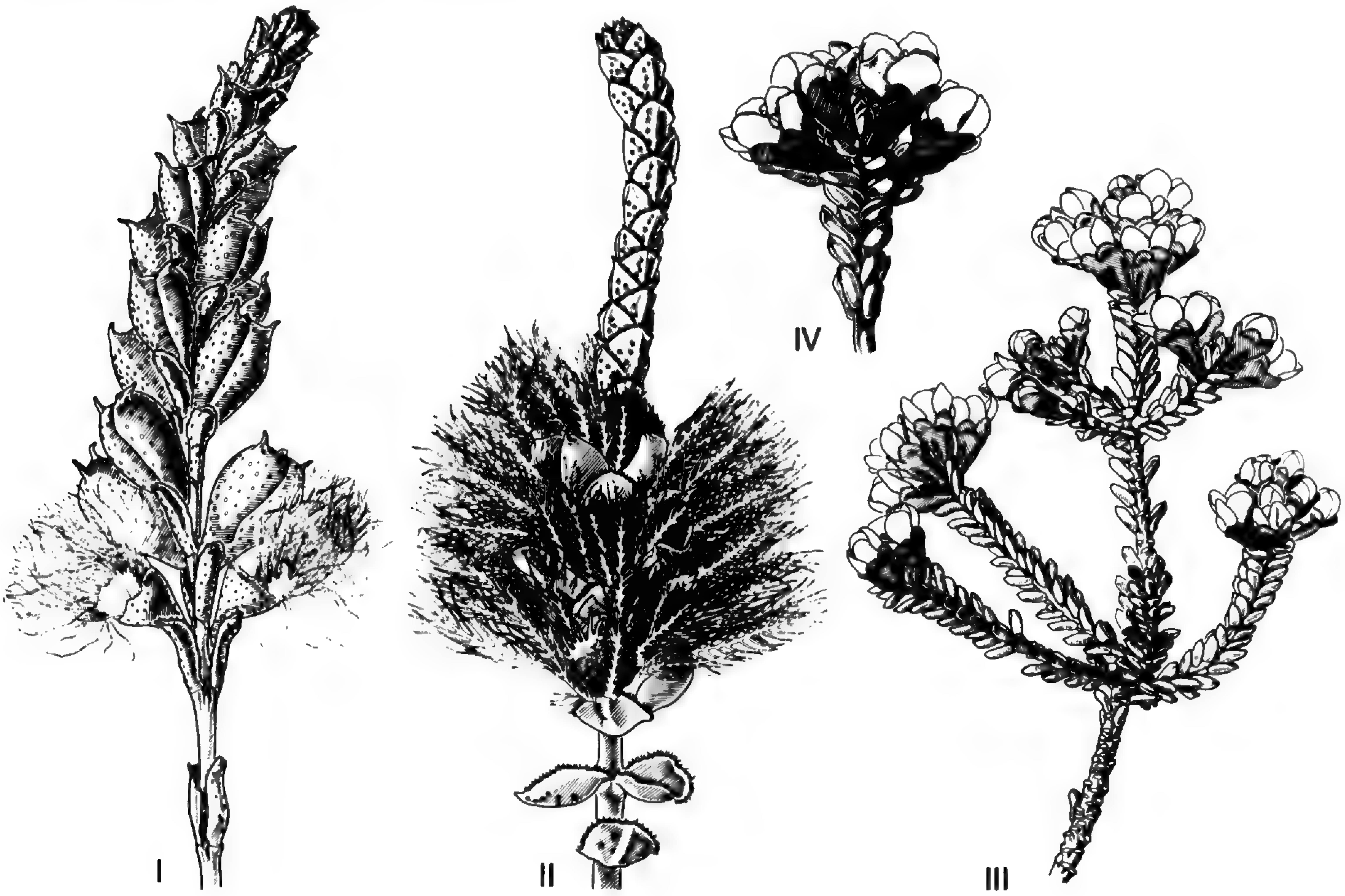

FIGURE 79. *Myrtaceae.—I.* Kunzea ericifolia (Meebold 11881).*—II.* Chamelaucium uncinatum; *flowering branch. (II From Troll.)*

uous, but the adjacent leaves are often greatly enlarged, petaloid, and colored, giving the capitate inflorescence a flowerlike shape (Fig. 82). For the western Australian species, Briggs & Johnson (1979: 201) found "a sequence from (for example) the little-modified *D. thymoides* Benth., through *D. virescens* (Meissn.) Benth., where the petaloid leaves are about as long as the perigynia ('floral tubes'), to the pendulous 'bells' . . . of *D. meeboldii* C. A. Gardn. ('Mondurup Bell') or *D. speciosa* (Meissn.) Benth., in which individual flowers are hidden by several series of long petaloid leaves," and the inflorescence axis "is anauxotelic" (Figs. 80 IV, 82). In *Actinodium cunninghamii* Schau. ex Lindley, the "daisy-like" flower heads have several rows of "rays" formed by modified sterile flowers (Figs. 80 V, 82). The axis of the capitulum "is somewhat swollen but not flat, and variation in the length of the peduncles of the monads brings the flowers to approximately the same level, although the outermost arise c. 2–5 mm below the innermost" (Briggs & Johnson, 1979: 202).

It is not rare that the development of triadic to uniflorous paracladia and the arrangement in leafy thyrsic, botrytic or spikelike proliferating inflorescences is limited to branches of more or less long main shoots

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FIGURE 78. *Myrtaceae.—I.* Verticordia pholidophylla.*—II.* V. spicata; *flowering branches. The apex of the inflorescence axis has returned to vegetative growth. (I. W. Australia: Watheroo,* Meebold 6619 *(M); II. W. Australia,* F. Mueller s.n. *(M).) III, IV.* Micromyrtus microphylla.*—III. Flowering branching system.—IV. Headlike condensed inflorescence with beginning proliferation (*L. Boorman *in 9.1908, New South Wales, Australia; M).*

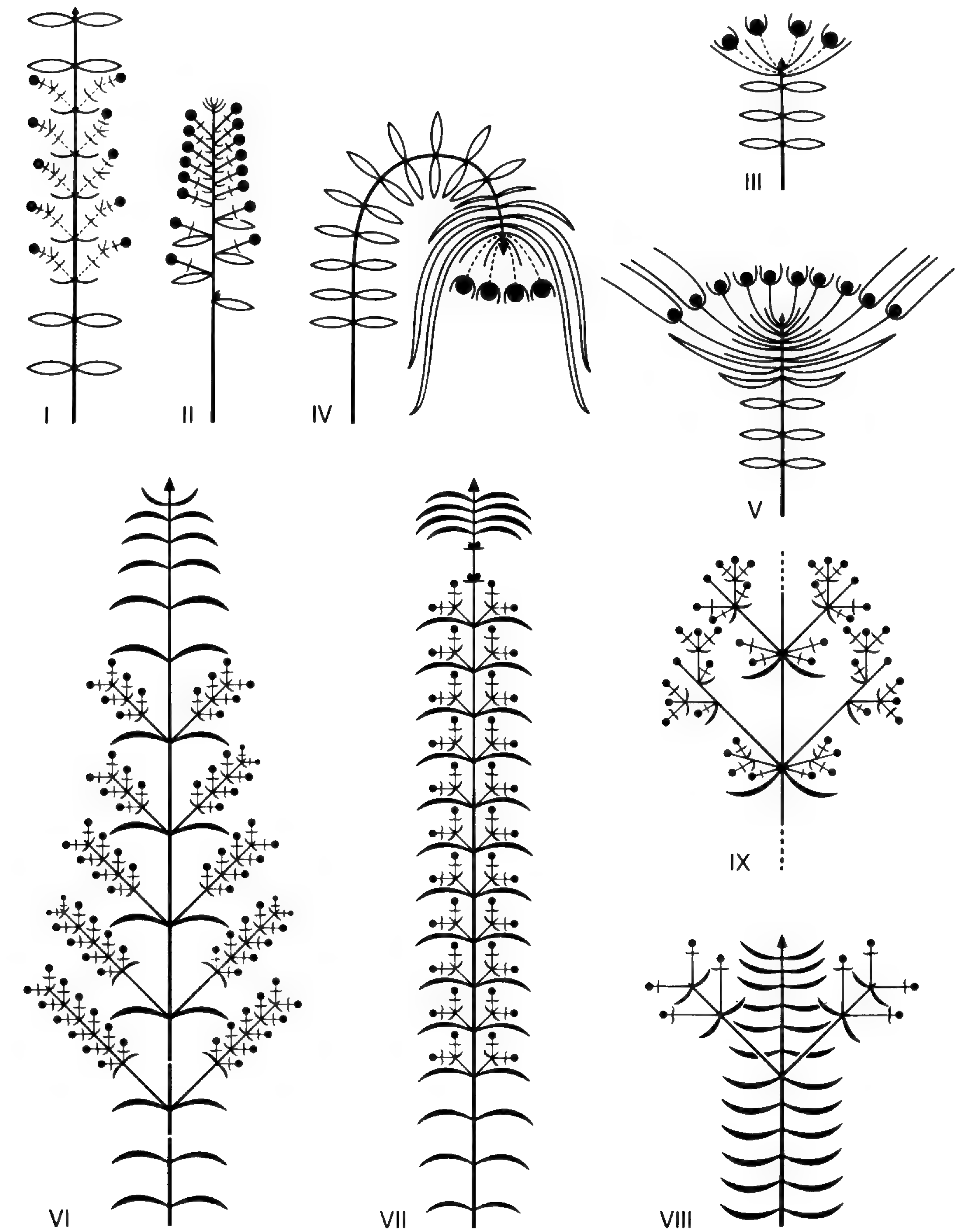

FIGURE 80. *Myrtaceae. Inflorescence diagrams.—I.* Melaleuca exarata.—*II.* Agonis juniperina *(W. Australia: Albany,* A. Meebold 10140, *(M)).—III.* Darwinia *with petaloid pherophylls (e.g.,* D. virescens*).—IV.* D. meeboldii.—*V.* Actinodium cunninghamii.—*VI.* Chamaelaucium gracile *(*E. Pritzel 638*); two pairs of paracladia omitted.—VII.* Hypocalymma angustifolium *(*Weberling 7011c*); the hypopodia of the two flowering branches remain undeveloped.—VIII.* Chamelaucium uncinatum.—*IX.* Myrceugenia exsucca *(paratype:* Martius; *M). (I, III–V from Briggs & Johnson.)*

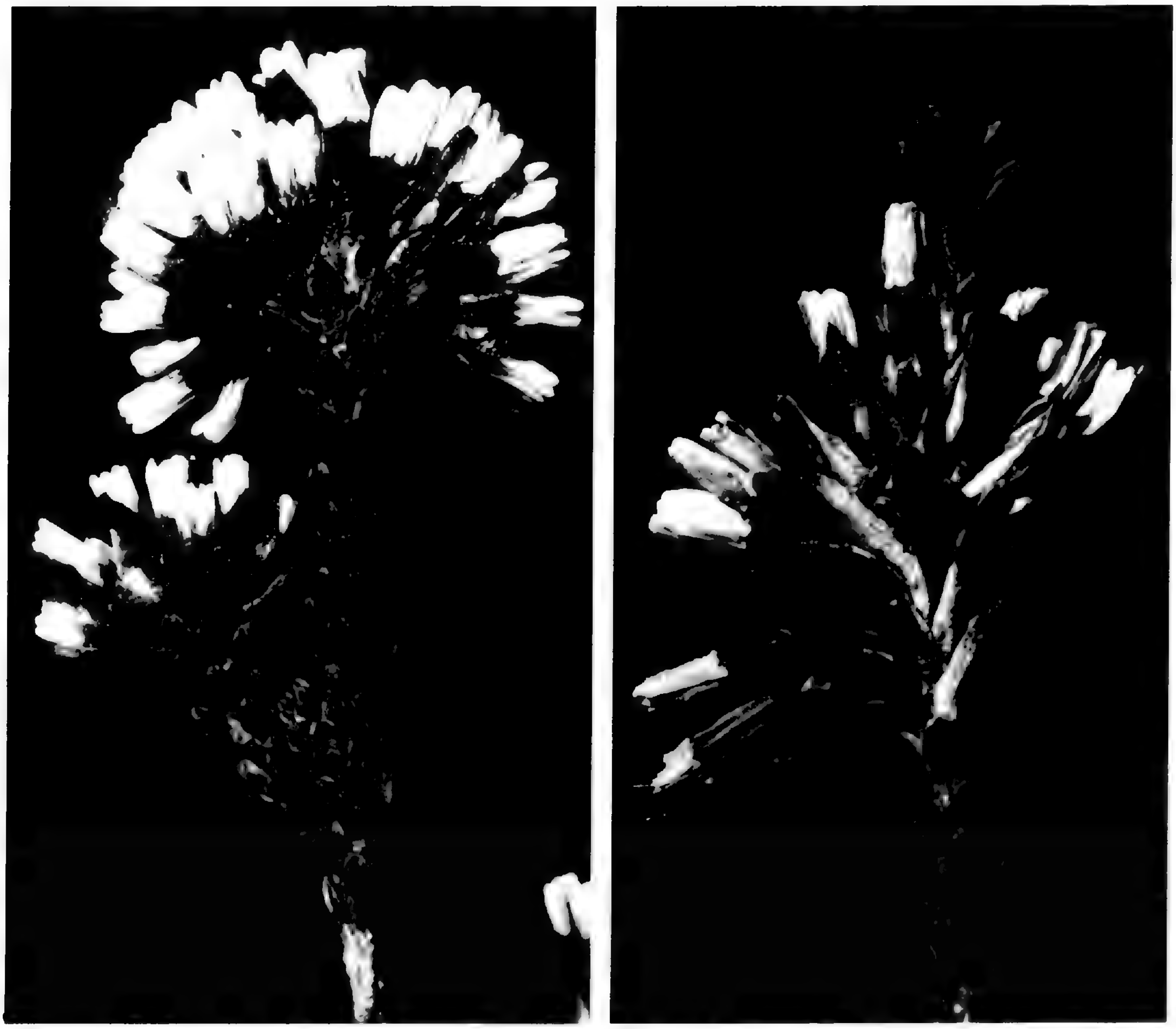

FIGURE 81. *Myrtaceae.* Darwinia vestita. *(Left,* Pritzel 11/1901; *right,* Meebold 1216 *(M).)*

that remain vegetative themselves. This applies to *Baeckea astartoides* Benth., *B. behrii* F. Muell., and others. The next step in this differentiation of a system of vegetative long shoots and flower-bearing short shoots may be that the short shoots develop and flower in the season that follows the development of the long shoot. This was observed in *Campomanesia xanthocarpa* Berg, in which the flower-producing short shoots bear cataphylls at their bases (also seen in *Myricariopsis baporetii* (Legrand) Kausel?; see Kausel, 1955–1957: 508, fig. 10). This characteristic "cauliflorous" position of the thyrsoid bracteose inflorescences in *Myrrhinium* species may be explained by an extreme delay of the development and flowering of such short shoots (cf. Fig. 83).

A remarkable reduction of flower-bearing lateral shoots can be observed in some species of *Chamelaucium* and *Hypocalymma.* In *C. uncinatum* Schau. (Fig. 79 II) leafy axes bear pairs of flowering branches that after the production of only two flowers terminate in a bud. This means that only the prophylls of the flowering branches are fertile. Sometimes, however, we can find the flowering branches producing two pairs of flowers before ending in a terminal bud (Fig. 80 VIII). By this observation we are justified to interpret the flower pairs as reduced (commonly anauxotelic) botrytic paracladia, especially as there are species of *Chamelaucium* with botrytic though bracteose flowering shoots (e.g., *C. gracile,* Fig. 80 VI). Whereas in the flowering shoots of *C. uncinatum* the hypopods of first

FIGURE 82. *Myrtaceae.—Left.* Darwinia meissneri (Meebold 1361 *(M)).—Right.* Actinodium cunninghamii *Schau.* (Meebold 1313 *(M)).*

and second order are well developed, they are completely reduced in the species of *Hypocalymma* (Fig. 80 VII). Thus the inflorescences of this genus consist of axillary sessile flower pairs including between the flowers a terminal bud that sometimes may become auxotelic. The same inflorescence structure was seen in *Myrceugenia campestris* (DC.) Legrand & Kausel. According to Briggs & Johnson (1979), even the uniflorous elements composing the spikelike inflorescences of *Melaleuca exarata* are lateral flowers of reduced lateral spikes. Except this single lateral flower, which according to Briggs & Johnson must be regarded as terminating a lateral axis of second order, we could only detect a series of about six bracts interpretable as the last remnant of the reduced spikes. In *N. nesophila* F. Muell. the dense spikelike inflorescence, which often proliferates, is composed of three-flowered cymes (Leins, 1965). A case similar to *Chamaelaucium* can be found in *Rhodomyrtus tomentosa* (Ait.) Wight (Fig. 71 VIII) and *R. parviflora* Alston, and in *Octamyrtus*. Here the prophylls of the flowering branches bear single flowers or triads, and the terminal bud at least produces one pair of small leaves.

Considering the indefinite character of the thyrsic or botrytic inflorescence axes and their main branches, which can be observed in some inflorescences, the question arises whether all of these inflorescences still may be classified as variants of the monotelic type. In many cases the answer is not simple, because the proliferation of various axes within the inflorescence may obscure the true morphological character.

In the thyrsoid paniculate inflorescences of *Syzygium* and many others mentioned above, there is no doubt about their monotelic character, even if the main axis of these inflorescences terminates in an anauxotelic or auxotelic bud. The same applies to the inflorescence of *Syzygium paniculatum*, which normally is a botryoid (Fig. 68 II) terminating a leafy shoot. The inflorescence of *S. jambos* (L.) Alston differs from these by the abortion of the terminal flower (Fig. 67). Troll (1969: 259) classified this inflorescence as a truncate monotelic synflorescence. Keeping in mind the flexibility in the formation of terminal flowers closing thyrsoid-paniculate inflorescences, which was demonstrated for several taxa of Myrtaceae, this view seems to be acceptable. Commonly the thyrsoid- or paniclelike flower-bearing branches—the paracladia—of such truncate monotelic systems are still provided with terminal flowers, revealing the monotelic character of the flowering system. Within *Eugenia*, one species with terminal flowers, *E. apiculata* DC. (Fig. 84 VI) was found by Sell (1982), but most of the species seem to have indeterminate flowering systems. The inflorescence structure depicted in Figure 84 I and II is not uncommon: the inflorescence axis terminates in an indefinite botrytic flowering system, and the branches inserted below this terminal botrys repeat this structure. Thus in all essential features this flowering system is in accordance with inflorescences of the polytelic type (Fig. 3 II) as characterized by Troll. According to Troll (1964–1969) and Weberling (1961, 1964, 1965, 1981, 1982, 1983a, b; Troll & Weberling, 1966), the polytelic type probably has been derived repeatedly from the monotelic during the evolution of the different groups of angiosperms by reduction of the terminal flower(s) and specialization of the paracladia of the monotelic system. As a result of this specialization the distal elements of the series of flower-bearing branches are reduced to single lateral flowers or lateral cymes (partial florescences, pf), which constitute elements of an apical system composed of lateral flowers only to which the term "florescence" is referred. The lower lateral branches repeat the structure of the main stem by producing (indefinite) florescences themselves, co-florescences, and thus are termed paracladia (pc) of the polytelic system (not to be mixed up with the paracladia of the monotelic systems).

FIGURE 83. *Myrtaceae.* Myrrhinium loranthoides; *flowering branch (I), flower (II), and fruit (III). (From Digilio & Legname.)*

Referring this typology to the inflorescences of *Eugenia polystachya* Rich. and *E. muricata* DC. (Fig. 84 I, II), we can regard the terminal botrys as the main florescence and the lateral axes with botrya as paracladia with co-florescences. In the same way the inflorescences of *E. patens* Poir. and several other species can be interpreted; rarely the single lateral flowers are replaced by triadic partial florescences (e.g., *E. muricata*, and according to Briggs & Johnson, 1979: 200, *E. dichotoma* DC.).

These polytelic forms of inflorescences can be derived from monotelic forms as repre-

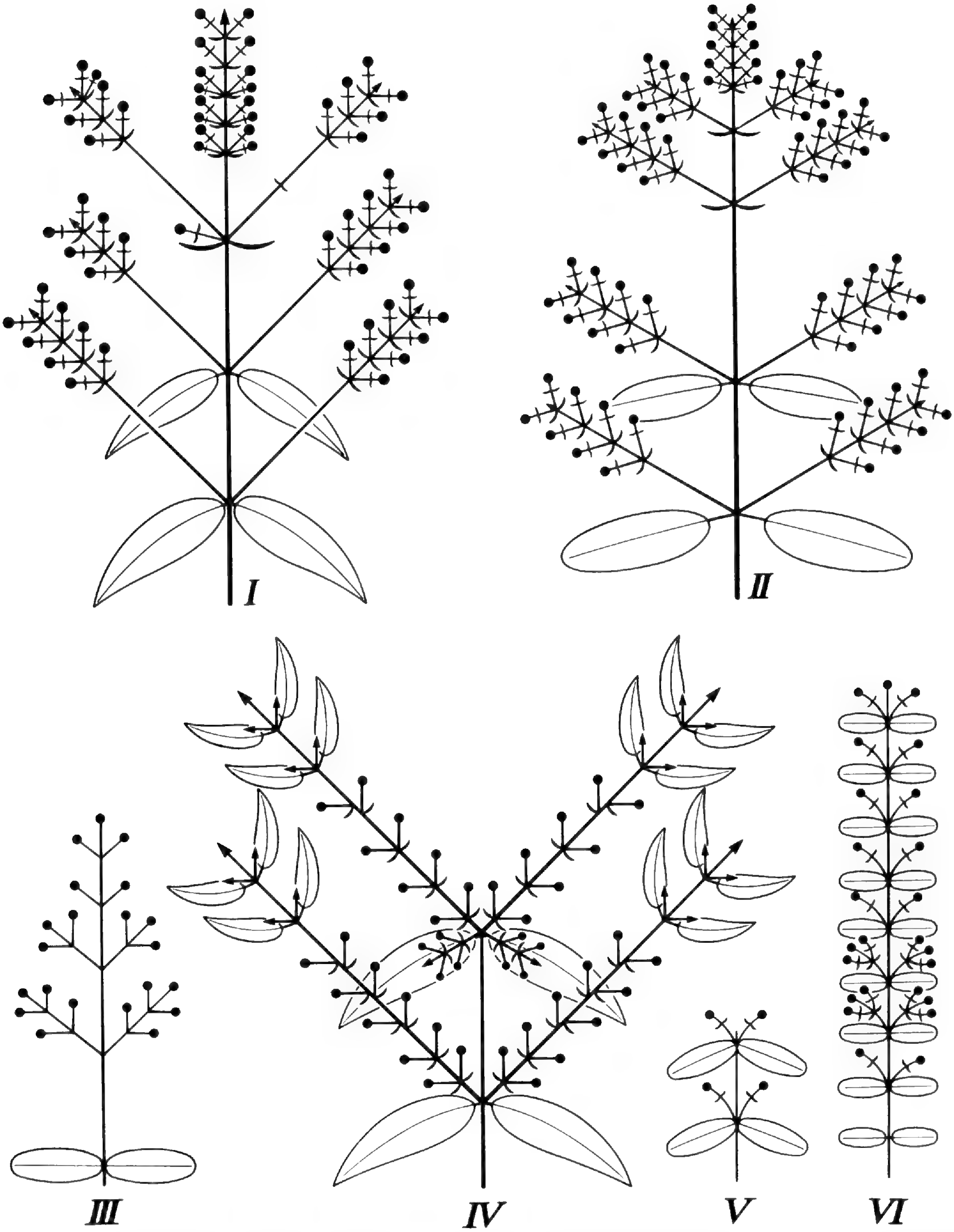

FIGURE 84. *Myrtaceae. Diagrams of flowering branches.—I.* Eugenia polystachya *(*J. M. Pires et al. 50523 *(M)).—II.* Eugenia muricata *(*Oldeman 2539*).—III.* Syzygium aromaticum *(*Oldemann B. 1096*).—IV.* Eugenia *cf.* uruguayensis *(*Weberling 5577*).—V.* E. sancta *(redrawn from Fl. Mart. XIV, 2: 26).—VI.* E. apiculata. *(II, III, V from Cremers, 1983/1986; VI from Sell, 1982.)*

sented even within *Eugenia* by species like *E. apiculata*. As mentioned before, this species has a thyrsoid-botryoid inflorescence that is still closed by a terminal flower. On the other hand, the pherophylls in this inflorescence are somewhat foliaceous. The same applies to *E. sancta* DC. (Fig. 84 V), with indefinite inflorescences.

In *Eugenia polystachya* the botrytic flowering systems end in a seemingly abortive bud. In others, however, such as *E.* cf. *uruguayensis* Cambess., they are auxotelic and produce a vegetative continuation of the bracteose botrytic axis (Fig. 84 IV). Proliferation also takes place in the botrytic leafy inflorescences of *E. parviflora* DC. (Sell, 1982) similar to the botrytic leafy proliferating inflorescences of many myrtoid and leptospermoid taxa mentioned above.

In general, a clear tendency towards the polytelic inflorescence structure can be confirmed for the Myrtaceae. In some transitional cases, however, and especially in cases of proliferating inflorescences, it can be difficult to decide whether the inflorescence of a certain taxon should be regarded as a (truncate) monotelic or a polytelic system.

The inflorescences of the Oliniaceae are monotelic throughout and follow the pattern of Myrtaceae with (thrysoid-)paniculate inflorescences, which we regard to be the central type within the whole order. The panicles are usually conical, caused by shortening of the internodes, but they can be contracted to somewhat globose heads, e.g., in *Olinia rochetiana* A. Juss. The ramification of the branches sometimes tends to be botryoidlike. In some species terminal as well as axillary panicles can be observed. This may be due to the considerably extended and sometimes irregular flowering season (Phillips, 1926): the lowermost paniclelike branches develop separately from the terminal panicle in a somewhat later stage of the flowering season, forming separate flowering systems.

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FLORA OF THE VENEZUELAN GUAYANA—IV

Julian A. Steyermark[1,2]

ABSTRACT

Recent expeditions in the Venezuelan Guayana to Cerro Yutajé, Murisipán-tepui, Camarcaibarai-tepui, and Cerro de la Neblina, have resulted in additional new taxa, especially in the Aquifoliaceae and Rubiaceae, of which the following are described: Paepalanthus holstii *(Eriocaulaceae)*; Rapatea chimantensis, Stegolepis minor *(Rapateaceae)*; Rauia subtruncata, Raveniopsis liesneri *(Rutaceae)*; Ochthocosmus micranthus *(Linaceae)*; Ilex abscondita, I. acutidenticulata, I. altiplana, I. attenuata, I. brevipedicellata, I. cardonae, I. ciliolata, I. davidsei, I. glabella, I. gransabanensis, I. guaiquinimae, I. holstii, I. ignicola, I. jauaensis, I. longipilosa, I. magnifructa *var.* minor, I. marahuacae, I. paujiensis, I. polita, I. spathulata, I. summa, I. wurdackiana *(Aquifoliaceae)*; Allophylus parimensis *(Sapindaceae)*; Coussarea evoluta, Faramea boomii, F. morilloi, F. paludicola, F. yavitensis, F. yutajensis, Ferdinandusa boomii, Morinda longipedunculata, Psychotria anartiothrix, P. edaphothrix, P. pectinata, P. steinii, P. thesceloantha, P. yutajensis, Rudgea corocoroensis, *and* Sabicea bariensis *(Rubiaceae)*.

ERIOCAULACEAE

PAEPALANTHUS

Paepalanthus holstii Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Dist. Piar, Murisipán-tepui, summit, 5°53'N, 62°3'W, 2,300 m, 22 Mar. 1987, *Bruce Holst 3523* (holotype, MO; isotype, VEN). Figure 1.

Herba perennis caulescens; caulibus elongatis 10–30 cm longis, parte foliacea 10–20 cm longa, dense foliosis; foliis supra argentiis, eis supremis supra sericeo-pubescentibus nitidis late lanceolatis apice prolongatis, acumine ligulato 1 mm longo, 4–5 cm longis 1–1.4 cm latis; pedunculo pubescenti; capitulis 8–10 mm diam.; bracteolis involucri atrobrunneo-nigris late triangulari-ovatis acuminatis 2–2.5 mm longis, basi 1.5 mm latis extus sericeo-pubescentibus marginibus ciliolatis intus glabris; bracteis receptaculi subligulatis apice abrupte acutis extus dense pilosis aliter glabris 2.5–2.7 mm longis 0.6–1 mm latis; bracteolis masculinis oblanceolatis obtusis dorsaliter carinatis 2.5 × 0.7 mm parte apicali extus dense pilosis; sepalis masculinis spathulatis apice rotundatis 2 mm longis 0.5 mm latis extus praeter apicem dense pilosum glabris intus glabris; corollae masculinae tubo anguste infundibuliformi 2.2 mm longo ad medium 0.7 mm lato basi 0.1 mm lato.

Perennial caulescent herb with elongated stems 10–30 cm long, the foliose portion 10–20 cm long, densely foliose. Leaves, especially the uppermost, densely silvery, sericeous and shining above, older ones glabrous both sides, many (11–17) nerved, broadly lanceolate, acute, the apex prolonged into a short, narrowly ligulate, obtuse acumen 1 mm long, 4–5 cm long, 1–1.4 cm wide, the margins densely ciliate on youngest leaves, eciliate or nearly so. Peduncles several, 10–16 cm long, 1 mm diam., several-costate, sparsely pilosulous or glabrescent except beneath the head where densely antrorsely pilose with ascending, subappressed hairs. Heads semihemispheric, 8–10 mm broad, 5 mm high. Involucral bractlets brownish black, with dark brown lower margins, the remainder black, broadly triangular-ovate, acuminate, 2–2.5 mm long, 1.5 mm broad at base, sericeous pubescent along exterior length of black middle portion, glabrous throughout within. Receptacular bracts subligulate most of length,

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ANN. MISSOURI BOT. GARD. 75: 311–351. 1988.

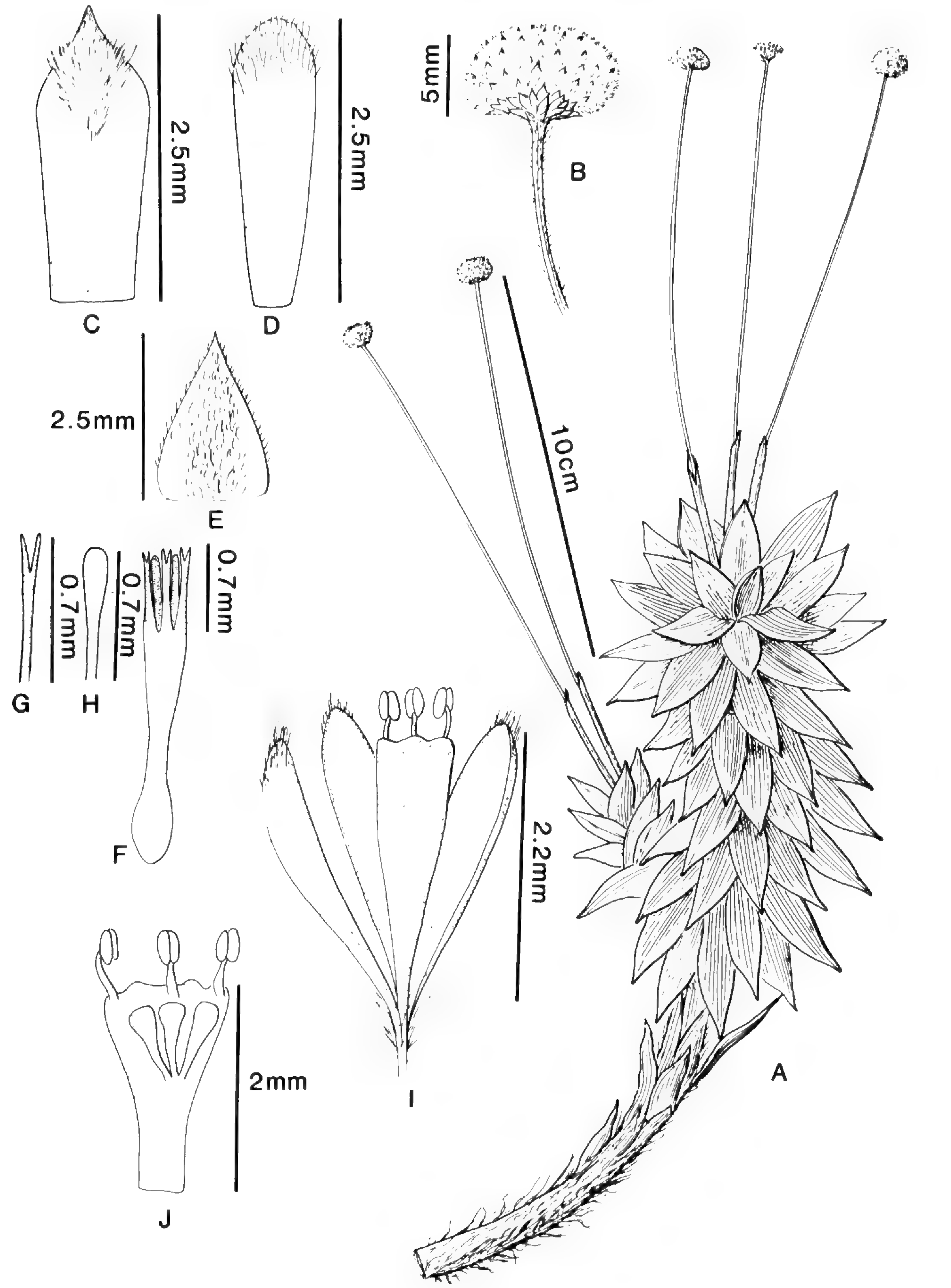

FIGURE 1. Paepalanthus holstii.—*A. Habit.—B. Inflorescence.—C. Receptacular bract.—D. Bractlet subtending pistillate flower.—E. Outer involucral bract.—F. Pistillate flower, corolla.—G. Outer segments of pistillate corolla.—H. Inner segments of pistillate corolla.—I. Staminate flower.—J. Interior of staminate corolla.*

abruptly ampliate above into a dark, acute apex, this densely pilose without, glabrous within, as is the rest of the bract, 2.5–2.7 mm long, 0.6–1 mm wide most of length.

Staminate florets: bractlet subtending flowers oblanceolate, obtuse, dorsally keeled, 2.5 mm long, 0.7 mm wide, densely villous without with erect villous hairs in apical portion, glabrous within. Staminate sepals separate, spathulate, rounded at apex, 2 mm long, 0.5 mm wide, densely villous within with long, erect hairs, glabrous on most of outer surface without except for long hairs around apex. Staminate corolla narrowly infundibuliform, gradually widened upward, 2.2 mm long, 0.7 mm wide above, 0.1 mm wide at base; stamens 3; anthers 0.2 mm long; filaments 0.2 mm long. Pistillate florets: corolla narrowly cylindric, 2.8 mm long, tubular, upper part 1.8 mm long, constricted to the ovary, 0.2 mm wide, outer segments linear, bifid at apex, 0.7 mm long, 0.1 mm wide, inner ones spathulate, truncate, 0.8 mm long.

This beautiful species with silvery foliage is well marked by its short, ovate-lanceolate leaves with a prolonged obtuse apex. From *Paepalanthus macrocaulon* Mold. var. *venamoensis* Mold. it differs in the densely sericeous median outer portion of the involucral bracts and shorter, silvery-sericeous upper surface of the younger leaves, while from *P. roraimensis* Mold. it is distinguished by the pubescent peduncle, involucral bracts pubescent throughout their median length outside, and the densely sericeous-silvery upper surface of the uppermost leaves.

It is a pleasure to name this species after Bruce K. Holst, who succeeded in collecting plants from the previously unexplored Murisipán-tepui and Aparamán-tepui.

RAPATEACEAE

RAPATEA

Rapatea chimantensis Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Chimantá Massif, lower southwestern slopes of Chimantá-tepui (Torono-tepui), 1,000 m, 24 May 1953, *Julian A. Steyermark 75584* (holotype, VEN; isotypes, MO, NY). Figure 2.

Planta herbacea terrestris ca. 1-metralis; vaginis 22–25 cm longis late alatis, parte superiore 7 cm anguste alata utroque latere 2–3 mm lato, basim versus una latere 20–30 mm lato; laminis basi abrupte constrictis late lineari-ligulatis apice tenuiter acuminatis basi abrupte cordatis 1.3 mm longis, 9–11.5 cm latis supra valde plicatis nervis primariis 35–45 elevatis acutis papillato-puberulentibus, subtus cristis rotundatis 1–1.5 mm latis dense papillato-puberulentibus; costa valde conspicua basim versus 3–4 mm lata; pedunculo 43 cm longo infra apicem 20 mm lato alibi 6 mm lato parte suprema 15 cm anguste alato 1–2 mm lato; capitulo subreniformi subcompresso semisphaerico 7 cm lato; spiculis numerosis 17–18 mm longis brevipedicellatis; bracteis involucralibus duobus anguste lanceolatis longiacuminatis basi late expansis 25 cm longis in dimidio superiore 15–17 mm latis basi 70 mm latis; bracteolis vix gradatis apice abrupte apiculatis 18 mm longis.

Terrestrial herbaceous plant ca. 1 m tall; leaf sheaths 22–25 cm long, broadly winged, upper 7 cm narrowly winged 2–3 mm wide on each margin, the wing widening below to 20–30 mm wide on one side; leaf blades erect-ascending, subcoriaceous, dull green above, silvery green below, abruptly constricted at the base, broadly ligulate-linear, slenderly acuminate at the apex, abruptly cordate at the base, 1.3 mm long, 9–11.5 cm wide, conspicuously plicate on upper surface with 35–45 elevated acute nerves on either side of the midrib separated by broad depressions 1–2 mm wide, papillate-puberulent, the lower surface with 42–49 rounded, shallowly convex ridges 1–1.5 mm wide, densely papillate-puberulent; midrib 3–4 mm wide below. Peduncle 43 cm long, 6 mm wide except at the expanded summit where 20 mm wide, finely costate, narrowly winged 1–2 mm wide in the uppermost 15 cm. Flowering head subcompressed, subhemispheric, 7 cm wide. Involucral bracts narrowly lanceolate, slenderly acuminate at the apex, broadly expanded at base, 25 cm long, 15–17 mm wide in upper half, 70 mm wide at base, three times longer than wide. Bracteoles submembranous, scarcely or not graduate, lanceolate, 18 mm long, the outer ones 18 × 3 mm, about equaling the spikelets, abruptly acuminate-pungent at the 3-nerved apex, the apiculate portion 1–2 mm long; other bracteoles subequal, ligulate-lanceolate, 12–14 × 4 mm with a cusp 1 mm long. Spikelets numerous, shortly pedicellate, 17–18 mm long. Sepals lanceolate, cuspidate, 9 × 2.5–3 mm. Anthers linear, bilobed at base, the connective triangular-lanceolate, acuminate, 2 mm long, the thecae

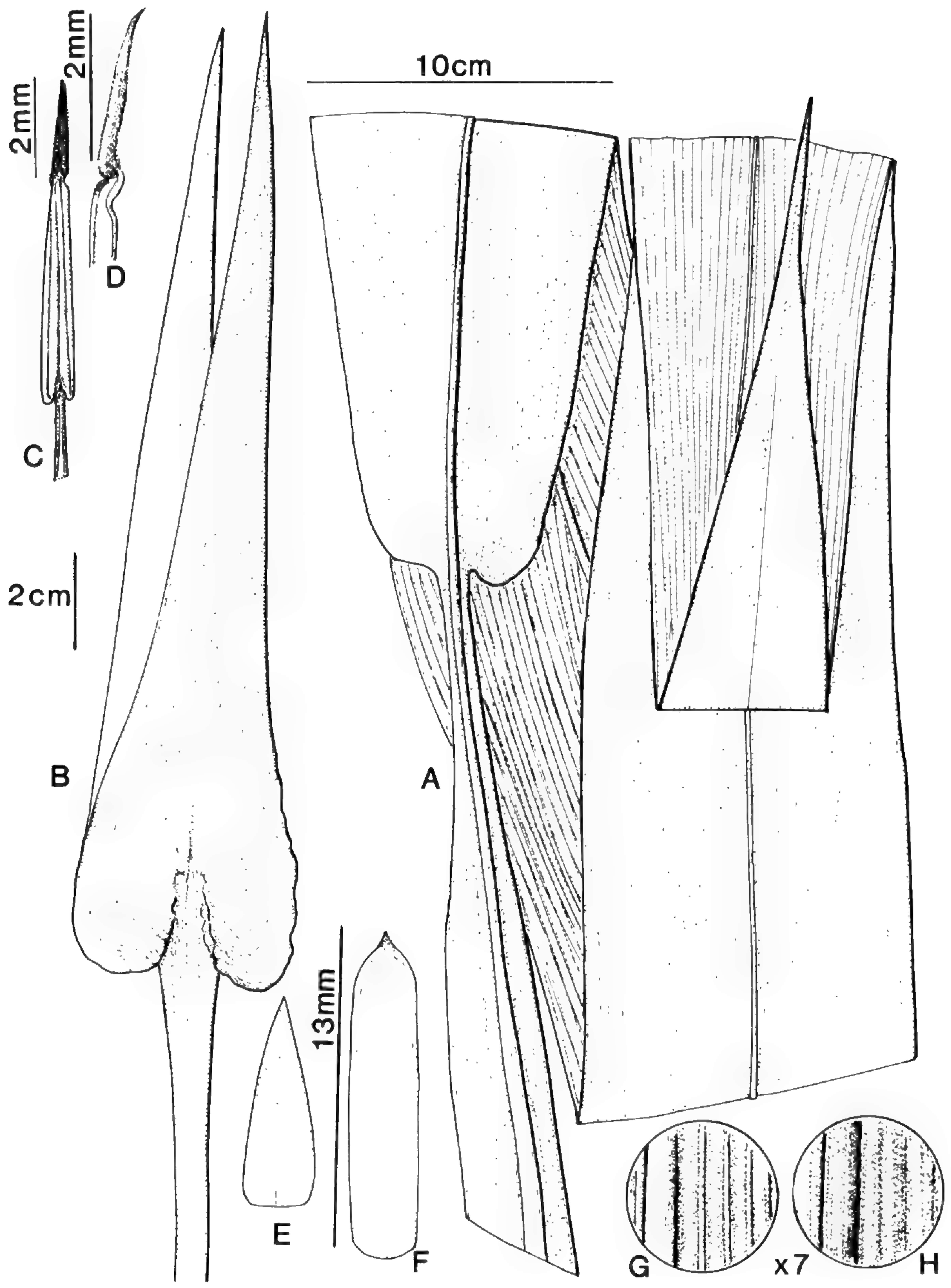

FIGURE 2. Rapatea chimantensis.—*A. Leaf blade and sheath.—B. Habit of cephalar bract with upper portion of peduncle.—C. Stamen, abaxial view.—D. Upper part of anther with connective, lateral view.—E. Sepal.—F. Outer bracteole.—G. Detail of upper leaf surface.—H. Detail of lower leaf surface.*

4.5–5 mm long, 0.7 mm wide toward the apex, 1 mm wide at base; filaments 2 mm long.

This taxon resembles *Rapatea fanshawei* Maguire but differs in having much longer involucral bracts which are more prominently narrowed above the base, longer, more narrowly winged peduncles, and outer bracteoles about equaling the spikelets. There are further differences in the leaf surfaces. In *R. fanshawei* the lower leaf surface has acutely elevated lines of nerves, whereas those of *R. chimantensis* have the nerves shallowly convex with rounded ridges. Moreover, the upper leaf surface of *R. chimantensis* has nerves more strongly elevated and more widely spaced than those in *R. fanshawei*. The leaf blades are longer and wider in *R. chimantensis*. Although related to *R. fanshawei*, the relatively equal length of the bractlets would ally the new taxon to *R. steyermarkii* Maguire.

STEGOLEPIS

Stegolepis minor Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Sierra de Lema, cabeceras del Río Chicanán, 80 km (en linea recta) al suroeste de El Dorado, 6°5′N, 62°W, 500 m, on banks and bluffs at base of uppermost waterfall of headwaters of Río Chicanán at base of high NE-facing sandstone bluffs, 28 Aug. 1961, *Julian A. Steyermark 89577* (holotype, VEN; isotype, NY).

Herbae perennes 0.5–0.6-metralis; vaginis subinduratis valde nervatis 14–25 cm longis 7 cm latis, valde scarioso-marginatis auriculus rotundatis; laminis ubique viridibus late linearibus apice subfalcate acutis 60 cm longis 6.5 cm latis tenuiter nervatis, costa subtus supra elevato; pedunculo apice subcompresso 1.5–2.5 mm lato sub apice 2.5–4 mm dilatato; capitulis compressis 13–14-floris 1.5 cm altis 2.3–3 cm latis; spiculis 13–14, lanceolato-ellipticis, sepalis inclusis 11–12 mm longis 3–5 mm latis; bracteolis castaneis subfructu laxe patentibus inferioribus late triangularibus acutis vel acuminatis carinatis 2–3.5 mm longis 1.5–2.5 mm latis medianis superioribusque lineari-lanceolatis acuminatis ecarinatis 5–8 mm longis 1.5–2.5 mm latis; sepalis sub fructu erectis haud deflexis anguste lanceolatis acutis 9–10 mm longis 2.5 mm latis.

Perennial herbs 0.5–0.6 m tall. Leaf sheaths subindurated, strongly nerved, 14–25 cm long, 7 cm wide, the margins broadly scarious, the auricles rounded. Leaf blades deep green both sides, broadly linear, subfalcately acute at apex, 60 cm long, 6.5 cm wide, finely nerved; midrib elevated above. Peduncle 0.5–0.6 mm long, subcompressed, 1.5–2.5 mm wide, 2.5–4 mm wide below the dilated apex. Heads compressed, 13–14-flowered, 1.5 cm high, 2.3–3 cm broad. Spikelets 13–14, lance-elliptic, 11–12 mm long including the sepals, 3–5 mm wide. Bracteoles castaneous-brown, spreading loosely in fruit, the lower ones broadly triangular, acute to acuminate, carinate, 2–3.5 mm long, 1.5–2.5 mm wide, the middle and upper bracteoles linear-lanceolate, acuminate, ecarinate, 5–8 mm long, 1.5–2.5 mm wide. Fruiting sepals erect, not deflexed, narrowly lanceolate, acute, 9–10 mm long, 2.5 mm wide.

The type specimen was previously identified by Maguire as "probably *Stegolepis ferruginea*." That taxon and the related *S. steyermarkii* Maguire, however, have essentially globose, noncompressed heads. *Stegolepis minor* is related to *S. ptaritepuiensis* Steyerm. and *S. celiae* Maguire. From *S. ptaritepuiensis* the new taxon differs in having much smaller heads and spikelets, and much broader leaves with a conspicuous elevated midrib on the upper surface. It is distinguished from *S. celiae* by the smaller heads with fewer, shorter spikelets, slenderer peduncles, conspicuous upper midrib, and conspicuously nerved, subindurate leaf sheath.

RUTACEAE

RAUIA

Rauia subtruncata Steyermark, sp. nov. TYPE: Venezuela. Bolívar: 20–25 km SW of Manteco, on road to San Pedro de las Dos Bocas, 7°10′N, 62°55′W, 200 m, 1–3 Aug. 1978, *Ronald Liesner & Angel González 5991* (holotype, VEN; isotype, MO). Figure 3.

Arbor 6-metralis, foliorum laminis elliptico-ovatis vel oblongo-ellipticis abrupte longiacuminatis 10.5–23 cm longis 4–9.5 cm latis, nervis lateralibus utroque latere 9–10 subtus elevatis supra sulcatis, venulis tertiariis supra inconspicuis; calyce campanulato 4.5 mm longo summo 3 mm lato basi 1.8 mm lato truncato; corolla alba cylindrica 18 mm longa, tubo 8–9 mm longo basi 2 mm lato extus dense brevistrigilloso sub anthesi sine glandulis negris, lobis 7–8 mm longis 1–1.5 mm latis; staminodiis tribus subulatis 9 mm longis; antherae fertilis connectivo late lanceolato attenuato 1.5 mm longo 0.4 mm lato minute pulverulento.

Tree 6 m tall; stems glabrous or with sparingly evanescent, minutely appressed, scattered pubescence. Leaves alternate or rarely opposite, 1-foliolate; leaf blades elliptic-ovate or oblong-elliptic, abruptly long-acuminate, the acumen 2 cm long, acute at base with 2 thickened glands at junction with petiole, 10.5–23 cm long, 4–9.5 cm wide, glabrous both sides; lateral nerves 9–10 each side, ascending at a 45° angle, elevated below, inconspicuous and slightly impressed above; tertiary venation conspicuous below, reticulate and slightly elevated, above slightly less manifest. Inflorescences terminal, corymbose-paniculate, many-flowered, 4–7.5 cm long, 4–8.5 cm wide, long pedunculate, with

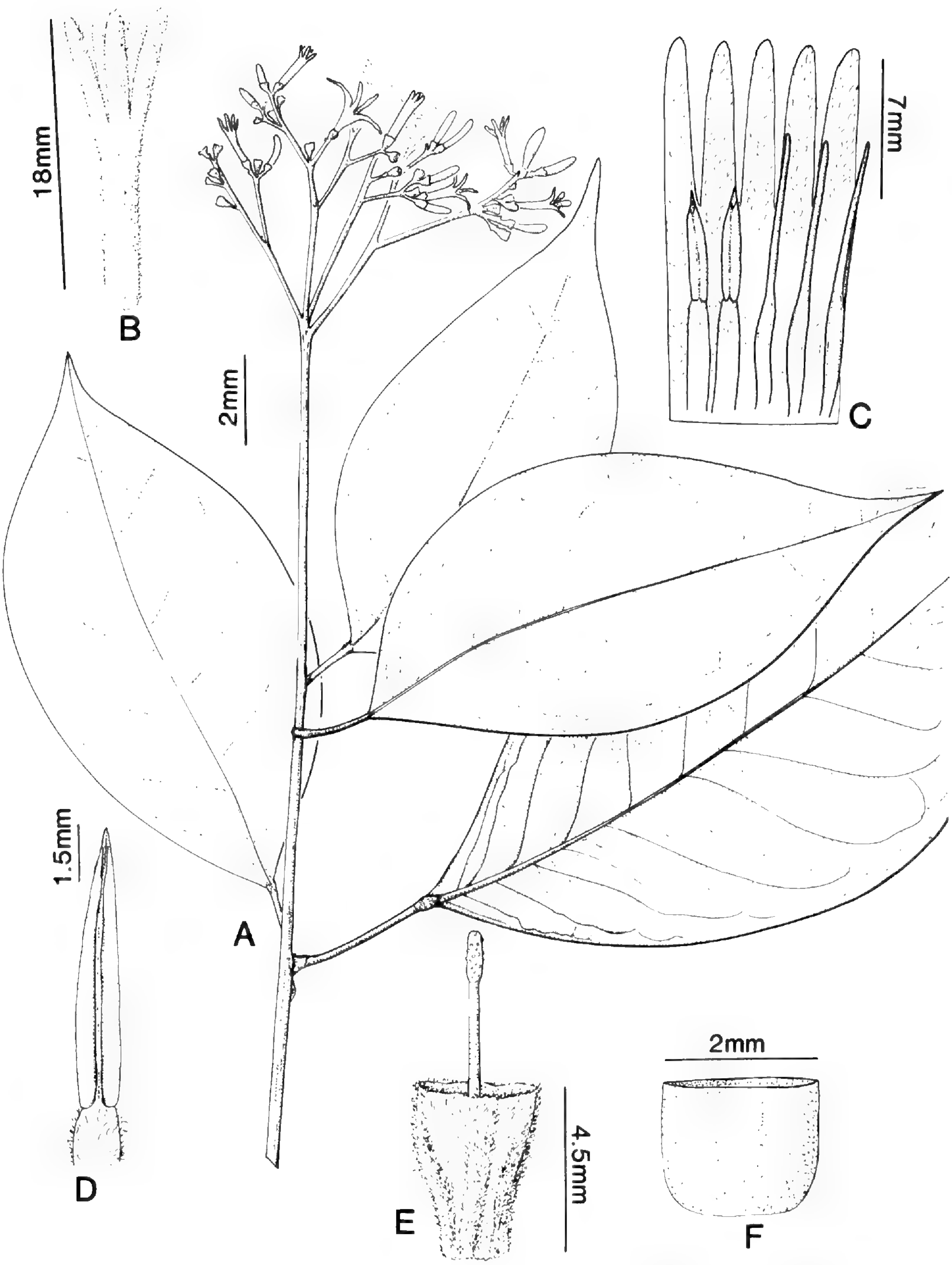

FIGURE 3. Rauia subtruncata.—*A. Habit of flowering branch.—B. Corolla, before anthesis.—C. Interior of corolla, showing two fertile anthers and three staminodia.—D. Anther with upper portion of filament.—E. Calyx.—F. Disk.*

2–4 unequal, main dichasially branched axes; each dichasium cymosely flowered; peduncle elongated, 7–11 cm long, 2–3 mm diam., glabrous to shortly appressed-pubescent below the axes of the inflorescence; each main axis 1.5–4 cm long in unbranched portion, 1–1.5 mm wide, longitudinally striate, densely appressed-pubescent with buff hairs; calyx thick textured, obtusely 5-angulate, campanulate, 4–5 mm long, 3 mm wide at summit where subtruncate or barely subundulately toothed, constricted 1.5 mm above base, 1.8 mm wide at base, densely appressed without with congested buff pubescence, glabrous within, with scattered black, resinous glands; corolla white, cylindric, 18 mm long, 2 mm wide at base, densely short-strigillose without, in anthesis lacking black resinous glands, the tube 8–9 mm long, densely pilosulous within for 4 mm between the filaments and staminodia, glabrous in the basal 2 mm; lobes 5, thickish, linear-ligulate, subobtuse, 7–8 mm long, 1–1.5 mm wide, minutely pilosulous within; fertile anthers 2, curved, 4.8 mm long, 0.6–0.7 mm wide including the connective; connective lanceolate, attenuate, 1.5 mm long, 0.4 mm wide; filaments united to the tube 4 mm above its base, free for 1–2 mm, glabrous in lowest 3 mm, densely pubescent in upper half; staminodia 3, subulate, free for 9 mm, attached to tube 6 mm from base, pilosulous but glabrous in uppermost 4 mm, glabrous ventrally, pilosulous dorsally; disk cupular, 1.8 mm long, 2 mm wide, slightly undulate at the truncate summit; ovary 1.2 mm high, 1.5 mm broad, glabrous.

This species differs from *Rauia resinosa* Nees & C. Martius in having a longer, broader calyx which is subtruncate at the summit, longer and broader corolla lobes and corolla tube, three instead of five staminodia, lance-attenuate prolonged connective of the fertile anthers, proportionately broader leaf blades, less elevated lateral nerves on the lower surface and less sulcate on the upper surface, and more evident tertiary venation of the upper surface.

RAVENIOPSIS

Raveniopsis liesneri Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Río Negro, Cerro de la Neblina, Camp 4, 15 km NNE of Pico Phelps, N branch of river in canyon, 0°51′N, 65°57′W, 780 m, 15–18 Nov. 1984, *Ronald Liesner 16605* (holotype, MO; isotype, VEN). Figure 4.

Caules stellato-pubescentes, foliis trifoliatis; calycis lobis ovato-oblongis apice late rotundatis 2–3 mm longis 1–1.5 mm latis stellato-pubescentibus; corolla cylindrico-infundibuliformi 17–19 mm longa summo 4.5–5 mm lata basi 2–2.5 mm lata stellato-pubescenti; staminodiis tribus subulatis 1.8 mm longis 0.1 mm latis inaequalibus; stylo 8–12 mm longo glabro.

Shrub 1 m tall, stems stellate-pubescent with the branched stellate hairs closely aggregated in the lower part of the main axis. Leaves trifoliate, the terminal leaflet the largest, symmetric, subacute to obtuse at apex, 2.5–6.5(–8) cm long, 1.2–2.5 cm wide, glabrous above except for the stellate midrib and lateral nerves, densely white stellate beneath, the pubescence concealing the surface; lateral nerves sulcate above, slightly elevated below, 7–9 each side, ending at the margins; petiolule of terminal leaflet 5–15 mm long, stellate; lateral leaflets mainly asymmetric, oblique at base, oblanceolate to oblong, subacute to obtuse at apex, 2.5–5.5 cm long, 1–2 cm wide, the lower side rounded at base, the upper side acute; lateral nerves 5–7 each side; petiolule of lateral leaflets 1–3 mm long or subsessile; petiole 0.5–3 cm long, densely stellate-pubescent. Inflorescence axillary or terminal, dichasial, the axes unilaterally racemose, 1.5–6 cm long, densely stellate-pubescent; peduncle 4–4.5 cm long, densely stellate-pubescent; terminal flower present or absent at apex of peduncle. Calyx 5 mm long, the tube 3 mm long, 1.5 mm wide at base, 3.5 mm wide at junction with calyx lobes; calyx lobes 5, slightly unequal, ovate-oblong, broadly rounded at apex, 2–3 mm long, 1–1.5 mm wide, the larger lobe 1.5 mm wide, the others 1 mm wide. Corolla straight or nearly so, or very slightly curved in bud, cylindric-infundibuliform, 17–19 mm long, 2–2.5 mm wide at base, 4.5–5 mm wide at summit, stellate-pubescent externally, within minutely pubescent in lines in the lower ⅓ below the staminodia; longer corolla lobes ovate-oblong, rounded at apex, 3.5–4 mm long, 2–2.5 mm wide; 3 shorter lobes ovate-oblong, rounded at apex, 2 mm long, 1.2 mm wide; 3 staminodia subulate, 1.8 mm long, 0.1 mm wide, one of them shorter than the other two. Fertile anther narrowly oblong,

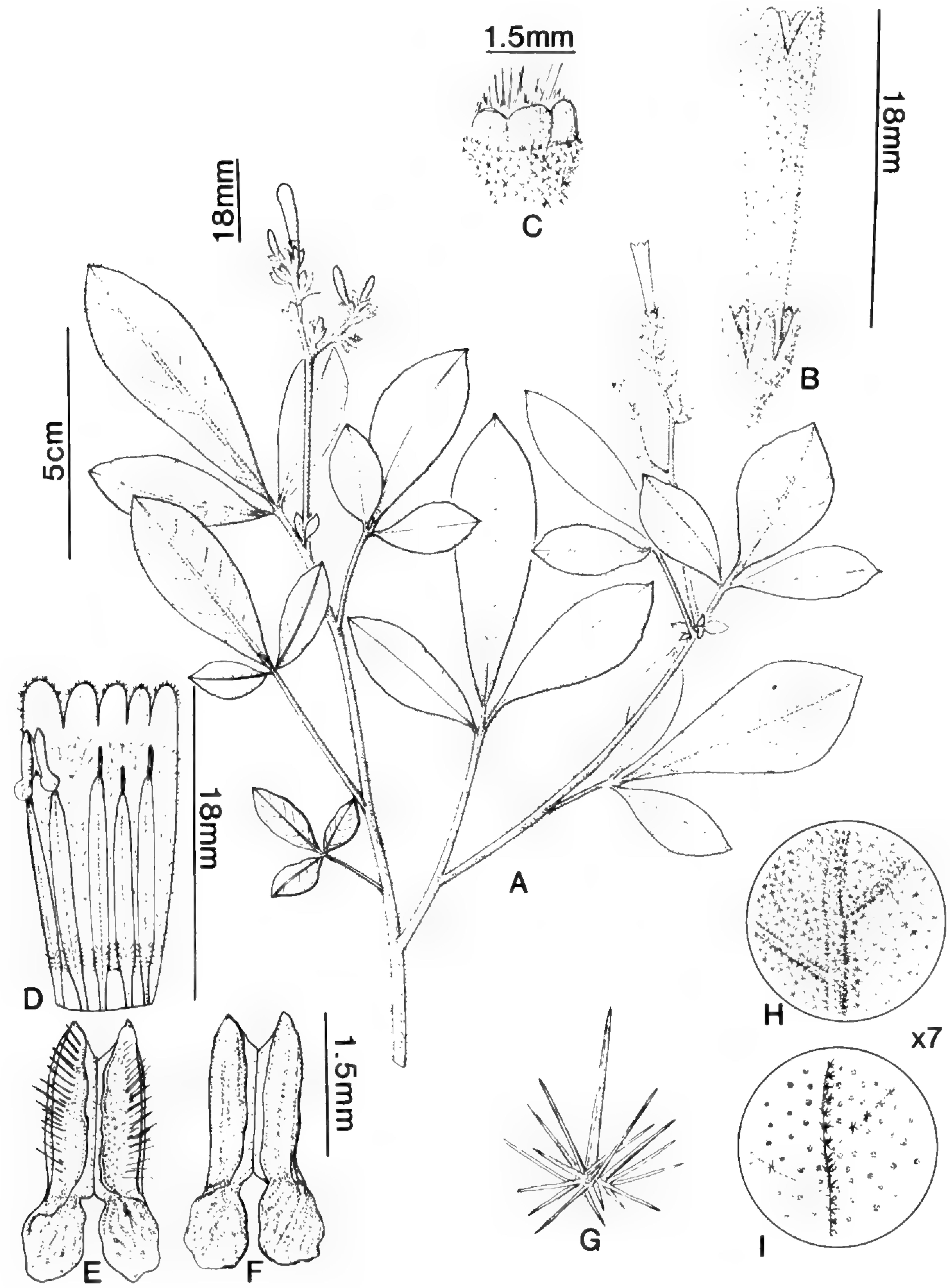

FIGURE 4. Raveniopsis liesneri.—*A. Habit of flowering branch.—B. Flower.—C. Disk with upper part of ovary and receptacle.—D. Interior of corolla, showing two fertile stamens and three staminodia.—E. Fertile stamens, abaxial view.—F. Fertile stamens, adaxial view.—G. Stellate hair from stem.—H. Enlarged section of lower portion of leaf surface.—I. Enlarged section of upper portion of leaf surface.*

minutely mucronate at apex, 2.5 mm long, glabrous; basal appendages suborbicular, rounded, venose, 1 mm long, 1 mm wide. Style 8–12 mm long, glabrous; ovary pilose; disk cupular, 0.75 mm high, 1.5 mm diam.

This species is related to *Raveniopsis stelligera* Cowan of Cerro Duida and Yutajé. It differs in the small corollas, more narrowly oblong, rounded calyx lobes, shorter staminodia, and shorter style. Five species and one variety of the genus are now recorded from Cerro de la Neblina.

LINACEAE

OCHTHOCOSMUS

Ochthocosmus micranthus Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Ayavaparú, 10 km southwest of Wadacapiap, 5°18′N, 60°58′W, 1,100 m, 13 Nov. 1986, *Lionel Hernández 348* (holotype, MO; isotype, VEN). Figure 5.

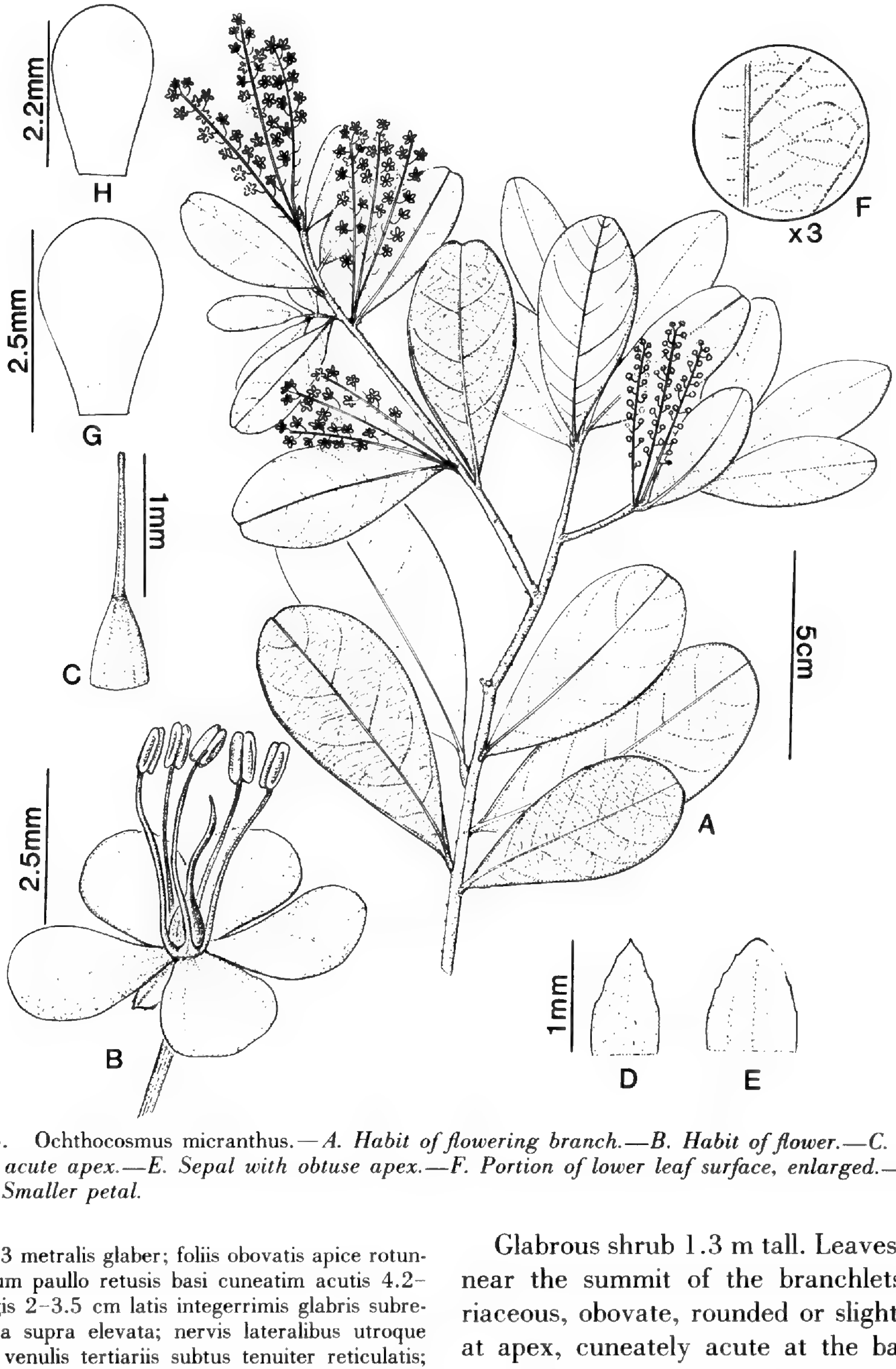

FIGURE 5. Ochthocosmus micranthus.—*A. Habit of flowering branch.—B. Habit of flower.—C. Pistil.—D. Sepal with acute apex.—E. Sepal with obtuse apex.—F. Portion of lower leaf surface, enlarged.—G. Larger petal.—H. Smaller petal.*

Frutex 1.3 metralis glaber; foliis obovatis apice rotundatis interdum paullo retusis basi cuneatim acutis 4.2–7.5 cm longis 2–3.5 cm latis integerrimis glabris subrevolutis; costa supra elevata; nervis lateralibus utroque latere 4–8; venulis tertiariis subtus tenuiter reticulatis; petiolis 2–5 mm longis; inflorescentia fasciculatis axillaribus racemosis 3.5–5.5 cm longis 7–9 mm latis; pedicellis filiformibus 3–3.5 mm longis; bracteis sub pedicellis lanceolato-subulatis vel lanceolatis 1 mm longis apice appendice fuscata praeditis deciduis; floribus parvis, sepalis quinque parum inaequalibus oblongo-ovatis apice subobtusis raro subacutis 1–1.5 mm longis 0.7 mm latis plerumque integris praeter aliquot apicem versus 1–2 prominentibus; petalis leviter inaequalibus majoribus late obovatis rotundatis 2.5 × 1.7 mm, minoribus oblongo-obovatis rotundatis 2.2 × 1.3 mm; antheris oblongis 0.8 mm longis, filamentis 3 mm longis; ovario ovoideo-conico 0.7 × 0.7 mm, stylo 1 mm longo.

Glabrous shrub 1.3 m tall. Leaves crowded near the summit of the branchlets, subcoriaceous, obovate, rounded or slightly retuse at apex, cuneately acute at the base, 4.2–7.5 cm long, 2–3.5 cm wide, entire, glabrous, subrevolute; midnerve elevated above and below; lateral nerves 4–8 each side, arcuate-ascending at a 30–45° angle, anastomosing near the margins, impressed above, slightly elevated below; tertiary venation finely reticulate and elevated below, impressed above. Inflorescence fasciculate, axillary in the upper leaf axils with usually 3 peduncles, racemose, 3.5–5.5 cm long, 7–9 mm wide; pedicels filiform, 3–3.5 mm long. Bracts subtending pedicels lance-subulate or lanceolate, 1 mm long with a darkened attenuate apical projection. Flowers small for the genus. Sepals 5, slightly unequal, hyaline, oblong-ovate, subobtuse or one of them sometimes acute or subacute at the apex, 1–1.5 mm long, 0.7 mm wide, mainly entire, but with one or two of them with minute projections toward the apex. Petals slightly unequal, the larger broadly obovate and rounded at apex, 2.5 × 1.7 mm, the smaller ones oblong-obovate, rounded, 2.2 × 1.3 mm. Stamens 5; anthers oblong, 0.8 × 0.3 mm; filaments 3 mm long. Ovary ovoid-conic, 0.7 × 0.7 mm, style erect for 1 mm, then spreading upwardly 0.5–0.8 mm long. Fruit not seen.

Paratype. VENEZUELA. BOLÍVAR: same locality as type, 15 Nov. 1986, *Hernández 359* (VEN).

This species is distinguished from the other known members of the genus by its smaller petals and sepals. The entire leaves with non-thickened, eglandular margins of the sepals are additional distinguishing characters. In the key to species previously published (Steyermark & Luteyn, 1980), *Ochthocosmus micranthus* would fall into the group including *O. multiflorus* and *O. longipedicellatus*.

LITERATURE CITED

STEYERMARK, J. & J. LUTEYN. 1980. Revision of the genus *Ochthocosmus* (Linaceae). Brittonia 32(2): 128–143.

AQUIFOLIACEAE

Since the treatment of *Ilex* by Edwin (1965) for *Botany of the Guayana Highland*, in which 55 taxa were treated, including 22 new species and seven varieties, many additional collections resulting from expeditions into this region have accumulated. A study of these new collections of *Ilex* have yielded a large number of new taxa. For the examination of types and other critical material, the author wishes to thank the curators of the herbaria of F, NY, and US for their courtesy in making these loans and gifts available.

One of the difficulties in studying the genus has been that a fair number of new taxa are based on either fruiting material or on staminate or pistillate specimens only. Furthermore, some of the descriptions by Edwin included references to so-called black pubescence on various parts of the plant. However, a careful examination of the type material of these "pubescent" specimens reveals that the so-called black trichomes are only artifacts consisting of fungal hyphal threads. This has been verified by Dr. Richard Harris of the New York Botanical Garden (pers. comm.). Added to the difficulties are differences in the position and type of inflorescence of the staminate and pistillate plants, the latter often having axillary solitary inflorescences only, whereas the staminate plants may bear either axillary fasciculate, or axillary solitary and lateral inflorescences. The terminology used in the present description for the inflorescences is that employed and illustrated by Edwin (1965, fig. 26). Another difficulty in the examination of herbarium material is the interpretation of the punctate or epunctate lower leaf surface. It is possible to misinterpret a leaf surface that appears dotted with dark punctations only to discover that such dots represent merely artifacts of lichens or fungi. This difficulty is well exemplified in the interpretation by Loesener (1901) of the lower surface of the leaf of *Ilex vacciniifolia* Klotzsch (p. 22, loc. cit.). In this case, Loesener intepreted the black dots as fungi, but an examination of conspecific material collected at the type locality and elsewhere indicates that the dots represent actual punctations.

ILEX

Ilex abscondita Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, Camp 7, south slopes of Cañon Grande, 0°55′N, 66°0′W, 1,900 m, 30 Nov. 1984, *Croat 59478* (holotype, MO; isotypes, NY, VEN).

Frutex vel arbor 3–5 metralis; foliis late obovatis apice rotundatis basi cuneatis 5.5–9 cm longis 4–6 cm latis integerrimis glabris subtus punctatis, costa leviter sulcata intus minute puberulenti; nervis lateralibus utroque latere 5–7 supra sulcatis intus minute puberulentibus; venatione tertiaria subtus obsoleta; petiolis 7–13 mm longis glabris; inflorescentiis masculinis axillaribus lateralibusque, foemineis axillaribus solitariis; pedunculis minute puberulis, fructiferis 6.5–11 mm longis; baccis immaturis 7–9 mm longis 6 mm diam.

Shrub or tree 3–5 m tall. Leaves subcoriaceous, broadly obovate, broadly rounded at apex, cuneate at the base, 5.5–9 cm long, 4–6 cm wide, entire, glabrous, revolute, entire, glabrous, dark punctate beneath; midnerve shallowly sulcate above with a minute puberulence within; lateral nerves 5–7 on each side, sulcate above with a minute puberulence within. Petioles 7–13 mm long, glabrous. Staminate inflorescence axillary and lateral, 3-flowered. Pistillate inflorescence axillary, solitary. Peduncle and pedicels minutely puberulent, the fruiting peduncle 6.5–11 mm long. Immature fruit ovoid, 7–9 mm long, 6 mm diam.

Paratype. VENEZUELA. Same locality and date as type, *Croat 59500* (MO, VEN).

This species differs from *Ilex sipapoana* Edwin in the broader obovate leaves rounded and broadest at summit and in the absence of tertiary venation on the lower surface. The new taxon differs from *I. magnifructa* Edwin in the longer petioles, sulcate puberulent interior of the lateral nerves of the upper leaf surface, and the shorter fruiting pedicels.

Ilex acutidenticulata Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Atabapo, Cerro Marahuaca, below Salto Los Monos on tributary of headwaters of Río Iguapo, 3°35′N, 65°23′W, 1,500–1,650 m, 12 Mar. 1985, *Ronald Liesner 18595* (holotype, MO; isotype, VEN). Figure 6B.

Arbor 3–8-metralis; foliis lanceolato-ellipticis vel elliptico-oblanceolatis apice acutis vel abrupte acuminatis basi acutis 5–8.5 cm longis 1.5–3 cm latis, marginibus superioribus 1–3-denticulatis, glabris subtus minute punctatis, nervis lateralibus utroque latere 5–7 paullo adscendentibus; petiolis 8–10 mm longis glabris; infructescentiis axillaribus lateralibusque solitariis fasciculatisque; pedicellis 3–5 mm longis; baccis globosis 5 × 5 mm; pyrenis dorsaliter unicanaliculatis.

Tree 3–8 m tall. Leaves lance-elliptic or elliptic-oblanceolate, acute to abruptly acuminate at apex, acutely narrowed at base, 5–8.5 cm long, 1.5–3 cm wide, upper ¼–⅓ part of the margins with 1–3 slender, acute teeth, glabrous, minutely punctate beneath; lateral nerves 5–7 each side, slightly ascending at 25–30° angle, slightly elevated below; tertiary venation slightly manifest below. Infructescence axillary and lateral, solitary and fasciculate, fruiting pedicels 3–5 mm long, minutely puberulent. Fruit globose, 5 × 5 mm. Immature pyrenes dorsally 1-canaliculate.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro de la Neblina, Camp 7, south slopes of Cañon Grande, along river below camp, 0°55′N, 66°0′W, 1,800 m, 29 Nov. 1984, *Croat 59450* (MO, VEN).

From *Ilex microdonta* Reissek of southern Brazil the new taxon differs in having fewer and smaller teeth confined to the upper leaf margins, punctate lower leaf surface, less ascending lateral nerves, and shorter pedicels. It is distinguished from *I. karuaiana* Edwin by the fewer, sharper teeth, less prominently reticulate upper leaf surface, and shorter pedicels.

Ilex altiplana Steyermark, sp. nov. TYPE: Venezuela. Bolívar: between San Ignacio de Yuruani and San Francisco de Yuruani, bordering small stream between km 251.5 and 253 south of El Dorado on road to Santa Elena, 1,200 m, 4 Jan. 1975, *Julian A. Steyermark 111402* (holotype, VEN).

Arbor 3–20-metralis, ramulis superne minute puberulis glabrescentibus; foliorum laminis elliptico-ovatis vel oblongo-ellipticis apice abrupte acutis vel acuminatis utrinque glabris, costa media subtus interdum minute sparsimque puberulenti excepta; petiolis 3–7 mm longis minute puberulentibus vel glabris; inflorescentia foeminea solitaria axillari lateralique, pedicellis 4.5–9 mm longis subanthesi minute puberulis sub fructu glabris; stigmate elongato late tholiformi 1 mm longo; fructu subgloboso 4–5 × 4–5 mm, pyrenes quattuor dorsaliter unisulcatis.

Tree 3–20 m tall, upper part of stems minutely pubescent or glabrescent in age. Leaves subcoriaceous or firmly membranous, ovate- or oblong-elliptic, abruptly acute or acuminate at apex, acute at base, 4–6.5 cm long, 2–2.5 cm wide, epunctate, glabrous both sides except minutely and sparsely puberulent on the lower midrib of younger leaves; lateral nerves 4–8 on each side, inconspicuous, slightly ascending, not sulcate on upper side; midrib sulcate above, slightly elevated below. Petioles 3–7 mm long, minutely puberulent or glabrous. Pistillate inflorescence solitary, axillary and lateral, 1–4-flowered; pedicels 4.5–9 mm long, minutely puberulent in anthesis, glabrous in fruit. Stigma broadly dome-shaped, elongated, conspicuous, 1 mm long. Fruit subglobose, 4–5 × 4–5 mm, glabrous. Pyrenes 4, brown, trigonous, 3.5 mm long, 2 mm wide, dorsally unisulcate.

Paratypes. VENEZUELA. BOLÍVAR: Gran Sabana, 152 km south of El Dorado, 1,350–1,400 m, 20 Dec. 1970, *J. Steyermark, G. C. K. & E. Dunsterville 104090* (VEN); km 119 south of El Dorado, 1,030 m, *Steyermark et al. 93037* (VEN).

This species shows a close affinity to *I. macarenensis* Cuatrec. of Colombia, but differs in the larger stigma and shorter petioles. Additionally, the leaf apex is shortly and obtusely acute to acuminate rather than narrowly cuspidate, the combined pistillate peduncle and pedicel is longer, and the lateral nerves are not prominently sulcate as in *I. macarenensis*.

Ilex attenuata Steyermark, sp. nov. TYPE: Brazil. Amazonas: Sierra Pirapucú, Comissão de Limites BR-1, 1,250 m, 24 Jan. 1966, *Nilo T. Silva & Umbelino Brazão 60873* (holotype, MO; isotypes, INPA, G, VEN, NY).

Arbor, 12-metralis, foliis oblongo-ellipticis vel late elliptico-lanceolatis apice longiattenuatis obtuse acuminatis, acumine 1–2 cm longo, 3–5 mm lato, basi obtusis vel subacutis 7–13.7 cm longis 2.5–4.7 cm latis, utroque margine remote 7–10-crenulatis glabris subtus punctatis; nervis lateralibus utroque latere 6–7 superne impressis inconspicuis; nervulis tertiariis subtus reticulatis elevatis; petiolis 7–14 mm longis glabris; infructescentiis solitariis axillaribus lateralibusque; pedunculis pedicellisque minute puberulis; bracteis sub pedicellis lanceolatis acuminatis usque 0.5–1 mm longis; florum foemineorum calyce 2–3 mm lato dense puberulo, lobis late rotundatis vel subtruncatis 1.5–2 mm latis dense puberulis ciliatisque tubo longiore; bacca globoso 5–6 × 5–6 mm; pyrenes trigonis 4 mm longis dorsaliter 3–4-costatis.

Tree 12 m tall. Leaves subcoriaceous, oblong-elliptic or broadly elliptic-lanceolate, narrowed to a long-attenuate, obtusely acuminate apex, the acumen 1–2 cm long, 3–5 mm wide, obtuse to subacute at base, 7–13.5 cm long, 2.5–4.7 cm wide, each margin with 7–10 crenulations 3–8 mm distant, glabrous, dark punctate beneath; midnerve sulcate above; lateral nerves 6–7 each side, inconspicuously impressed above, irregularly anastomosing; tertiary venation reticulately elevated below. Petiole 7–14 mm long, glabrous. Infructescence near apex of branchlets, solitary, axillary and terminal. Pistillate flowers either on simple pedicels 6–7 mm long, or, if these in 3s at the end of a peduncle, 3–4 mm long. Peduncle and pedicels minutely puberulous, the puberulence in vertical lines. Bracts subtending pedicels lanceolate, acuminate, 0.5–1 mm long. Pistillate calyx 2–3 mm wide, densely puberulous, the lobes broadly rounded or subtruncate, 1.5–2 mm wide, densely puberulous and ciliate, longer than the tube. Fruit globose, 5–6 × 5–6 mm; pyrenes trigonous, 4 mm long, 3–4-dorsally costate.

In leaf shape this taxon resembles *Ilex symplociformis* Loes. of Brazil, but is distinguished by having a solitary, axillary and lateral pistillate inflorescence, longer peduncles and pedicels, the latter subtended by acuminate bracts, leaf blades with fewer and more distant crenulations, and suborbicular, rounded calyx lobes.

Ilex brevipedicellata Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Atabapo, Cerro Marahuaca, "Sima Camp," south-central portion, forested slopes along eastern branch on Caño Negro, 3°43′N, 65°31′W, 1,140 m, 21–22, 24 Feb. 1985, *Julian A. Steyermark & Bruce Holst 130531* (holotype, MO; isotype, VEN). Figure 6D.

Arbor 15-metralis, foliis oblongo-obovatis apice rotundatis saepe emarginatis basi acutis 4–7 cm longis 2.5–3.5 cm latis integerrimis glabris subtus valde negro-punctatis; nervis lateralibus utroque latere 5–6; nervulis tertiariis obsoletis; petiolis 4–8 mm longis glabris; inflorescentiis solitariis axillaribus lateralibusque, pedicellis 1–1.5 mm longis glabris; calyce sub fructu 2.5 mm lato, lobis suborbicularibus 1.5 mm latis minute ciliolatis.

Tree 15 m tall. Leaves firmly membranous or chartaceous, revolute, oblong-obovate, rounded and often emarginate at apex, acute at base, 4–7 cm long, 2.5–3.5 cm wide, entire, glabrous, strongly black punctate beneath; midnerve sulcate above; lateral nerves 5–6 each side, faint beneath; tertiary venation obsolete. Inflorescence solitary, axillary and lateral. Pedicels 1–1.5 mm long, 0.8 mm wide, glabrous. Calyx lobes in fruit suborbicular, rounded, 1.5 mm wide, 0.5 mm long, minutely ciliolate; calyx tube puberulent to glabrescent.

This species differs from *Ilex sessilifructa* Edwin of Cerro de la Neblina in the shorter pedicels and more manifest lateral nerves on both leaf surfaces. It differs from *I. culmenicola* Steyerm. of Cerro Duida in the very short pedicels and rounded leaf apex and from *I. gleasoniana* Steyerm. of Cerro Duida in the larger, nonmucronate leaf apex, shorter pedicels, more abundantly punctate leaves, and the more conspicuous lateral nerves on the lower leaf surface.

Ilex cardonae Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: orillas del Río Castanho, afluente del Padauiri que cae del Río Negro y éste último al Amazonas, 100–140 m, 16–24 Feb. 1946, *Felix Cardona 1480* (holotype, VEN).

Arbor, ramulis glabris; foliis oblongo-ellipticis apice acutis basi acutis 11–13 cm longis 3.5–4.5 cm latis obscure repando-crenulatis epunctatis glabris; petiolis 6–8 mm longis glabris; inflorescentia masculina fasciculata axillari lateralique; pedunculis 3–5-floris 3–4 mm longis puberulis; pedicellis 1–2 mm longis puberulis; floribus 4-meris, calycis lobis suborbicularibus rotundatis extus puberulis.

Tree with glabrous stems. Leaves submembranous or chartaceous, oblong-elliptic, acute at apex and base, 11–13 cm long, 3.5–4.5 cm wide, obscurely repand-crenulate, epunctate, glabrous; main lateral nerves 7–8 each side, ascending at an angle of 45–60°, impressed above, slightly elevated below; upper midrib shallowly sulcate, lower midrib elevated; tertiary venation grossly reticulate below. Petioles 6–8 mm long, glabrous. Inflorescence staminate, fasciculate, axillary and lateral. Peduncles 3–5-flowered, 3–4 mm long, puberulous. Pedicels 1–2 mm long, puberulous. Flowers 4-merous. Calyx lobes suborbicular, rounded, puberulous without.

This species is related to *I. tateana* Steyerm. of Cerro Duida and Marahuaca, but differs in the thinner, smaller, epunctate leaf blades, puberulous peduncles, pedicels, and calyx lobes.

Ilex ciliolata Steyermark, sp. nov. TYPE: Venezuela. Bolívar: 0.4 km north of El Pauji on trail to Uaiparú, 4°30'N, 61°35'W, 800–900 m, 4 Nov. 1985, *Ronald Liesner 19479* (holotype, MO; isotype, VEN).

Arbor 5-metralis, ramulis superioribus juvenilibusque minute puberulis; foliis elliptico-ovatis vel oblongo-ovatis apice acutis obtusis vel rotundatis basi acutis vel subacutis 4.5–6.5 cm longis 2–3.3 cm latis integerrimis subtus obscure minuteque pallide punctatis, subtus costa nervis lateralibusque minute puberulis superne costa sulcata et prope margines puberulis, marginibus revolutis ciliolatis aliter glabris; nervis lateralibus utroque latere plerumque 5; petiolis 4–7 mm longis minute puberulis glabrescentibus; inflorescentiis masculinis solitariis axillaribus lateralibus; pedunculo 2.5–3 mm longo; pedicellis 2.5–6 mm longis; pedunculis pedicellisque minute puberulis; calycis lobis suborbicularibus 1 mm latis; fructu globoso 4 × 4 mm.

Tree 5 m tall; young stems and uppermost branches minutely puberulent. Leaves elliptic-ovate to oblong-ovate, acute, obtuse, or rounded at the apex, acute to subacute at base, 4.5–6.5 cm long, 2–3.3 cm wide, entire, obscurely and minutely pale punctate beneath, the lower midrib and lateral nerves minutely puberulent, the midrib above and marginal upper surface puberulent, the margins revolute, minutely ciliolate; lateral nerves mainly 5 each side. Staminate inflorescence solitary, axillary and lateral, cymosely flowered with a peduncle 2.5–3 mm long or epunctate, pedicels 2.5–6 mm long; peduncle and pedicels minutely puberulent. Calyx lobes suborbicular, 0.5 mm long, 1 mm wide, erose-ciliolate; petals 3 mm long, 1 mm wide. Fruit globose, 4 × 4 mm.

This taxon is characterized by the abundance of minute pubescence near the margins of the upper surface of the leaf blades, on the lower midrib and lateral nerves, peduncles, pedicels, as well as the upper portions of the stems. It is related to *Ilex sulcata* Edwin and *I. steyermarkii* Edwin of higher altitudes in Estado Bolívar, which differ in their glabrous vegetative parts. From *Ilex steyermarkii* it differs further in having both axillary and lateral inflorescences. In his description of *I. steyermarkii*, Edwin (1965) mistook small, black hairlike fungal structures occurring upon the leaf margins as true trichomes. Descriptions of such artifacts are frequently encountered in a number of species described in the above mentioned publication.

Ilex davidsei Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, lower part of the Río Baria, 1°27′–1°10′N, 66°32′–66°25′W, inundated forest along river, 80 m, 22–23 July 1984, *Gerrit Davidse 27719* (holotype, MO; isotype, VEN).

Arbor 8-metralis, ramulis juvenilibus minute puberulentibus glabrescentibus; foliis elliptico-oblongis vel anguste ellipticis apice in acumen obtusum 5–12 mm longum 3–5 mm latum productis basi acutis vel subacutis, 4–7.5 cm longis 1.5–3 cm latis, marginibus 2–4 remote crenulatis glabris subtus punctatis; nervis lateralibus utroque latere 5–6; nervulis tertiariis subtus vix manifestis; petiolis 5–8 mm longis glabris; inflorescentiis masculinis solitariis axillaribus racemose denseque ca. 25-floris 1.3–1.7 cm longis 7 mm latis, rhachidi minute puberulenti; floribus 4-meris, pedicellis 0.5–1 mm longis minute puberulentibus; calycis lobis suborbicularibus rotundatis 1 mm latis valde ciliolatis aliter glabris; petalis oblongo-obovatis 1.5 mm longis; inflorescentiis foemineis solitariis axillaribus densifloris racemosis 1.2–1.5 cm longis 0.6–0.7 mm latis; pedicellis 1 mm longis puberulentibus; calycis lobis suborbicularibus rotundatis ciliolatis 1.2 mm latis ciliolatis.

Tree 8 m tall. Young stems minutely puberulent, glabrescent. Leaves elliptic-oblong or narrowly elliptic, the apex prolonged into an obtuse acumen 5–12 mm long, 3–5 mm wide, acute to subacute at base, 4–7.5 cm long, 1.5–3 cm wide, the margins with 2–4 remote crenulations, glabrous, punctate below; lateral nerves 5–6 each side, slightly manifest below; tertiary venation scarcely apparent below, obsolete above. Petioles 5–8 mm long, glabrous. Staminate inflorescences solitary, axillary, racemose, densely ca. 25-flowered, 1.3–1.7 cm long, 7 mm wide, rachis minutely puberulent; flowers 4-merous; pedicels 0.5–1 mm long, minutely puberulent. Calyx tube 1.5 mm wide, glabrous; calyx lobes suborbicular, rounded, 1 mm wide, conspicuously ciliolate, glabrous elsewhere. Petals oblong-obovate, broadly rounded at apex, 1.5 mm long, 1 mm wide, ciliolate on upper margins. Pistillate inflorescence solitary, axillary, elongated, simply racemose, 1.2–1.5 cm long, 0.6–0.7 mm wide; pedicels 1 mm long, puberulent. Rachis puberulent. Calyx 2.5 mm wide, lobes suborbicular, rounded, 1.2 mm wide, ciliolate.

Paratype. VENEZUELA. BOLÍVAR: Río Pacimoni between Caño Arapacua and Caño Boridahari, 110 m, *Maguire & Wurdack 34905* (NY).

This taxon is characterized by the short, densely flowered, racemose, solitary, axillary inflorescence and leaves with a pronounced, elongated, obtuse acumen and remotely few crenate margins. It shows affinities with members of section 3 (*Thyrsiflorae*), section 4 (*Symplociformes*), and section 5 (*Brachythyrsae*) of Loesener (1901). From *Ilex conocarpa* Reissek and *I. symplociformis* Reissek it differs in the more remotely, fewer-crenate leaf margins, smaller leaves with a more pronounced elongated apex, and a shorter, narrower inflorescence. It is distinguished from *I. casiquiarensis* Loes. by the smaller leaves with fewer lateral nerves and by more congested inflorescences with shorter staminate lateral axes and shorter pedicels.

Ilex glabella Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro de la Neblina, Camp 4, 15 km NNE of Pico Phelps, north branch of river in canyon, 0°51′N, 65°57′W, 780 m, 15–18 Mar. 1984, *Ronald Liesner 16688* (holotype, MO; isotype, VEN).

Arbor, ramulis glabris; foliis oblongo-lanceolatis apice obtuse vel acute subacuminatis basi rotundatis 10–15 cm longis 4.5–6 cm latis integerrimis glabris subtus punctatis; nervis lateralibus principalibus utroque latere 11–13; venulis tertiariis subtus manifeste reticulatis; petiolis 10–11 mm longis glabris; inflorescentiis masculinis subterminalibus vel terminalibus axillaribus fasciculatisque, pedunculis quattuor 5–8 mm longis unusquisque 5-floris umbellatis; pedicellis 3–4.5 mm longis; floribus 4-meris, calyce glabri 2.5 mm lato, lobis suborbiculari-ovatis apice subacutis vel apiculatis 0.8 × 0.8 mm.

Tree with glabrous branchlets. Leaves subcoriaceous, oblong-lanceolate, obtusely to acutely subacuminate at apex, rounded at base, 10–15 cm long, 4.5–6 cm wide, entire, glabrous, subrevolute; midnerve shallowly sulcate above; principal lateral nerves 11–13 on each side, slightly ascending at 10–20° angle, impressed above, somewhat manifest beneath; tertiary venation manifestly reticulate below. Petiole 10–11 mm long, glabrous. Staminate inflorescence subterminal in the uppermost leaf axils or terminal, axillary, fasciculate with 4 peduncles 5–8 mm long, each bearing 5 umbellately arranged pedicellate flowers; pedicels 3–4.5 mm long, glabrous. Flowers 4-merous; calyx 2.5 mm wide, glabrous; lobes suborbicular-ovate, narrowed to a subacute or apiculate apex, 0.8 × 0.8 mm, glabrous. Petals ligulate-oblong, rounded at apex, 1.5 mm long, 1 mm wide.

In Loesener's monograph (1901) this species would fall in subsection A, *Punctatae* Loes., section 9 *Micranthae* Loes. of series *Paltoria* (Ruiz & Pavon) Maxim. From *Ilex tarapotina* Loes. of Peru it differs in the glabrous stems and inflorescences, shorter peduncles with longer pedicels, glabrous calyx, and larger leaf blades with rounded bases. *Ilex glabella* differs from *I. andarensis* Loes. of Peru by having glabrous peduncles, pedicels, calyx, and branchlets and by having more numerous, less ascending lateral nerves of the leaf blades.

Ilex gransabanensis Steyermark, sp. nov. TYPE: Venezuela. Bolívar: road from Ikabarú to Santa Elena, 16 km north of Ikabarú, 4°20'N, 61°45'W, 750 m, 26 July 1982, *Croat 54158-A* (holotype, MO; isotype, VEN).

Frutex 1.5-metralis, ramulis glabris; foliis obovato-oblongis vel oblongo-ovatis apice rotundatis obtusis vel subobtusis basi obtusis vel subacutis 5–9.5 cm longis, 3.5–5 cm latis integerrimis glabris subtus punctatis; costa supra subelevata vel subimpressa 1 mm lata; nervis lateralibus supra obsoletis vel impressis utroque latere 6–11; petiolis 9–13 mm longis glabris; inflorescentia foeminea axillari lateralique solitaria vel fasciculata; pedunculo fructifero 1 mm longo fructifero puberulo, pedicellis sub fructu 2–5 mm longis puberulis; calycis lobis sub fructu suborbicularibus rotundatis 2 mm latis ciliolatis aliter glabris; bacca globoso 6 × 6 mm; pyrenis trigonis 4 mm longis dorsaliter laevibus.

Shrub 1.5 m tall. Branchlets glabrous. Leaves coriaceous, shining above, obovate-oblong or oblong-ovate, rounded, obtuse or subobtuse at apex, obtuse to subacute at base, 5–9.5 cm long, 3.5–5 cm wide, entire, glabrous, punctate below, slightly recurved on margins; midrib subelevated, subimpressed above, 1 mm wide; lateral nerves obsolete or impressed above, 6–11 each side, forking before reaching margins, not manifestly anastomosing. Petioles 9–13 mm long, glabrous. Pistillate inflorescence axillary and lateral, solitary or fasciculate, fruiting peduncle 1 mm long, puberulent; fruiting pedicels 1–2 on a peduncle, 2–5 mm long, puberulent. Calyx minutely puberulent, the lobes in fruit suborbicular, rounded, 1–1.5 mm long, 2 mm wide, ciliolate. Fruit globose, 6 × 6 mm. Pyrenes trigonous, 4 mm long, dorsally smooth above, without ridges.

This taxon resembles *Ilex tepuiana* Edwin in leaf shape but differs in the dorsally smooth pyrenes and much longer petioles. From *I. solida* Edwin it is differentiated by the much shorter fruiting pedicels and much longer petioles, while from *I. fanshawei* Edwin it may be distinguished by the dorsally smooth achenes and rounded leaf apex.

Ilex guaiquinimae Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Cerro Guaiquinima, southeast-central part of the summit, 5°44'4"N, 63°41'8"W, 730–900 m, 24 May 1978, *Julian A. Steyermark, Paul Berry, G. C. K. & E. Dunsterville 117276* (holotype, VEN; isotype, MO).

Arbor, ramulis glabris; foliis late oblongis apice late rotundatis basi acutis vel subacutis 10–16 cm longis 6.5–8 cm latis integerrimis glabris subtus punctatis; costa superne leviter lateque sulcata subtus manifeste elevata; nervis lateralibus utroque latere 6–7 angulo 30–45° adscendentibus 1.5 1.7 cm remotis; petiolis 10–18 mm longis glabris; inflorescentia foeminea solitaria axillari lateralique pedunculo sub fructu 3–5 mm longo glabro; pedicellis 3 mm longis glabris; calyce glabro, lobis leviter suborbicularibus rotundatis; bacca globosa 5 mm longa 5.5 mm diam.; pyrenis 5 mm longis dorsaliter late unisulcata.

Tree with glabrous branchlets. Leaves broadly oblong, broadly rounded at apex, acute to subacute at base, 10–16 cm long, 6.5–8 cm wide, entire, glabrous, punctate below; midrib 2 mm wide, shallowly and widely sulcate above, conspicuously elevated below; lateral nerves slender, 6–7 each side, ascending at an angle of 30–45°, 1.5–1.7 cm apart, impressed or slightly elevated above, slightly elevated below, branching before reaching margin; tertiary venation slightly evident above, obscure below. Petioles 10–18 mm long, glabrous. Pistillate inflorescence solitary, axillary, lateral. Fruiting peduncle 3–5 mm long, glabrous; pedicels 3 mm long, glabrous. Calyx glabrous, the lobes shallowly suborbicular, rounded. Fruit globose, 5 mm long, 5.5 mm diam. Pyrenes 5 mm long, 3 mm wide, dorsally broadly 1-sulcate.

Closely related to *Ilex jenmanii* Loes., from which it differs in the fewer lateral nerves more distantly separated (15–17 mm vs. 4–10 mm in *I. jenmanii*), broadly oblong leaves rounded at the apex, punctate lower leaf surface, shallowly and widely sulcate upper midrib, and solitary, axillary, and lateral inflorescence. From *I. marginata* Edwin it is distinguished by the ascending lateral nerves of the leaf blades.

Ilex holstii Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Atabapo: Cerro Marahuaca, "Sima Camp," south-central portion of forested slopes along east branch of Caño Negro, 3°43'N, 65°31'W, 1,140 m, 21–22, 24 Feb. 1985, *Julian A. Steyermark & Bruce Holst 130481* (holotype, MO; isotype, VEN).

Arbor 4-metralis, ramulis glabris; foliis lanceolatis apice acuminatis basi acutis vel subacutis 5.5–8 cm longis 1.3–2.5 cm latis integerrimis glabris subtus ut videtur epunctatis; nervis lateralibus angulo 5–20°; petiolis 6–10 mm longis glabris; inflorescentia foeminea solitaria axillari lateralique, pedunculo 2–7 mm longo glabro vel absenti; pedicellis tenuibus solitariis vel duobus 4–7 mm longis 0.3–0.5 mm latis; calyce glabro 2.5 mm lato, lobis vix manifestis truncatis; bacca 4–6 × 4–6 mm; pyrenis 4, trigonis 4 mm longis dorsaliter late 1-sulcatis.

Tree 4 m tall with glabrous branchlets. Leaves subcoriaceous, lanceolate, acuminate at apex, with an attenuate mucro 0.5 mm long, acute or subacute at base, 5.5–8 cm long, 1.3–2.5 cm wide, 2.7–4 times longer than broad, entire, glabrous, the midnerve shallowly sulcate above, slightly elevated below; lateral nerves obsolete above, manifestly impressed below, subhorizontally spreading at an angle of 5–20°, tertiary venation faintly reticulate below. Petioles 6–10 mm long, glabrous. Pistillate inflorescence solitary, axillary, lateral. Fruiting peduncle when present 2–7 mm long, glabrous; fruiting pedicels solitary or 2 together, slender, 4–7 mm long, glabrous. Calyx in fruit glabrous, 2.5 mm diam., the lobes scarcely evident, truncate. Fruit globose, 4–6 × 4–6 mm. Pyrenes 4, trigonous, 4 mm long, 2–2.5 mm wide, broadly unisulcate dorsally.

This species is similar to *Ilex oliveriana* Loes. in unisulcate pyrenes, leaf shape and mucronate apex, and the size of the fruit; but it differs in the longer petioles, more prominently impressed, subhorizontal lateral nerves, and longer mucros of the leaf blades. From *I. macarenensis* it differs principally in the dorsally unisulcate achenes.

Ilex ignicola Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aratitiyope, 70 km south-southwest of Ocamo, 2°10'N, 65°34'W, 990–1,100 m, 24–28 Feb. 1984, *Julian A. Steyermark, Paul Berry & Francisco Delascio 130112* (holotype, MO; isotype, VEN).

Arbor 6-metralis, ramulis novellis minute puberulis vel glabris; foliis elliptico-oblongis apice anguste obtusis vel subacutis basi acutis vel subacutis 5.5–8 cm longis 2.5–

3.5(–4) cm latis integerrimis glabris; costa superne subelevata vel leviter sulcata plerumque puberula subtus impressa vel elevata plerumque puberula; nervis lateralibus utroque latere 7–9; petiolis 5–9 mm longis minute puberulis glabrescentibus; inflorescentia foeminea solitaria axillari lateralique, pedicellis 3–4 mm longis minute puberulis; calyce sub fructu puberulo, lobis leviter suborbicularibus rotundatis 1 mm latis puberulis; bacca subobovoidea 7–8 mm longo 5 mm lato; pyrenis quattuor trigonis 4–5 mm longis dorsaliter late 1-sulcatis.

Tree 6 m tall; young stems minutely puberulent, glabrescent. Leaves subcoriaceous, elliptic-oblong, narrowly obtuse or subacute at apex, acute to subacute at base, 5.5–8 cm long, 2.5–3.5(–4) cm wide, entire, glabrous, subrevolute; midnerve subelevated or shallowly sulcate above, puberulous, impressed or elevated below, mainly puberulous; lateral nerves 7–9 each side, inconspicuous, scarcely evident below, impressed above, ascending at a 45° angle; tertiary venation obsolete above, scarcely evident beneath. Petioles 5–9 mm long, minutely puberulous or glabrescent. Pistillate inflorescence solitary, axillary, lateral. Pedicels 3–4 mm long, minutely puberulent. Calyx puberulous in fruit, the lobes shallowly suborbicular, rounded, 1 mm wide, puberulent. Fruit subobovoid, 7–8 mm long, 5 mm broad. Pyrenes 4, trigonous, 4–5 mm long, 2 mm wide, dorsally broadly unisulcate, the sulcation sharply angled.

This species is marked by the usually minutely puberulent upper and lower midnerves, the puberulent pedicels and calyx, and the slightly longer than broad subobovoid fruits with unisulcate pyrenes.

Ilex jauaensis Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Meseta de Jaua, Cerro Jaua, southwest summit, 4°48′50″N, 64°34′10″W, gallery forest along tributary of Río Marajano, 1,750–1,800 m, 22–28 Feb. 1974, *J. A. Steyermark, V. C. Espinoza & C. Brewer-Carías 109294* (holotype, VEN; isotype, MO).

Arbor 4-metralis, ramulis glabris; foliis oblongo-obovatis apice rotundatis retusis basi acutis vel obtusis 4–5.5 cm longis 2–3 cm latis integerrimis glabris subtus punctatis; nervis lateralibus utroque latere 5; venulis tertiariis obsoletis; petiolis 5 mm longis glabris; inflorescentia foeminea solitaria axillari lateralique; pedicellis sub fructu 13–14 mm longis glabris; calyce sub fructu glabro, lobis leviter suborbicularibus 2 mm latis; bacca in sicco 7 mm longo, 8 mm diam., in vivo 9 mm longo 10 mm diam.; pyrenis trigonis 4.5–6 mm longis dorsaliter late unisulcatis, cristis marginalibus prominentibus.

Tree 4 m tall with glabrous branchlets. Leaves coriaceous, oblong-obovate, mainly rounded at the retuse apex, acute to obtuse at base, 4–5.5 cm long, 2–3 cm wide, entire, glabrous, punctate below; lateral nerves 5 each side, narrowly sulcate above, slightly manifest and subelevated below; tertiary venation not evident. Petioles 5 mm long, glabrous. Pistillate inflorescence solitary, 1-flowered, axillary, lateral. Fruiting pedicels 13–14 mm long, glabrous. Calyx glabrous in fruit, the lobes shallowly suborbicular, 2 mm wide. Fruit 7 mm long, 8 mm wide (dried state), 9 mm long, 10 mm wide (living state). Pyrenes trigonous, 4.5–6 mm long, 3–4 mm wide, with prominent marginal ridges.

Paratype. VENEZUELA. BOLÍVAR: Cerro Marutani, 1,420 m, *Steyermark et al. 124032* (VEN).

The retuse, mainly rounded leaf apex distinguishes this taxon from *Ilex sulcata* Edwin and *I. tiricae* Edwin; the longer petioles, shorter leaves, and oblong-obovate leaf shape differentiate it from *I. lasseri* Edwin; the longer petioles, shorter pistillate pedicels, and obtuse to acute leaf base distinguish it from *I. solida*; and the longer and less thickened petioles differentiate the new species from *I. tepuiana* Edwin.

Ilex longipilosa Steyermark, sp. nov. TYPE: Venezuela. Bolívar: 3 km south of El Pauji, non-forested south slope and summit of El Abismo, 4°30′N, 61°35′W, 800–1,050 m, 11 Nov. 1985, *Ronald Liesner 19878* (holotype, MO; isotype, VEN). Figure 6A.

Frutex 1.5-metralis, ramulis dense hirtellis pilis usque 0.5 mm longis instructis; foliis cuneiformi-obovatis vel suborbiculari-ovatis apice rotundatis abrupte apiculatis basi cuneatis 4–7 cm longis 2.5–5.5 cm latis plerumque integris vel raro 1–2-denticulatis subtus costa valde pilosa pilis 0.3–0.9 mm munitis; nervis lateralibus subtus pilosulis pilis divaricatis instructis alibi subtus sparse pilosulis vel glabratis, subtus minute punctatis; nervis lateralibus utroque latere 6–8 angulo 10–20° divaricatis; venulis tertiariis subtus grosse reticulatis; petiolis 3–7 mm longis dense hirtellis pilis patentibus; inflorescentia foeminea solitaria axillari lateralique 10–20 mm longo ramosa 5–6 axibus 4–10 mm longis praedita; pedunculo 4–9 mm longo puberulo; pedicellis 1.5–2 mm longis puberulis; bracteis deltoideo-lanceolatis acutis vel acuminatis 1.2 mm longis 0.5 mm latis glabris vel extus basi paucipilosis; floribus 4-meris, calycis lobis suborbicularibus rotundalis vel paullo subacutis 1.3 mm latis leviter irregulariterque erosis; petalis obovato-oblongis rotundatis 3 mm longis 2 mm latis.

Shrub 1.5 m tall, the branchlets densely hirtellous with spreading hairs up to 0.5 mm long. Leaves cuneiform-obovate or suborbicular-ovate, abruptly apiculate at the rounded apex, cuneate at base, 4–7 cm long, 2.5–5.5 cm wide, mainly entire or rarely with 1–2 minute toothlike projections, subrevolute, the lower midrib strongly pilose with spreading hairs 0.3–0.9 mm long, the lateral nerves beneath with spreading hairs, the lower surface pilosulous to glabrate, the upper surface glabrous except for the minutely puberulent sulcate midrib, minutely punctate on lower surface; midnerve sulcate above, elevated below; lateral nerves 6–8 each side, divaricately spreading at a 10–20° angle, slightly manifest below, inconspicuous and faintly sulcate above. Petioles 3–7 mm long, densely hirtellous with spreading hairs. Pistillate inflorescence solitary, axillary, lateral, 10–20 mm long, cymosely or paniculately branched with 5–6 lateral axes 4–10 mm long; peduncle 4–9 mm long, shortly puberulous; pedicels 1.5–2 mm long, shortly puberulous. Bracts deltoid-lanceolate, acute to acuminate, 1.2 mm long, 0.5 mm wide, mainly glabrous or with a few hairs at the outer base. Flowers 4-merous; calyx lobes suborbicular, rounded or slightly subacute, 1.3 mm wide, the margins slightly irregularly erose. Petals obovate-oblong, rounded, 3 mm long, 2 mm wide.

From the taxa placed by Loesener (1901) in his section 7 *Megalae*, subsection *Pedicellata* Loes., especially *Ilex villosula* Martius, *I. velutina* C. Martius, *I. brasiliensis* (Sprengel) Loes., and *I. theezans* var. *riedelii* Loes., the new species differs in its solitary, axillary, and lateral (vs. fasciculate) inflorescences, punctate lower leaf surface, and differently shaped leaves. The longer pubescence of the new species is somewhat reminiscent of *I. maguirei* Wurdack of Cerro de la Neblina, which differs in its rounded leaf bases, differently shaped leaves, shorter petioles, pubescent, elongated fruit, and only 1–3-flowered inflorescences.

Ilex magnifructa Edwin, var. **minor** Steyermark, var. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Ualipano, orillas del Río Parucito, 6°N, 65°43′W, 1,760 m, Feb. 1962, *Felix Cardona 2943* (holotype, US; isotype, MO).

A var. *magnifructa* pedicellis fructiferis 5–10 mm longis recedit.

Leaf blades broadly oblong-obovate, rounded at apex, broadly rounded or obtuse at base, 7.5–10.5 cm long, 4–8 cm wide. Petioles 2–3 mm long. Calyx lobes 4, deltoid, acute. Fruiting pedicels 5–10 mm long.

This variety differs from var. *magnifructa* in the shorter fruiting pedicels.

Ilex marahuacae Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Marahuaca, "Sima Camp," south-central portion, forested slopes along E branch of Caño Negro, 3°43′N, 65°31′W, 1,140 m, 21–22, 24 Feb. 1985, *J. A. Steyermark & B. K. Holst 130425* (holotype, MO; isotype, VEN).

Arbor 4-metralis, ramulis glabris; foliorum laminis ovatis vel oblongo-ovatis apice obtuse vel argute acuminatis, acumine 8–10 mm longo, basi rotundatis vel subobtusis 6.5–11 cm longis 2.5–4.5 cm latis punctatis glabris, marginibus remote obscureque crenulato-serrulatis; venulis tertiariis supra reticulatis aliquantum impressis; petiolis 6–8 mm longis; infructescentia solitari axillari; floribus 4-meris; pedunculo 5–6 mm longo glabro 2–3-flora; calycis lobis suborbicularibus rotundatis minute erosis sparsim ciliatis; pyrenis 4 trigonis dorsaliter laevibus vel sublaevibus.

Tree 4 m tall, the stems glabrous. Leaf blades subcoriaceous, ovate or oblong-ovate, obtusely to acutely acuminate at apex, the acumen 8–10 mm long, rounded to subobtuse

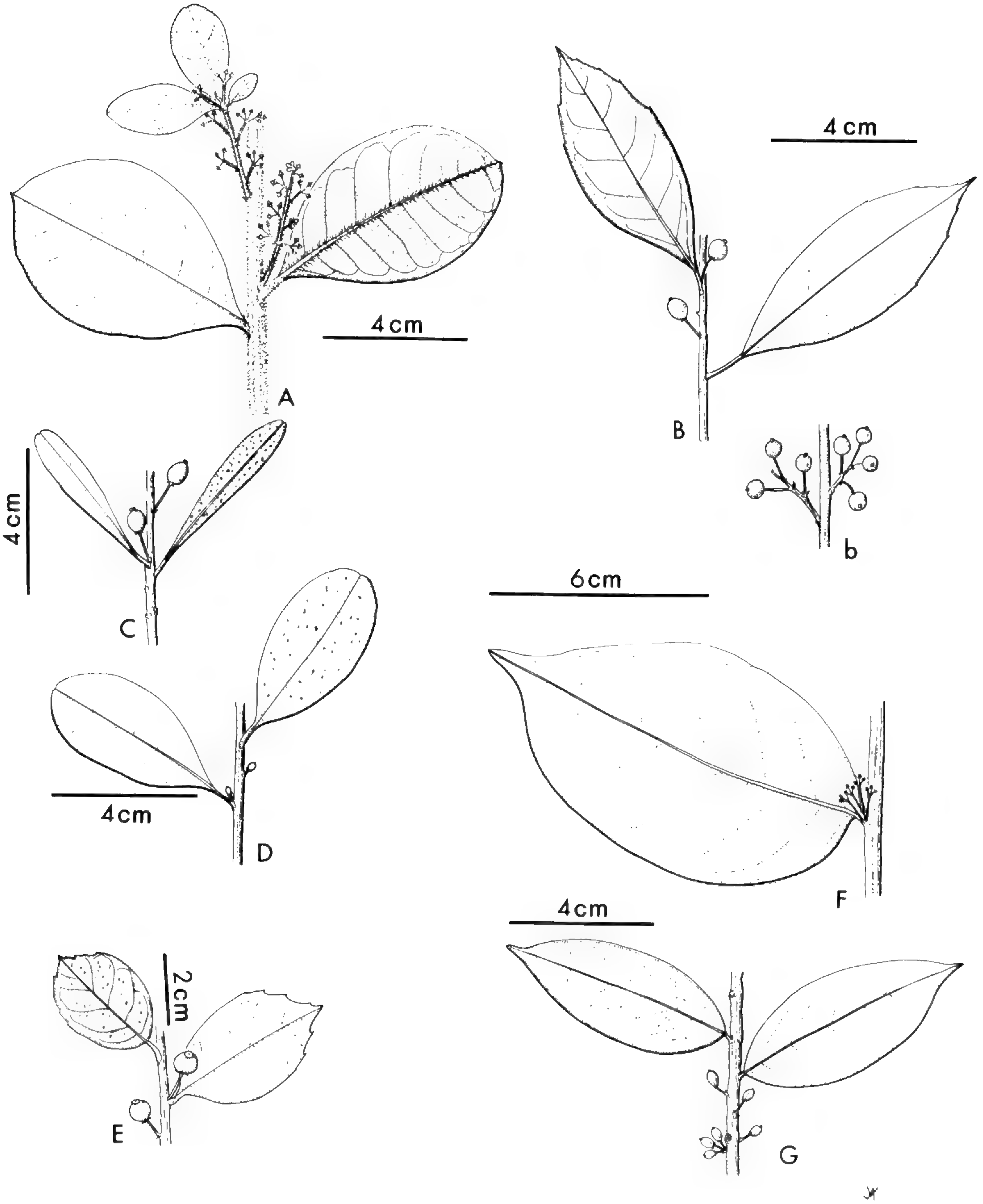

FIGURE 6.—*A.* Ilex longipilosa, *portion of flowering branch, staminate.*—*B.* Ilex acutidenticulata.—*b. Branched fruiting peduncles.*—*C.* Ilex spathulata.—*D.* Ilex brevipedicellata.—*E.* Ilex summa.—*F.* Ilex wurdackiana, *staminate branch.*—*G.* Ilex wurdackiana, *portion of fruiting branch.*

at base, 6.5–11 cm long, 2.5–4.5 cm wide, punctate, glabrous; lateral nerves 4–5 each side with less conspicuous intermediate nerves, subhorizontally spreading at 10–20°, impressed above, slightly elevated below; tertiary venation reticulate and rather conspicuously impressed above, subobsolete below. Petioles 6–8 mm long, glabrous. Infructescence solitary, axillary. Peduncle 5–6 mm long, 2–3-flowered, glabrous. Pedicels 3 mm long, glabrous. Flowers 4-merous. Calyx lobes shallowly suborbicular, rounded, 0.3 mm long, 1 mm wide, minutely erose, sparsely ciliolate. Calyx tube glabrous. Fruit globose, 5 mm diam. Pyrenes 4, trigonous, 5 mm long, 3 mm wide, dorsally smooth or essentially so.

This taxon is characterized by the elongated acumen of the obscurely crenulate-serrulate leaves, the solitary axillary inflorescence, the dorsally smooth pyrenes, and the epunctate leaves.

Ilex paruensis Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Atabapo, Serranía del Parú (Aroko), sector centro-sur, sabanas herbáceas en el borde sur de la tercera meseta central, 4°27′N, 65°32′W, 1,100 m, 7 Oct. 1979, *O. Huber 4437* (holotype, VEN).

Frutex 2-metralis, ramulis pubescentibus pilis arcte verticaliterque seriatis dispositis; foliorum laminis late obovatis apice rotundatis minute mucronulatis basi acutis 2.5–3.5 cm longis 1.5–2.3 cm latis subtus epunctatis supra arcte negro-punctatis scrobiculatisque, subtus costa media pubescenti pilis brevibus patentibus munita supra sulcata minute puberulenti; petiolis 2 mm longis crebiter minuteque puberulis; infructescentia foeminea solitaria fasciculata axillari lateralique; pedunculis 1–3-floris usque 3 mm longis dense puberulis, pedicellis 1–3 mm longis dense puberulis; calycis lobis fere obsoletis repando-rotundatis apice paullo apiculatis; stigmate depresso latiori quam longiori; fructu subgloboso 3 mm diam. (immaturo).

Shrub 2 m tall; stems minutely pubescent in vertical lines. Leaf blades coriaceous, broadly obovate, rounded at the minutely mucronulate apex, acute at the base, 2.5–3.5 cm long, 1.5–2.3 cm wide, epunctate below, scrobiculate and densely black-puncticulate above, the midrib puberulent below with spreading hairs, minutely puberulent in the sulcation above, elsewhere glabrous on both surfaces or sparsely puberulent near base of upper surface, revolute; lateral nerves 4–5 each side, inconspicuous both sides, faintly impressed below. Petioles 2 mm long, densely and minutely puberulent. Infructescence solitary or fasciculate, axillary and lateral. Peduncles 1–3-flowered, up to 3 mm long, densely puberulent. Pedicels 1–3 mm long, densely puberulent. Calyx lobes scarcely developed, broadly shallowly repand-rounded, slightly apiculate at the apex, glabrous. Stigma broadly flattened and depressed at the slightly umbonate summit. Immature fruit subglobose, 3 mm diam.

This species is related to *I. vacciniifolia* Klotzsch, from which it differs in the epunctate lower leaf surface, strongly black puncticulate upper surface, shorter fruiting peduncles and pedicels, mucronulate leaf apex, and glabrous, subobsolete calyx lobes.

Ilex paujiensis Steyermark, sp. nov. TYPE: Venezuela. Estado Bolívar: 3 km south of El Pauji, 4°30′N, 61°35′W, 900 m, 19 Oct. 1985, *Ronald Liesner & Bruce Holst 18796* (holotype, MO; isotype, VEN).

Arbor 4-metralis, ramulis glabris; foliis obovatis apice rotundatis interdum retusis basi cuneatis 6.5–11 cm longis 2.5–4.5 cm latis integerrimis glabris subtus valde negro punctatis; costa superne anguste sulcata; nervis lateralibus utroque latere 7–9; venulis tertiariis subtus tenuibus; petiolis 5–10 mm longis 1.5–2 mm diam. glabris; inflorescentia foeminea solitaria axillari lateralique; pedicellis fructiferis 2–3 mm longis minute puberulentibus; calyce minute puberulenti, lobis suborbicularibus rotundatis ciliolatis vel obsolete erosis 1 mm latis; petalis 3–3.5 mm longis 1.5 mm latis minute papillatis marginibus papillato-ciliolatis; bacca globoso 6 × 6 mm.

Tree 4 m tall with glabrous branchlets. Leaves coriaceous, obovate, rounded and sometimes retuse at apex, cuneately narrowed at base, mainly 6.5–11 cm long, 2.5–4.5 cm wide, 2–2½ times longer than broad, entire, glabrous, strongly black-punctate beneath, the upper midnerve narrowly sulcate; lateral nerves 7–9 each side, slightly elevated or impressed above, finely impressed below; tertiary venation faintly manifest beneath. Petioles 5–10 mm long, 1.5–2 mm wide, glabrous. Pistillate inflorescence solitary, axillary, lateral. Fruiting pedicels 2–3 mm long, minutely puberulent. Calyx tube minutely puberulent; calyx lobes suborbicular, rounded, some of them minutely ciliolate, others obsoletely erose, 1 mm wide. Petals 3–3.5 mm long, 1.5 mm wide, minutely papillate on the lower half of the upper surface, the margins papillate-ciliolate. Fruit globose, 6 × 6 mm.

Paratype. VENEZUELA. BOLÍVAR: region of ríos Icabarú and Hacha, 450–850 m, *Bernardi 2622* (VEN).

The elongate petioles and short fruiting pedicels ally this taxon to *Ilex gransabanensis* Steyerm., but *I. paujiensis* differs in having the punctations on the lower leaf surface larger and more conspicuous, less conspicuous lateral nerves, more cuneately acute leaf bases, and narrowly sulcate upper midnerves.

The collection of *Bernardi 2622* at VEN, presently treated as a paratype of *Ilex paujiensis*, was identified by Edwin as *I. andarensis* Loes. and forms the basis for his inclusion of that species in his treatment for the Venezuelan Guayana (1965). *Ilex andarensis*, originally described from Andara Mountain, Peru, was based on a *Spruce s.n.* collection and is completely different from the *Bernardi 2622* specimen, having, among other differences, ovate, oval-oblong, or elliptic leaf blades which are obtuse, rounded, or cuneately obtuse at the base and acute or obtusely acuminate at the apex with an acumen 7–12 mm long.

Ilex polita Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Guayaraca, southern base, Auyán-tepui, between escarpment and Río Guayaraca, 5°44′N, 62°32′W, 950 m, 25–27 Nov. 1982, *G. Davidse & O. Huber 22679* (holotype, MO; isotype, VEN).

Frutex 2-metralis, ramulis glabris; foliis superne nitidis ovatis ovalibus oblongis vel elliptico-oblongis apice obtuse vel rotundatis basi obtusis vel rotundatis 4–7.5 cm longis 1.8–4.5 cm latis integerrimis glabris subtus epunctatis; costa supra anguste paullo sulcata; nervis lateralibus utroque latere 5–9; petiolis 4–10 mm longis glabris; inflorescentia foeminea solitaria axillari lateralique; pedunculo sub fructu 7–10 mm longo; pedicellis sub fructu 3–5 mm longis ubi solitariis 1–2 mm longis ubi inflorescentiis ramosis; floribus 4-meris; calycis tubo minute puberulo, lobis suborbicularibus apice rotundatis vel subacutis 1.2–1.5 mm latis marginibus ciliolatis.

Shrub 2 m tall with glabrous branchlets. Leaves coriaceous, shining and mainly enervate above, ovate, oval, oblong, or elliptic-oblong, obtuse or rounded at apex, obtuse or rounded at base, 4–7.5 cm long, 1.8–4.5 cm wide, entire, glabrous, epunctate below, 1.3–2.6 times longer than broad, revolute; midnerve narrowly and shallowly sulcate above, somewhat elevated below; lateral nerves 5–9 each side, ascending at an angle of 15–20°, obsolete above, faintly impressed or slightly elevated below; tertiary venation slightly manifest below. Petioles 4–10 mm long, glabrous. Pistillate inflorescence solitary, axillary, lateral. Peduncle 7–10 mm long in fruit. Pedicels, when solitary, 3–5 mm long in fruit, 1–2 mm long in fruit in cymose inflorescences, sparsely puberulent. Flowers 4-merous. Calyx tube sparsely and minutely puberulent, the lobes suborbicular, rounded or slightly subacute at apex, 0.5 mm long, 1.2–1.5 mm wide, ± densely ciliolate.

Paratypes. VENEZUELA. BOLÍVAR: Auyán-tepui, Guayaraca, 950 m, *Davidse & Huber 22733* (MO, VEN); Río Aparamán, affluent of Río Acanán near Yuray-merú rapids, 1.5 km S of SW corner of Amaruay-tepui, 5°54′N, 62°15′W, 500 m, *Liesner & Holst 20114* (MO, VEN).

This species is characterized by the combination of its densely ciliolate calyx lobes, shallowly sulcate upper midnerve, and oblong, elliptic-oblong, ovate, or oval leaf blades lustrous on the upper surface and obtuse or rounded at the apex.

Ilex spathulata Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Atabapo, Cerro Marahuaca, slopes upstream from Río Yameduaka, 3°38′N, 65°28′W, 1,225 m, 17–18 Feb. 1985, *Ronald Liesner 17599* (holotype, MO; isotype, VEN). Figure 6C.

Frutex 2-metralis; ramulis glabris; foliis anguste spathulatis apice rotundatis emarginatis basi conspicue angustatis 2.5–4.5 cm longis 0.5–1.2 cm latis integerrimis glabris subtus punctatis; costa superne sulcata; nervis lateralibus principalibus 5–6; venulis tertiariis obsoletis vel fere; petiolis 5–8 mm longis glabris; inflorescentia foeminea solitaria axillari, 1–2-flora; pedicellis sub anthesi 4–4.5 mm longis sub fructu 10–12 mm longis minute puberulentibus; calyce sub anthesi 0.7–1 mm longo 1.5 mm lato glabro, lobis suborbicularibus rotundatis; inflorescentia masculina fasciculata vel solitaria axillari lateralique cymosa 2–5-flora, pedunculo 1.5 mm longo puberulenti, pedicellis 2 mm longis; bacca (immatura) globosa 6 × 5.5 mm.

Shrub 2 m tall, the branchlets glabrous. Leaves subcoriaceous, narrowly spathulate, rounded and emarginate at apex with a thickened blunt tip in the sinus, conspicuously narrowed at the base and decurrent, 2.5–4.5 cm long, 0.5–1.2 cm wide, (2½–)4½–5 times longer than broad, entire, glabrous, punctate beneath, revolute; midnerve sulcate above; principal lateral nerves 5–6 each side, impressed above, slightly elevated below; tertiary venation obsolete or inconspicuous above, slightly more conspicuous below. Petioles 5–8 mm long, glabrous. Pistillate inflorescence solitary, axillary, lateral, 1–2-flowered. Pedicels in flower 4–4.5 mm long, in fruiting specimens 10–12 mm long, minutely puberulent. Calyx 0.7–1 mm long, 1.5 mm wide in anthesis, glabrous; lobes suborbicular, rounded, 0.5 mm long, 0.8 mm wide. Petals 2–2.5 mm long, 1 mm wide. Staminate inflorescence fasciculate or solitary, axillary and lateral, cymosely 2–5-flowered, pedunculate; peduncle 1.5 mm long, puberulent; pedicels 2 mm long. Immature fruit globose, 6 mm × 5.5 mm.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Marahuaca, same locality as type, 19 Feb. 1985, *Liesner 17688* (MO, VEN).

This taxon is characterized by the narrowly spathulate leaves, mainly 4½–5 times longer than broad and the completely glabrous calyx. From *Ilex huachamacariana* Edwin it may be distinguished by having shorter fruiting pedicels, more conspicuous lateral nerves, and more conspicuous tertiary venation on the lower leaf surface. From *I. gleasoniana* Steyerm. it differs in the much narrower and thinner leaf blades and in the glabrous calyx.

Ilex summa Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Dist. Piar, Camarcaibarai-tepui, summit, 5°53′N, 61°59′W, 2,400 m, 26 Mar. 1987, *Bruce K. Holst 3617* (holotype, MO; isotype, VEN). Figure 6E.

Frutex 2-metralis, ramulis glabris; foliis ovatis apice apiculatis vel subacutis basi rotundatis vel late obtusis 2.5–4.3 cm longis 1.5–3 cm latis, marginibus superioribus tertiis dentibus 3–5 acutis vel setulosis praeditis glabris ubique punctatis valde revolutis; costa superne sulcata; nervis lateralibus utroque latere 4–5 supra manifeste sulcatis subtus elevatis divaricatis; venulis tertiariis supra obsoletis subtus grosse reticulatis; petiolis 3–6 mm longis glabris; inflorescentia foeminea solitaria axillari lateralique; pedunculis sub fructu 4–6 mm longis; pedicellis sub fructu 4–9 mm longis glabris; bacca globoso 6–7 mm diam.; pyrenis 4 trigonis 4–4.5 mm longis dorsaliter unisulcatis.

Shrub 2 m tall with glabrous branchlets. Leaves coriaceous, ovate, apiculate or subacute at apex, rounded or broadly obtuse at base, 2.5–4.3 cm long, 1.5–3 cm wide, 1.4–1.6 times longer than broad, the upper ⅓ of the margins with 3–5 acute to setulose teeth, glabrous, black-punctate on upper and lower surfaces, the margins strongly revolute; midnerve sulcate above with minute puberulence in sulcation, elevated below; lateral nerves 4–5 each side, prominently sulcate above, elevated below, spreading divaricately, dichotomously branched 2–4 mm from the margins; tertiary venation obsolete above, grossly reticulate below. Petioles 3–6 mm long, glabrous. Pistillate inflorescence solitary, axillary, lateral. Peduncles in fruit 4–6 mm long, glabrous. Pedicels in fruit 4–9 mm long, glabrous. Stigma depressed in fruit. Fruit globose, 6–7 mm diam. Pyrenes 4, trigonous, 4–4.5 mm long, dorsally unisulcate.

This species differs from *Ilex acutidenticulata* Steyerm. in having smaller, broadly ovate leaves rounded or broadly obtuse at base and shortly apiculate at the apex; more numerous marginal teeth; shorter, glabrous petioles; and more divaricately spreading lateral nerves prominently sulcate above and elevated below.

Ilex wurdackiana Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Cerro Venamo, northwest slopes, SE of road camp km 125, to line of NE-facing, sandstone bluffs, 1,100–1,140 m, 21 Apr. 1960, *J. A. Steyermark & S. Nilsson 449* (holotype, VEN). Figure 6F, G.

Frutex epiphytica, ramulis superioribus puberulentibus; foliis rigidi-coriaceis subsessilibus late ovatis vel oblongo-lanceolatis apice acutis vel acuminatis basi late rotundatis vel subcordatis 4–10.5 cm longis 2–6 cm latis integerrimis glabris subtus valde punctatis; costa superne elevata nervis lateralibus utroque latere 4–6 supra subsulcatis vel valde sulcatis subtus elevatis; venulis tertiariis supra obsoletis subtus grosse reticulatis paullo elevatis; petiolis 1–3 mm longis glabris; inflorescentia masculina fasciculata axillari lateralique, pedunculis 7–8 filiformibus cymosis 4–6 mm longis glabris; pedicellis filiformibus 1–2 mm longis glabris; floribus 4-meris; calycis lobis suborbicularibus rotundatis 0.3–0.5 mm longis 0.7 mm latis glabris; inflorescentia foeminea solitaria axillari lateralique; pedicellis sub fructu 2.5–4 mm longis; bacca immatura ovoideo-subgloboso 2.5–3.5 mm longo 3 mm lato.

Woody epiphyte; upper portions of stems puberulent. Leaves stiff-coriaceous, subsessile, broadly ovate or oblong-lanceolate, acute to acuminate at apex, broadly rounded to subcordate at base, 4–10.5 cm long, 2–6 cm wide, entire, glabrous, strongly punctate beneath; upper midrib prominently elevated; lateral nerves 4–6 each side, subsulcate to prominently sulcate above, elevated below; tertiary venation obsolete above, grossly reticulate below. Petioles 1–3 mm long, glabrous. Staminate inflorescence fasciculate with 7–8 filiform, cymosely branched, glabrous peduncles 4–6 mm long; pedicels filiform, 1–2 mm long, glabrous. Flower 4-merous; calyx lobes suborbicular, rounded, 0.3–0.5 mm long, 0.7 mm wide, glabrous. Petals broadly oblong, rounded at apex, 0.7–1 mm long, 0.8 mm wide. Anthers suborbicular-oblong. Pistillate inflorescence solitary, axillary, lateral. Fruiting pedicels 2.5–4 mm long, glabrous. Stigma depressed-flattened. Immature fruit ovoid-subglobose, 2.5–3.5 mm long, 3 mm wide.

Paratype. VENEZUELA. BOLÍVAR: laderas del Cerro Uei, entre los brazos del Río Uei (afluente del Río Venamo y Cuyuni), selva nublada, 865–1,050 m, 27–28 Dec. 1970, *J. A. Steyermark, G. C. K. & E. Dunsterville 104565* (VEN).

This species is noteworthy in its epiphytic shrubby habit. Other distinguishing characters are the conspicuously elevated upper midrib, subsessile leaves, these entire or with a few minute excrescences, broadly rounded to subcordate at base, and the fasciculate staminate inflorescence with filiform peduncles and pedicels. The species is endemic to the region of the Cerro Venamo and tributaries of the Río Venamo and Río Cuyuni.

It is a great pleasure to dedicate this distinct species to Dr. John J. Wurdack, who has identified much material belonging to the genus *Ilex* and who has rendered invaluable help to the author on many occasions.

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SAPINDACEAE

ALLOPHYLUS

Allophylus parimensis Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Sierra Parima, vecindades Simarawochi, Río Matacuni, 3°49′N, 64°36′W, 6–7 km west of the Brazil–Venezuela frontier, 795–830 m, 18 Apr.–23 May 1973, *Julian A. Steyermark 107033* (holotype, MO; isotype, VEN). Figure 7.

Arbor 10-metralis, ramulis novellis modice pubescentibus pilis subadpressis praeditis; foliis trifoliolatis petiolatis, laminis lanceolato-ellipticis apice acuminatis basi acutis, foliolis lateralibus sessilibus 4–5 cm longis 1–1.3 cm latis (immaturis), terminali (intermedia) 5.5–6 cm longis 1.5–1.8 cm latis subintegris vel marginibus superioribus denticulatis 1–5 dentibus tenuibus adpressis setulosis instructis, supra glabris subtus praesertim costa sparsim adpresso-pubescentibus; nervis lateralibus utroque latere tenuibus 8–9; petiolis (novellis) 1.5–2.5 cm longis dense adpresso-pubescentibus; thyrsis anguste racemiformibus 3.5–5 cm longis 6–8 mm latis densifloris multifloris; floribus solitariis vel plerumque in cincinnis 2–3-floris dispositis vel interdum axibus infimis elongatis racemiformibus 5–6-floris; pedunculo pedicellisque atque rhachidi adpresso-pubescentibus; sepalis valde ciliatis exterioribus ubique glabris interioribus extus minute pulverulentibus intus glabris; petalis intus dense villosulis; filamentis glabris; disco modice hispidulo.

Tree 10 m tall; young branchlets moderately subappressed pubescent. Leaves 3-foliolate; leaflets lance-elliptic (immature) acuminate at apex, acute at base, the lateral sessile 4–5 cm long, 1–1.3 cm wide; terminal (intermediate) leaf subsessile, 5.5–6 cm long 1.5–1.8 cm wide, entire or the upper margins with 1–5 appressed, slender, setulose teeth, glabrous above, sparsely appressed-pubescent below on surface, midnerve, and lateral nerves; lateral nerves slender, 8–9 on both sides. Young petioles 1.5–2.5 cm long, densely appressed-pubescent. Inflorescence a narrow racemiform thyrse, axillary in the upper leaf axils, with 20–30 short, lateral, sessile or pedunculate cincinni, the upper axes mainly 1-flowered, the others usually 2–3-flowered, sometimes the lowest racemiform, elongated, 5–6-flowered and up to 12 mm long; rachis of inflorescence densely subappressed-pubescent, the hairs antrorsely suberect-ascending; pedicels 1–2 mm long, sparsely puberulous; peduncle 1–2 cm long, densely appressed-pubescent. Outer sepals ovate-oblong, rounded, cucullate, 1.5 mm long, 1 mm wide, strongly ciliate, elsewhere glabrous both sides; inner sepals with incurved margins, suborbicular from a short claw, broader than long, 1.3 mm long, 1.6 mm wide, strongly ciliate, glabrous within, minutely puberulent without. Petals broadly obovate or suborbicular, obovate, rounded at summit, narrowed to the base, 1.1 mm long, 0.7 mm wide above the middle, glabrous without, densely ciliate, within densely barbate-villosulous on the 2-lobed scale and lamina. Disk fleshy, shallowly lobed, moderately hispidulous. Filaments glabrous, 0.8 mm long. Ovary bilobed, suborbicular, densely hispidulous.

This species is allied to *Allophylus strictus* Radlk. and *A. laevigatus* (Turcz.) Radlk., from both of which it differs in the hispidulous disk, glabrous filaments, and sparsely pubescent style. It further differs in the sparingly 1–5-denticulate upper leaf margins with slender appressed teeth, the sparsely puberulous pedicels, more densely pubescent interior of the petals, more densely and closely flowered inflorescence with a densely pubescent rachis, and the sometimes racemosely elongated lowest axes bearing up to 6 flowers.

RUBIACEAE

COUSSAREA

Coussarea evoluta Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, on hills 1.5 km south of Base Camp on Río Mawarinuma, 0°50′N, 66°10′W, 140–340 m, 4 Dec. 1984, *R. Liesner & D. Bell 17493* (holotype, MO; isotype, VEN). Figure 8.

Stipulae suborbiculares late rotundatae 2–5 mm longae; inflorescentia magna longipedunculata 15–17 cm longa 7–10 cm lata pedunculo incluso, axibus lateralibus elongatis infimis 2–3.5 cm longis; corollae lobis ad dimidium vel magis longitudinem tubi corollae attingentibus recurvatis 7–10 mm longis; floribus sessilibus dense fasciculatis.

Tree, 8 m tall, the stem glabrous; stipule suborbicular, shallow, broadly rounded, 2–5 mm long, 5–8 mm broad, glabrous. Petiole 1.5–2.3 cm long, 3 mm thick, glabrous. Leaf blades large, subcoriaceous, oblong-elliptic, abruptly obtusely acuminate at apex, acumen 1–2 cm long, acute at base, 18–29 cm long, 5.5–13 cm wide, glabrous both sides, domatia absent; midrib prominent and elevated below, impressed above; lateral nerves 10–12 each side of the midrib, ascending from a 25–35° angle; tertiary venation grossly reticulate beneath with large areoles, subelevated on lower surface. Inflorescence pedunculate, 15–17 cm long including the peduncle, 7–10 cm wide at the base, cymose-paniculate, the lateral axes subverticillate; peduncle 6–7.5 cm long, microscopically sparsely puberulent; lowest axes verticillate or subverticillate, usually 3–4, widely spreading, 2–3.5 cm long, the other axes shorter, the lowest tier separated by 4–5 cm from the middle tier, the middle tier separated by 2–3.5 cm from the upper tier; lateral axes usually branched at the apex into 2–3 short, mostly unequal axes 7–15 mm long or unbranched, or with short axes 1–2 mm long, each ending in sessile groups of 2–7 flowers. Flowers sessile; calyx and hypanthium 2.5–3.5 mm long, microscopically sparsely puberulent; hypanthium obconic-urceolate or oblong-obconic, 1.2 mm long, 1 mm wide, obtusely ribbed, minutely puberulent; calyx tube deeply campanulate-urceolate, 2 mm long, 1.5 mm wide, minutely sparsely puberulent; calyx teeth 5, linear or subsubulate, recurved, 0.5 mm long, minute-

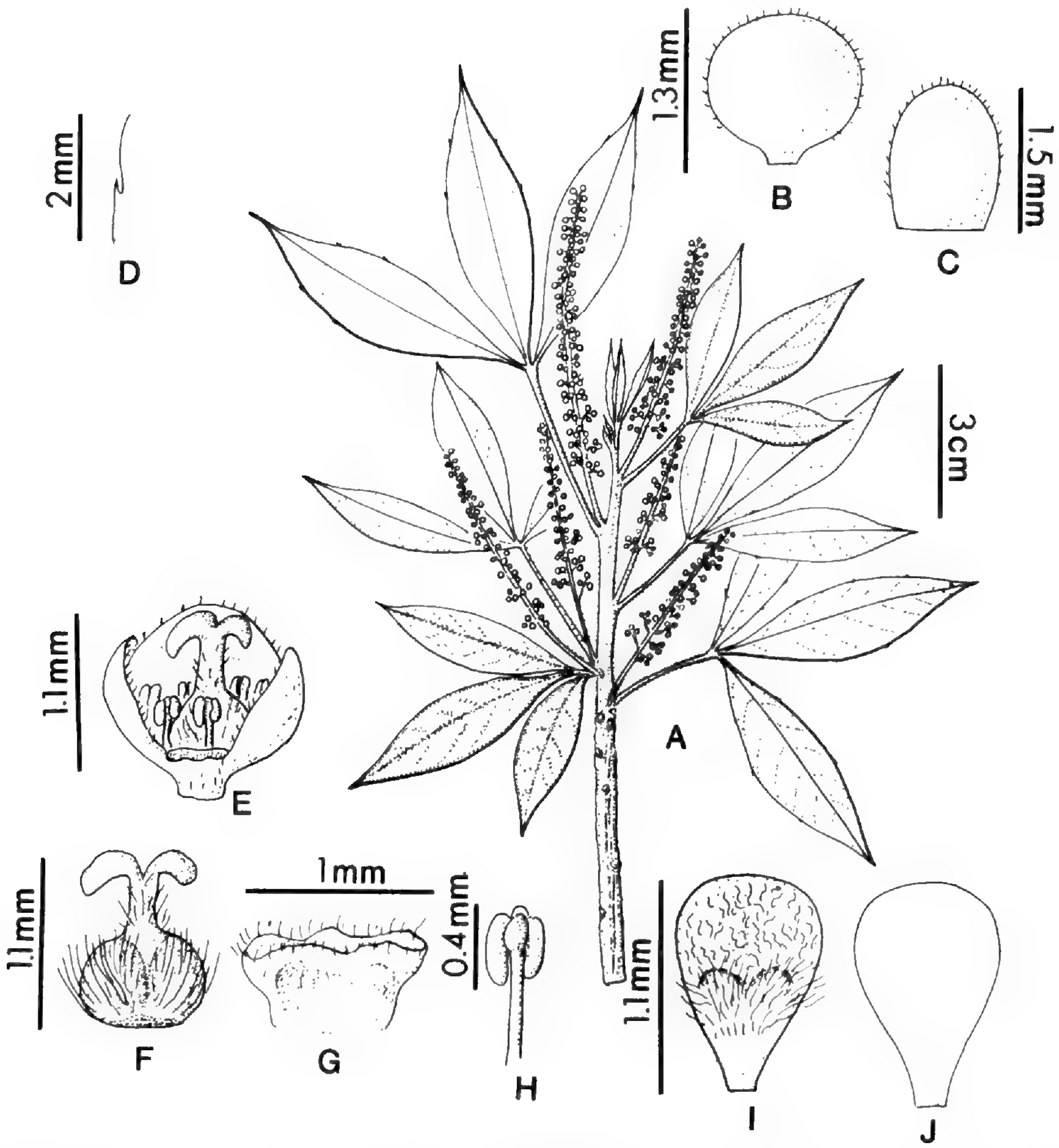

FIGURE 7. Allophylus parimensis.—*A. Habit of flowering branch.—B. Convex dorsal side, inner sepal.—C. Convex dorsal side, outer sepal.—D. Portion of upper margin of leaflet.—E. Flower with one of inner sepals removed.—F. Pistil.—G. Disk.—H. Stamen.—I. Petal, abaxial view.—J. Petal, adaxial view.*

ly hirtellous. Corolla salverform, tube 12.5–13 mm long, 1 mm wide; 4 corolla lobes linear, recurved, 7–10 mm long, 1 mm wide, glabrous within, microscopically puberulent without and at apex, the tube densely papillate-puberulent without. Stamens 4 in the upper 5 mm of corolla tube, included; anthers linear, 4.5 mm long, obtuse at apex with rounded connective, rounded at base. Disk short-columnar, truncate, 0.8 mm long.

This species is characterized by the large inflorescences with elongate lateral axes, compact clusters of sessile flowers, elongated peduncles, corolla lobes at least half the length of the corolla tube, and shallow, rounded stipules.

FARAMEA

Faramea boomii Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, Base Camp, Río Mawarinuma, terra firma forest, 0°50′N, 66°10′W, 4 Dec. 1984, 140 m, *B. Boom & A. Weitzman 5278* (holotype, MO; isotypes, NY, VEN, GH, PORT, K, BR, COL, U, INPA, P, MG, B, AAU, US).

Stipulae aristatae, aristis 2–3 mm longis; foliorum laminis elliptico-oblongis apice abrupte obtuseque caudatis 10–15.5 cm longis 3–6 cm latis, ad marginem valde incrassatis; inflorescentia latiore quam latiore, floribus breviter pedicellatis; pedicellis 1–1.5 mm longis glabris; bracteis nullis; corolla 25 mm longa, tubo 17 mm longo, lobis lineari-ligulatis 8–9 mm longis basi 1.5 mm latis; antheris 5 mm longis apice breviter cuspidatis.

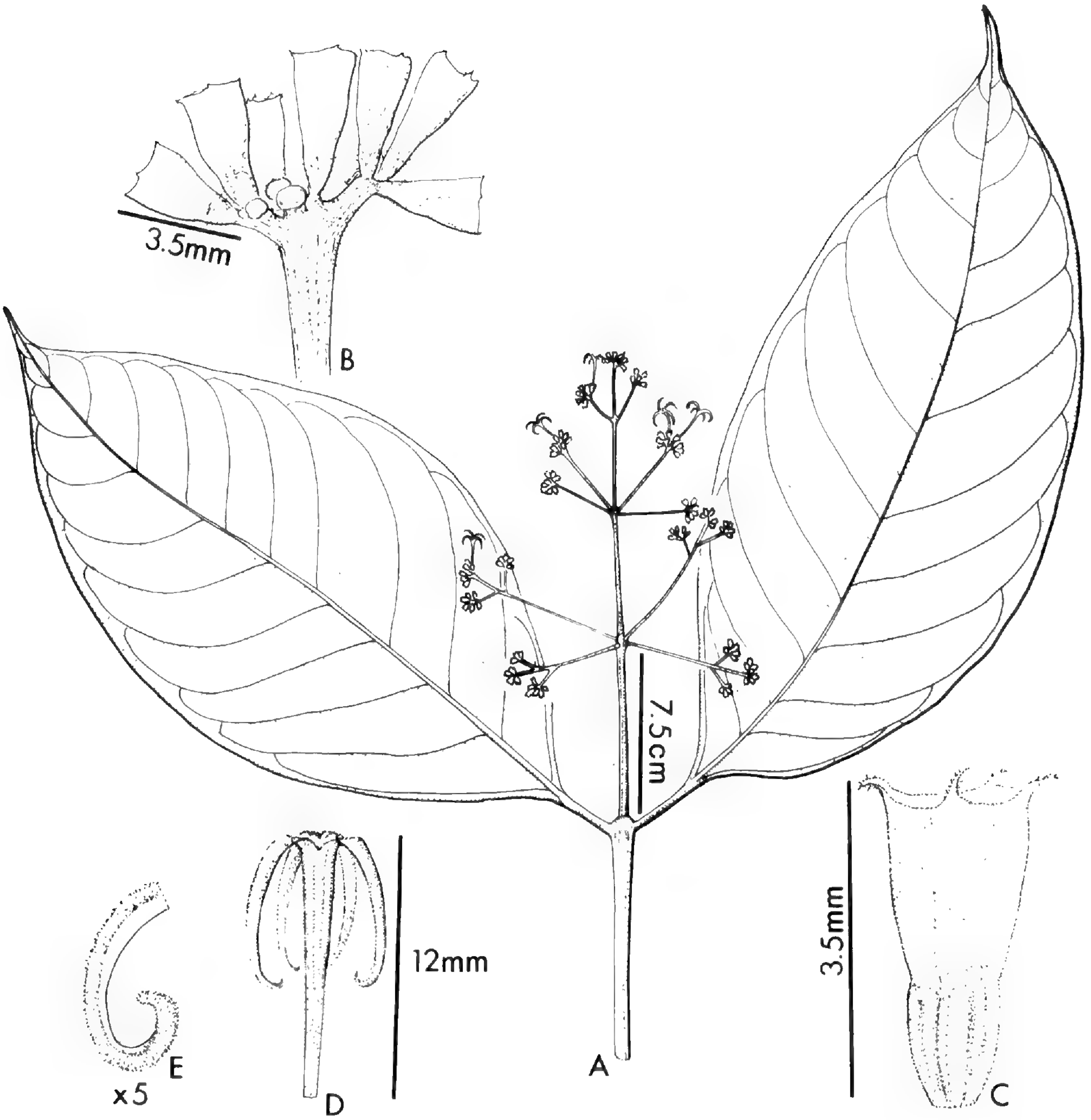

FIGURE 8. Coussarea evoluta.—*A. Habit of flowering branch.*—*B. Detail of portion of inflorescence, corollas absent.*—*C. Calyx and hypanthium.*—*D. Corolla.*—*E. Distal portion of corolla lobe.*

Tree 12 m tall, the young stems glabrous. Stipules persistent, laterally connate, the sheath 2–2.5 mm long, 3 mm wide, abruptly aristate, the arista indurated, 2–3 mm long, arising from just below the summit of the sheath, the part protruding above the summit 2 mm long. Leaf blades elliptic-oblong, abruptly obtusely caudate, acute at base, 10–15.5 cm long, 3–6 cm wide, the obtuse acumen 12–13 mm long, 1.5–2 mm wide, glabrous throughout, with a strong marginal nerve; principal lateral nerves widely spaced 8–13 mm distant, widely spreading-ascending at 10–25° angle, impressed above, slightly elevated below, the intermediate nerves finer and less conspicuous below; petiole 10–13 mm long, glabrous; tertiary venation scarcely evident above, grossly and irregularly reticulate below, slightly manifest. Inflorescence terminal, pedunculate, 3.5 cm long, 6 cm broad, cymosely branched in 3 main divaricately spreading, glabrous axes 10–13 mm long, 0.5 mm diam., each axis branched into 2 lateral axes 5 mm long, mainly 3-flowered with a central short axis bearing a solitary flower; central flower 1 mm long pedicellate, other flowers 1–1.5 mm long pedicellate; pedicels glabrous. Bracts obsolete, not manifest. Calyx and hypanthium 2.5 mm long, glabrous; hypanthium columnar-urceolate, 1.5

mm long, 1.2 mm wide; calyx broadly cupulate, truncate or essentially so at apex, 0.8–1 mm long, 1.2–1.3 mm wide, eglandular within. Disk shortly columnar, 0.8 mm long. Corolla white, salverform, 25 mm long, the tube 17 mm long, 2 mm wide above, narrowing to 0.8 mm wide at base; 4 lobes linear-ligulate, narrowed to a rounded apex, 8–9 mm long, 1.5 mm wide at base, 0.5 mm wide at apex. Stamens 4, included; anthers linear, in the upper third of the corolla tube, cuspidate at apex, 5 mm long, 0.5 mm wide, the cusp 0.3 mm long.

From *Faramea neblinae* Steyerm. this species differs in the aristate stipules, marginally thickened nerves of the leaves, shorter pedicels, and shorter calyx and hypanthium. From *F. crassifolia* Benth. it differs in the longer corolla and anthers, differently shaped leaves, more evident lateral and tertiary nerves on the lower leaf surface, and absence of inflorescence bracts. From *F. angustifolia* Benth. & Hook. it differs in the truncate calyx and longer corolla and anthers. It differs from *F. panurensis* Muell. Arg. by having apiculate anthers, shorter peduncles, thickened marginal nerves, longer anthers, and vaginate stipules.

Faramea morilloi Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Parcela Fénologica, 16 km de Cruce con la carretera a Puerto Ayacucho–Sanariapo, via a Gavilán, 100 m, 17 Nov. 1977, *G. Morillo 6716* (holotype, VEN).

Frutex 1.5–2-metralis glaber; stipulis aristatis, artistis 4–5 mm longis; foliis lanceolato-ellipticis apice acuminatis basi acutis 8–10.5 cm longis 1.5–3.5 cm latis; nervis lateralibus principalibus utroque latere 9–11; petiolis 2–3 mm longis; inflorescentia axillari solitaria; pedicellis sub anthesi 3–5 mm longis sub fructu 5–6 mm longis; bracteis duobus apice pedicelli insidentibus subulatis 10–12 mm longis; hypanthio calyceque 5 mm longis 1.1 mm latis, hypanthio 1 mm longo; calyce sub fructu deciduo; calycis tubo 2 mm longo lobis inaequalibus subulatis 1–2 mm longis; corolla hypocrateriformi, tubo 17 mm longo 1–1.2 mm lato, lobis quattuor angusto lanceolato-subulatis 7 mm longis 1–1.5 mm latis; staminibus quattuor inclusis, antheris linearibus 3 mm longis; stylo 15 mm longo; fructu subgloboso rugoso 9 mm longo 11 mm lato; seminibus orbicularibus 7 mm diam. dorsaliter 8-costatis.

Shrub 1.5–2 m tall, glabrous. Stipular sheath 2 × 2 mm, aristae acicular, 4–5 mm long. Leaves papyraceous, lance-elliptic, acuminate at apex, acute at base, 8–10.5 cm long, 1.5–3.5 cm wide; principal lateral nerves 9–11 each side, with fainter intermediate nerves, widely spreading, conspicuously elevated and anastomosing below, inconspicuously impressed above; tertiary venation faintly reticulate above. Petioles 2–3 mm long. Inflorescence solitary, axillary, shortly pedicellate. Pedicels in anthesis 3–5 mm long, in fruit 5–6 mm long. Two bracts at apex of pedicel subulate, 10–12 mm long. Calyx and hypanthium 5 mm long, 1–1.15 mm wide; hypanthium short-columnar, 1 mm long; calyx deciduous in fruit; calyx tube short-cylindric, 2 mm long, 1.5 mm wide, twice longer than the hypanthium, the lobes unequal, 2 elongated teeth with a lateral subulate appendage, one of the teeth with 2 shorter subulate projections 0.6 mm long on one side and another short subulate projection on the side of a longer tooth. Corolla hypocrateriform, the tube very slender, 17 mm long, 1–1.2 mm wide; 4 lobes narrowly lanceolate-subulate, recurved at tip, 7 mm long 1 mm wide above base, 1.5 mm wide at base. Stamens 4, included, inserted at the summit of the corolla tube. Anthers linear, 3 mm long; filaments 1 mm long, attached 4 mm below orifice of tube. Stigmas subulate, 3 mm long. Fruit depressed-globose, rugose, broader than high, 9 mm high, 11 mm broad. Seed 1, orbicular, 7 mm diam., with 8 longitudinal ridges radiating from dorsal side.

With its solitary axillary flowers, this taxon is related to *Faramea egregia* Sanders and *F. spathacea* Muell. Arg. ex Standley. From both of these it is distinguished by the smaller calyx and hypanthium, smaller corolla tube and lobes, and shorter petioles. The rugose fruits and ridged seeds are noteworthy. From *F. brevipes* Steyerm. it differs in the deciduous fruiting calyx, acutely acuminate leaves, and setaceous (vs. subfoliaceous) bracts subtending the calyx and hypanthium.

Faramea paludicola Steyermark & Boom, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Río Negro, upper Caño Baria, "swampy" area between Río Mawarinuma and headwaters of Río Baria, ca. 0°52′N, 66°15′W, 130 m, 26 Mar. 1984 (fl. buds), *R. Liesner 16960* (holotype, MO; isotypes, NY, VEN).

A *Faramea torquata* Muell. Arg. foliis nervis marginalibus valde prominentibus differt.

Shrub 2 m tall. Stipule with shallow coriaceous sheath broader than long, 7 mm wide, 4 mm high, glabrous, with a rigid awn 3 mm long arising from the center in a depression below the summit. Leaves coriaceous, elliptic-oblong, abruptly caudate at apex, acute at base, 23–30 cm long, 7–11 cm wide, conspicuously marginally nerved, glabrous on both sides, acumen obtuse, 13–18 mm long, 1.5–2 mm wide; lateral nerves strongly elevated below, impressed above, anastomosing 7–11 mm from margin, principal elevated nerves 15–18 each side; midrib stout, elevated above, impressed below; tertiary venation finely reticulate, subelevated both sides. Petiole glabrous, stout, vaginate in upper half, open adaxially, 15–17 mm long, 4 mm wide. Inflorescence slenderly pedunculate, terminal, 2–3 pedicels arising together, purple, 3–3.5 cm long, 1 mm wide, with 3–4 axes 8–12 mm long arising umbellately and divaricately, these separated 8–10 mm distance by a second higher tier of 3 axes 6–7 mm long, terminating in a final cluster of closely positioned several axes 2–3 mm long; axes of inflorescence purple, microscopically papillate but appearing glabrous; peduncle appearing glabrous, the base subtended by 2 bracteoles united by a suborbicular sheath 1 mm long terminating abruptly in a 2–2.5 mm glabrous awn. Flowers 3–5-umbellate at the ends of the lowest primary axes on pedicels 1–2 mm long. Flowers on purple pedicels, 2–3 mm long, 1 mm wide, ebracteolate. Calyx and hypanthium microscopically papillate-puberulent, 2–2.5 mm long; hypanthium obconic, 1.5–2 mm long, 2 mm wide at summit, gradually narrowed to a base 1 mm long; calyx 2–2.5 mm wide at summit, 0.8–1 mm high, subtruncate or slightly undulate; corolla green in bud, 4 mm long, 1 mm wide at base, 0.8 mm wide at the rounded tip, microscopically papillate-puberulent; corolla lobes in bud 2.5 mm long, ligulate, obtuse; anthers 1.5 mm long, filaments 1 mm long, attached at base of corolla; gynoecium immature. Fruit unknown.

Faramea yavitensis Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Yavita, 28 Jan. 1942, *Llewelyn Williams 14026* (holotype, VEN; isotype, F).

Frutex 2-metralis glaber; stipulis aristatis, aristis 4 mm longis; foliis elliptico-oblongis apice abrupte caudatis, acumine 7–12 mm longe, basi cuneatim acutis 12–16 cm longis 4–6.5 cm latis, nervis lateralibus utroque latere 7–10, venatio tertiaria inconspicua; petiolis 1.2–1.5 cm longis; infructescentia epedunculata, axibus secundariis tribus primariis umbellatis 2.7–3.2 cm longis; axibus secundariis tribus 8–10 mm longis apicem versus dilatatis ramosis, axibus sub fructu 4–5 mm longis; pedicellis sub fructu 4–5 mm longis; bracteis sub pedicellis subulatis persistentibus 2.5 mm longis; bracteis sub axibus primariis persistentibus subulatis 5.5 mm longis, sub axibus secundariis subulatis 3.5 mm longis; calycis tubo sub fructo persistenti 1–1.5 mm longo 1 mm lato, dentibus tribus vel quattuor, setaceis persistentibus sub fructu 2–3.5 mm longis; fructu subgloboso 4–5 mm longo 6–7 mm lato.

Glabrous shrub 2 m tall. Stipular teeth linear, 4 mm long, persistent on upper nodes, deciduous or not evident on lower nodes. Leaves elliptic-oblong, abruptly caudate at apex with acumen 7–12 mm long, cuneately acute at base, 12–16 cm long, 4–6.5 cm wide; lateral nerves 7–10 each side, divaricately spreading at an angle of 5–25°, elevated below, slightly elevated or impressed above; tertiary venation inconspicuous with large, areolate, impressed reticulation on both sides. Petioles 1.2–1.5 cm long. Infructescence epedunculate, the 3 primary rays umbellate, 2.7–3.2 cm long, 1.5 mm wide, each ray terminating in 3 secondary axes 8–10 mm long and dilated apically; secondary axes ending in branches with 2 lateral fruiting pedicels 4–5 mm long on either side of a central sessile fruit. Bracts at base of axes persistent, subulate, those subtending pedicels 2.5 mm long, those subtending secondary axes 3.5

mm long, those subtending primary axes 5.5 mm long. Calyx teeth persistent in fruit, setaceous, 2–3.5 mm long. Fruit depressed-globose, 4–5 mm high, 6–7 mm broad.

This taxon is related to *Faramea multiflora* A. Rich. and its varieties (for discussion of these, see Mem. New York Bot. Gard. 17: 390–395. 1967) but differs from it and related species in having the persistent fruiting calyx with elongated teeth.

Faramea yutajensis Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: below summit of east slope of unnamed peak, 8 km NW of Yutajé settlement, 4 km west of Río Coro Coro, west of Serranía de Yutajé, 5°41′N, 66°10′W, 1,500–1,760 m, 4 Mar. 1987, *R. Liesner & B. Holst 21640* (holotype, MO; isotype, VEN).

Frutex 2-metralis glaber; stipulis aristatis, aristis 2.2 mm longis; foliis oblanceolatis vel lanceolato-ellipticis apice abrupte obtuseque acuminatis basi acute attenuatis 8–14 cm longis 2–4.7 cm latis; acumen 5–12 mm longis, 3 mm latis, nervis lateralibus principalibus utroque latere 7–11 subhorizontaliter patentibus; venatio tertiaria subtus reticulata; petiolis 3–9 mm longis; inflorescentia terminali axillarique fere sessili vel pedunculata, pedunculo solitario 10–15 mm longo glabro infra apicem 2 mm lato basi 1.5 mm lato; bracteis duobus sub fructu ovatis acutis 13–23 mm longis 6–8 mm latis glabris; fructu globoso 9–10 mm longo 10–11 mm lato calyce persistente 2 mm longo 2.5 mm lato coronato.

Glabrous shrub, the stem 1-angled or ridged on each side. Stipular sheath triangular, carinate, 1 mm long, 1.2 mm wide at base, tapering into an acicular awn 2.2 mm long. Leaves oblanceolate or lance-elliptic, abruptly and obtusely acuminate at apex, the acumen 5–12 mm long, 3 mm wide, conspicuously acutely attenuate at base, 8–14 cm long, 2–4.7 cm wide, slightly decurrent on petiole; principal lateral nerves 7–11 each side, subhorizontally spreading, anastomosing near margin, slightly elevated below, slightly sulcate above, intermediate nerves shorter and less conspicuous; tertiary venation reticulate and slightly manifest below, faintly reticulate above. Petioles 3–9 mm long. Inflorescence terminal and axillary, nearly sessile or on a peduncle 10–15 mm long. Peduncles slightly dilated to 2 mm toward summit, 1.5 mm wide at base, solitary. Subtending two bracts at base of fruit ovate, acute, 13–23 mm long, 6–8 mm wide. Fruit globose, 9–10 mm high, 10–11 mm wide, crowned by the persistent calyx tube, this 2 mm long and 2.5 mm wide.

This species is distinguished by having solitary primary inflorescence axes with only one or few flowers which terminate the peduncle and by the subtending enlarged bracts. *Faramea yutajensis* differs from *Faramea anisocalyx* Poeppig & Endl. by having smaller green bracts and by having the solitary primary ray bearing one to few flowers. From *F. parvibractea* Steyerm. and *F. cardonae* Steyerm. it differs in the solitary peduncle with one to few flowers.

FERDINANDUSA

Ferdinandusa boomii Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, Base Camp, Río Mawarinuma, 0°50′N, 66°10′W, 8 Dec. 1984, 140 m, *B. Boom & A. Weitzman 5274* (holotype, MO; isotypes, NY, VEN, GH, INPA, PORT, U, COL, BR, K).

A *F. schultesii* Steyerm. corollis longioribus, pedicellis longioribus, foliis majoribus plerumque basi late rotundatis vel subcordatis recedit; corollis 40–41 mm longis, tubo 35 mm longo; pedicellis 2–4 mm longis; foliis 7.3–14 cm longis 5–9 cm latis basi rotundatis vel paullo subcordatis.

Tree 10 m tall; stems densely puberulent; petioles glabrous both sides, 8–15 mm long. Leaf blades coriaceous, ovate to oblong-ovate, abruptly shortly and obtusely acuminate at apex, rounded or slightly subcordate at the base, 7.3–14 cm long, 5–9 cm wide, the acumen 5–6 mm long, 2–3 mm wide, glabrous on both sides; lateral nerves 7–8 each side of midrib, arcuate-ascending to the margins; tertiary venation conspicuously reticulate above, the smaller areolae 2–3 mm diam. Inflorescence terminal with 3–5 pedunculate cymes, 4–4.5 cm long, 4–4.5 cm wide, each cyme 4–12-flowered; peduncle of each cyme 1–2 cm long, minutely puberulent-hirtellous with divaricate hairs; axes of cyme similarly pubescent. Calyx and hypanthium 2–2.5 mm long, the hypanthium columnar-obconic; calyx lobes 4, deltoid, obtusely acute, 0.2–0.5 mm long, 0.7 mm wide at base, sparsely short ciliolate on margins and in sinuses, apparently eglandular within. Disk shorter than to equaling calyx lobes. Corolla 40–41 mm long, glabrous without and within, the tube 35 mm long, 2.5 mm wide throughout except at orifice where 5 mm wide; 4 lobes 4 mm long, 4.5–5 mm wide, lobed above the middle, glabrous within and at sinuses; 4 stamens unequally inserted above style, in the upper ⅛ of the tube; anthers broadly oblong, 1.2 mm long, rounded at both ends; filaments 5 mm long. Style ending 7 mm below orifice of corolla.

From *Ferdinandusa schultesii* Steyerm. to which this species is related, it is separated by the longer corolla and corolla tube, longer pedicels, and larger leaves generally broadly rounded to subcordate at the base.

MORINDA

Morinda longipedunculata Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro de la Neblina, Canyon Grande, along Río Mawarinuma between the mouth of the canyon and the first major fork of the river, 7 airline km ENE of Puerto Chimo, 0°50′N, 66°02′W, 350–400 m, 9–14 July 1984, *G. Davidse & J. S. Miller 27327* (holotype, MO; isotype, VEN). Figure 9.

Frutex 2-metralis; foliis late oblanceolatis apice abrupte caudatis basi cuneatis 17–30 cm longis 6–8 cm latis supra glabris subtus modice hirtellis pilis patentibus instructis; pedunculis axillaribus 20 cm longis breviter puberulis; floribus 4-meris; calyce cupuliformi-campanulato 1.5 × 1.5 mm subtruncato extus hispidulo; corolla cylindrica extremitatibus angustatis alabastro 8 mm longa extus hispidula.

Shrub 2 m tall; upper part of stems densely pubescent with short, appressed-ascending hairs. Stipule deeply bifid, short-pubescent without, the subulate teeth 2.5 mm long. Petioles 1.5–2 cm long, moderately hirtellous. Leaf blades membranous, broadly oblanceolate, abruptly caudate at apex, long tapering to a cuneate decurrent base, 17–30 cm long, 6–8 cm wide, upper surface with scattered, pale raphides, glabrous, the lower surface moderately hirtellous with spreading hairs; midrib and lateral nerves densely pubescent with spreading hairs 0.5–0.6 mm long; lateral nerves 9–10 each side; tertiary venation inconspicuous below, scarcely manifest above. Peduncles axillary, greatly elongated, equaling or slightly shorter than leaves, 20 cm long, 2 mm wide, moderately shortly puberulous, apically branched into 3–4 primary axes 9 mm long in anthesis, the primary axes again branched into 3–4 secondary axes 3–4 mm long (in anthesis), 10 mm long (in fruit). Bracts at base of secondary axes shallowly 3–4-lobed, 2 mm long (fruiting). Flowers 4-merous, at summit of secondary axes, congested, sessile, several. Calyx cupuliform-campanulate, 1.5 × 1.5 mm, subtruncate with shallowly raised border, hispidulous without. Corolla cylindric-tubular, 8 mm long (late bud), 1.5 mm wide at the middle, slightly narrower at apex and base, outer surface hispidulous except glabrous in basal 1.2 mm; tube glabrous within; lobes suborbicular, rounded, 0.5 × 0.5 mm. Stamens inserted in the lower third of the corolla; anthers linear-oblong, 2.2 mm long. Disk cupuliform, 0.5 mm high. Ovary 4-celled. Fruit dark red, globose, 7–8 mm long, 8–8.5 mm diam., umbonate, 4-seeded.

This taxon is noteworthy for the exceptionally elongated peduncle.

PSYCHOTRIA

Psychotria anartiothrix Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, lower part of Río Baria, inundated forest along river, 1°10′N, 66°25′W, 22–23 July 1984, 80 m, *Gerrit Davidse 27651* (holotype, MO; isotype, VEN).

Frutex 2-metralis, stipularum aristis acicularibus 5–6 mm longis minute puberulentibus glabrescentibus; foliis elliptico-lanceolatis extremitatibus acutis 4–8.5 cm longis 1–2.5 cm latis; inflorescentia dense cymoso-corymbosa,

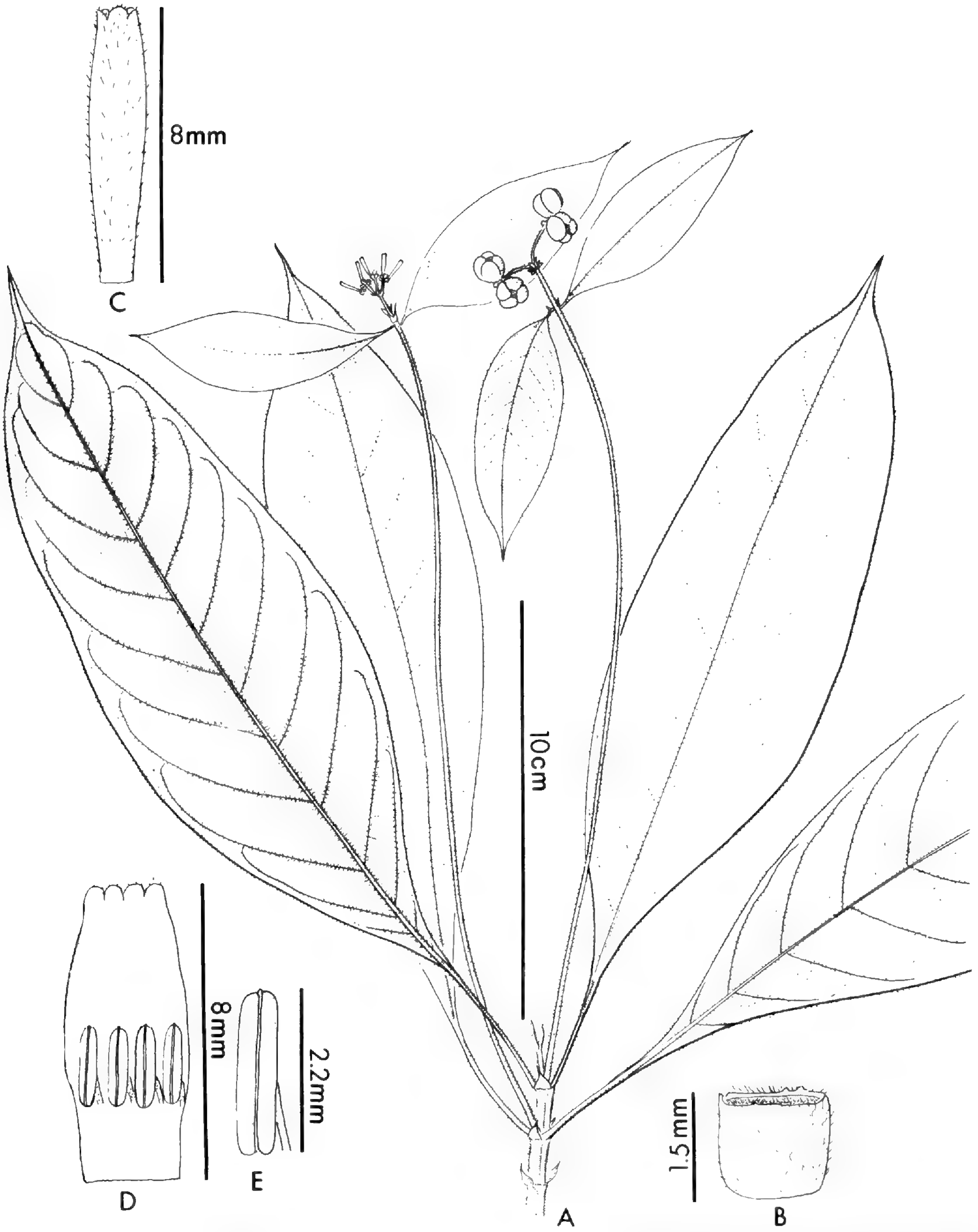

FIGURE 9. Morinda longipedunculata.—*A. Habit of flowering and fruiting branch.—B. Calyx and hypanthium.—C. Corolla, late bud stage.—D. Corolla, interior view.—E. Stamen, ventral view.*

axibus principalibus tribus angulis superioribus seriebus verticalibus pilis brevibus divaricatis rigidiusculis praeditis; corollae tubo hypanthioque similiter pubescentibus.

Shrub 2 m tall with glabrous stems. Stipular sheath 1 mm long, 2 mm wide, truncate, bearing on each side 2 acicular teeth 5–6 mm long arising 0.3 mm below summit of sheath, minutely puberulent becoming glabrous. Leaf blades subcoriaceous, elliptic-lanceolate, acute at base and apex, 4–8.5 cm long, 1–2.5 cm wide, glabrous throughout except for minutely hispidulous puberulous midrib on lower side, or completely glabrous; lateral nerves 8–9 on each side of midrib, arcuately ascending at 15–30°, subelevated below, slightly anastomosing near (1–2 mm) the margin, inconspicuous above; tertiary nerves slightly evident both sides. Inflorescence densely cymose-corymbose, 8 mm high, 1.6 cm broad, pedunculate; peduncle 1.4–1.8 cm long, 1 mm diam., microscopically puberulent on the angles with spreading hairs. Three main axes of inflorescence 2–3 mm long, 0.5–1 mm wide, densely flowered, shortly branched, microscopically puberulent with spreading, stiff, puberulent-hispidulous hairs in vertical lines on the angles. Flowers sessile; calyx and hypanthium 1.2 mm long in anthesis; hypanthium short-columnar, 0.5 mm long, 0.4 mm wide, minutely hispidulous on angles, glabrous elsewhere; calyx cupulate, 5-lobed, 0.7 mm long, 1.1 mm broad; teeth broadly shallowly triangular, subacute, 0.5 mm long, 0.8 mm wide, ciliolate on margins, dorsally puberulent, eglandular within. Corolla white, cylindric, broadened at orifice, 5 mm long; tube 3.5 mm long, 0.7 mm wide except 1 mm wide at orifice and 0.9 mm wide at base, sparsely puberulent-hispidulous in lines without, pilose in upper 1.5 mm within; 5 lobes fleshy and thickened with a corniculate apex 1.5 mm long, 0.6 mm wide, puberulent in lines. Stamens 5, included, attaining the orifice, the upper half of corolla; anthers linear, obtuse at apex, 0.8 mm long. Stigmas 2, rhomboid-ligulate, truncate at apex, papillate-puberulent, 0.3 mm long; style filiform, papillate, 3 mm long. Disk depressed cupulate, shorter than calyx lobes, 0.4 mm high. Fruit orange, globose, 5 × 5 mm; pyrene dorsally acutely 3-costate, ventrally flat with a narrow sulcate depression along the middle.

The minute puberulence of short, stiffish, divaricate hairs in more or less irregular vertical lines along the upper angles of the inflorescence axes, exterior of corolla tube, and the hypanthium is characteristic of this taxon.

Psychotria edaphothrix Steyermark, sp. nov. TYPE: Venezuela. Bolívar: 0–3 km west of El Polo (8.6 km west of El Pauji), 4°30′N, 61°40′W, 650–800 m, 5 Nov. 1985, *R. Liesner 19595* (holotype, MO; isotype, VEN). Figure 10.

Frutex 3-metralis; stipulae vagina 2 mm longa 5.5 mm lata glabra in dentes duos triangulari-lanceolatos longiattenuatos 4 mm longos 1.5 mm latos glabros desinenti; foliorum laminis oblongo-ellipticis vel late oblanceolatis apice acuminatis basi acutis utrinque glabris; nervis lateralibus principalibus utroque latere 17–21; venulis tertiariis cum nervis lateralibus conspicue transversim conjunctivis; inflorescentia capitulis subhemisphaericis tribus densifloris praedita, pedunculo 1.2–6 cm longo dense tomentoso pilis brunneis divaricatis munito; hypanthio dense tomentoso-hirsutulo; calycis lobis 0.8 mm longis ciliatis; corolla alba, sub anthesi 14 mm longa basi 2 mm lata omnino symmetrica, tubo intus basi pilis brevibus vestito.

Shrub 3 m tall, the stem glabrous. Stipule sheath 2 mm high, 5.5 mm wide, glabrous with 2 triangular-lanceolate, long-attenuate teeth on each side, 4 mm long, 1.5 mm wide at base, interior of sheath with numerous aculeiform processes. Leaves oblong-elliptic to broadly oblanceolate, acuminate at apex, acute at base, (9.5–)17–25 cm long, (3–)6–8.5 cm wide, glabrous both sides; lateral nerves 17–21 each side, ascending at an angle of 25–35°, elevated below, impressed above; tertiary veinlets conspicuously transversely connecting the secondary nerves, conspicuously elevated below with reticulate pattern. Inflorescence 2.5–4 cm high, 2.5–6 cm wide, divided into 3 densely-flowered, subhemispherical heads, these 1.7–2.5 cm high, 1–3 cm broad; peduncle 1.2–6 cm long, 1.5–2.5 mm wide, densely brown tomentose with spreading hairs. Main axes of inflorescence 0.8–2 cm long, ascending to divaricate, densely brown tomentose. Bracts of inflorescence lanceolate, caudate-acuminate, arising at the sides and apices of the axes, but not at their bases. Flowers 15–21 in one branched axis, 42–63 in one inflorescence, sessile, each flower subtended laterally by 2 lanceolate, caudate bracts 6 mm long, 1 mm wide, puberulous on both sides, the 2 bracts subtended by a larger middle bract 9 mm long, 2.5 mm wide, oblanceolate, acuminate-caudate, puberulous on both sides, with a larger outer bract, this lanceolate, caudate-acuminate, 13 mm long, 3 mm wide, puberulous on both sides. Calyx and hypanthium 2 mm long, the hypanthium 0.5 mm high, 1.5 mm wide,

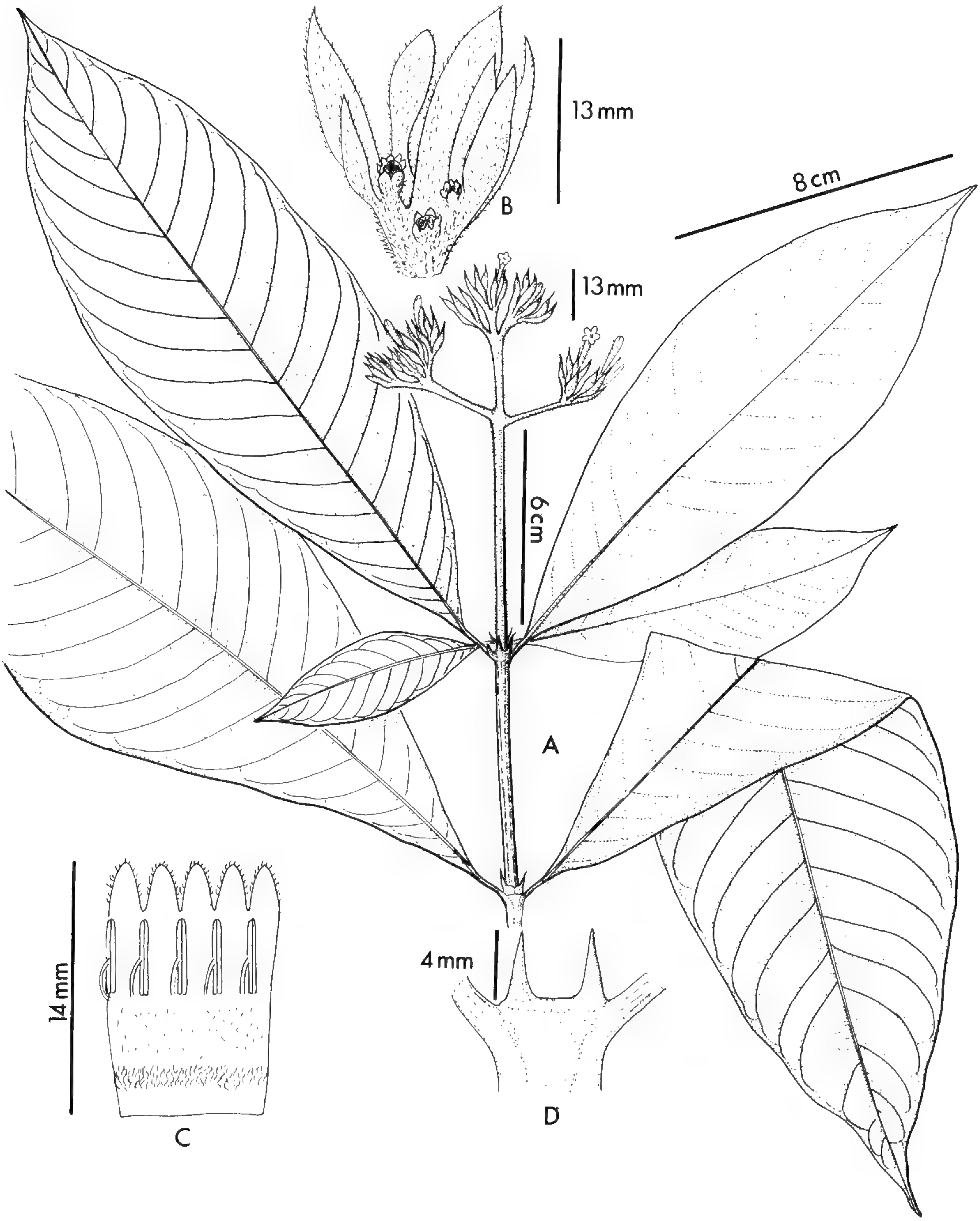

FIGURE 10. Psychotria edaphothrix.—*A. Habit of flowering branch.—B. Portion of inflorescence, corollas absent.—C. Corolla, interior view.—D. Stipule with bases of petioles.*

densely brown tomentose-hirsutulous; calyx lobes 5, deltoid, obtusely acute, 0.8 mm long, 1 mm wide at base, ciliate, glandular within in sinuses. Corolla white, cylindric, symmetric, 14 mm long, 3.5 mm wide below orifice, 2 mm wide at base, densely pilosulous without with spreading hairs, glabrous without at the very base, within shortly pubescent at base with a zone of hairs 1 mm above base; corolla lobes oblong-ovate, 2 mm long, 1.2–1.5 mm wide. Stamens 5, included in the upper half; anthers linear, obtuse at apex, 3 mm long, the filaments inserted half way up corolla tube. Disk subcupulate, about the height of the calyx tube.

Psychotria edaphothrix is somewhat intermediate between *Palicourea* and *Psychotria*, in some respects resembling *Palicourea longistipulata* (Muell. Arg.) Standley in the densely pubescent zone confined to the interior base of the corolla tube, aculeiform structures within the stipular sheath, pubescent exterior of the corolla, and large leaves with numerous lateral nerves. It differs, however, in the large subtending bracts of the compact inflorescence, densely tomentose calyx, glabrous stem and leaves, and white, symmetrical corolla and white bracts. In other respects the new taxon resembles *Psychotria maturacensis* Steyerm. of the Neblina area, but the stipular sheath is conspicuously bidentate on each side, the hypanthium is densely tomentose, the calyx lobes are conspicuous and densely ciliate, and the leaves have more lateral nerves on each side. Since the corolla is symmetrical and shows no gibbosity at base, I am including it in *Psychotria* as a borderline species.

Psychotria pectinata Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, white water tributary of Río Mawarinuma, ca. 3 km upstream (SE) of Base Camp, 0°49'N, 66°08'W, 150 m, 17 July 1984, *Ronald Liesner 15955* (holotype, MO; isotype, VEN). Figure 11.

Frutex 0.75–2 metralis, caulibus glabris; stipulae dentibus setaceis 4–5 mm longis 0.2–0.3 mm latis dense pectinato-ciliatis pilis brunneo-hirtellis vestitis; foliorum laminis anguste oblanceolatis vel lanceolato-ellipticis apice acutis vel acuminatis basi cuneatim acutis utrinque glabris 10–15 cm longis 1.5–2.5 cm latis; inflorescentia monocephala vel in capitula tria vel quattuor ramosa 5–6 mm longo 10–11 mm lato densiflora; pedunculo 3–13 mm longo 1 mm lato glabro; bracteis sub inflorescentia duas, anguste lanceolatis 4 mm longis; floribus parvis, corollae tubo 2 mm longo, lobis 1.8 mm longis valde corniculatis; fructu elliptico-oblongo 9 mm longo 5 mm lato obtuse 10-costato.

Shrub 0.75–2 m tall, the stems glabrous. Stipular sheath 2.5–3 mm long, 4 mm wide with 2 elongated, setaceous or lance-linear teeth 4–5 mm long, 0.2–0.3 mm wide, densely pectinate-ciliate with brown, hirtellous hairs. Petiole 5–15 mm long, glabrous. Leaves lanceolate-elliptic or narrowly oblanceolate, acute to acuminate at apex, cuneately acute at base, partly decurrent on the petiole, 10–15 cm long 1.5–2.5 cm wide, glabrous on both sides; lateral nerves 8–10 each side of the midrib, 1.5–3 mm distant, slightly impressed on both sides, the midrib slightly raised above. Inflorescence capitate, 5–6 mm high, 10–11 mm broad, monocephalous or branched into 3–4 heads, 15–40-flowered, axillary or terminal, with 2 spreading bracts at the base at the summit of the peduncle. Peduncle erect, 3–13 mm long, 1 mm wide, glabrous. Each axis of the inflorescence bearing ca. 5 closely crowded, pedicellate flowers and subtended by 3–4 lanceolate, acute, brown-ciliate bracts 1.5 mm long. Pedicels 0.5–1 mm long, glabrous. Calyx tube and hypanthium 1.5–2 mm long, glabrous; hypanthium obconic, 1 mm long, 1–1.5 mm above; calyx lobes 5, conspicuous, spreading and slightly squarrose, lanceolate, acute, 0.8–1.5 mm long, 0.5–0.6 mm wide, ciliolate. Disk higher than calyx tube in anthesis, fleshy, oblong-ovoid. Corolla white, small, the tube broadly cylindric, 2 mm long, 1.5 mm wide at summit, 1.3 mm wide at base, glabrous without; lobes 5, recurved, 1.8 mm long, 0.8 mm wide, conspicuously corniculate, the tube densely pubescent within at orifice. Stamens at orifice, slightly protruding above the tube; anthers 0.5 mm long; filaments 0.4 mm long. Style filiform, glabrous, 2 mm long, exserted. Fruit elliptic-oblong, 9 mm long, 5 mm wide, glabrous, obtusely 10-costate, crowned by the persistent calyx.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro de la Neblina, Río Mawarinuma, upstream from Base Camp, 0°50'N, 66°10'W, 140 m, 2 May 1984, *Stein, Gentry & Thomas 1715* (MO, VEN); Cerro de la Neblina, Caño Blanco, white water tributary of Río Mawarinuma, ca. 3 km upstream (SE) of Base Camp, 0°49'N, 66°8'W, 150 m, *Miller 1766* (MO, VEN); same locality, *Boom et al. 5714* (MO, GH, INPA, PORT, U, NY, VEN); same locality, *Croat 59612* (MO, VEN).

This species is readily distinguished by the densely hirtellous, pectinate-ciliate stipular

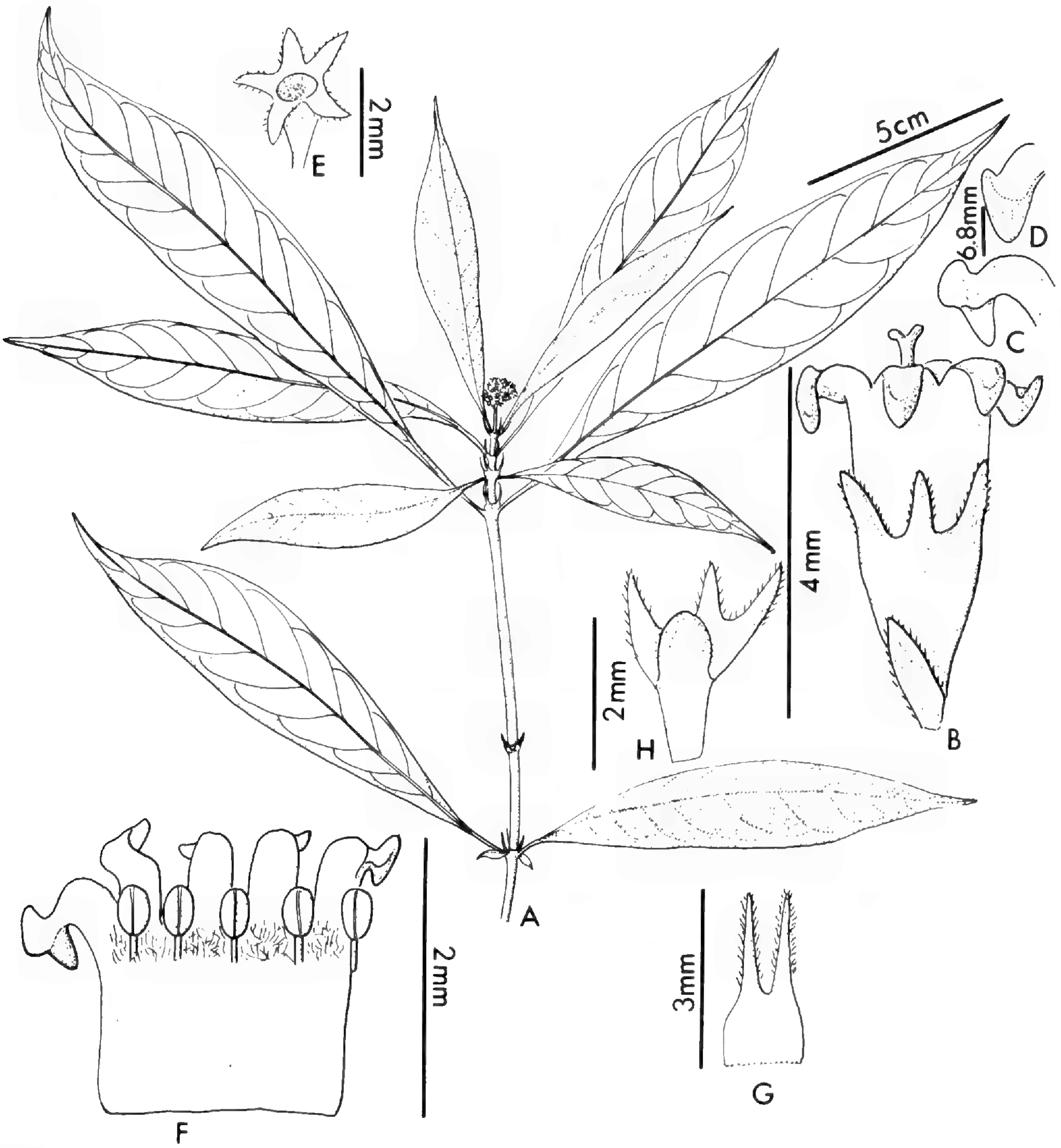

FIGURE 11. Psychotria pectinata.—*A. Habit of flowering branch.—B. Flower from outer portion of inflorescence with a subtending bract.—C, D. Showing corniculate corolla lobe.—E. Calyx and hypanthium.—F. Corolla, interior view.—G. Stipule.—H. Disk and portion of calyx and hypanthium.*

teeth, densely flowered heads of small flowers, brown-ciliate, elongate calyx lobes, and strongly corniculate corolla lobes. It was noted that within a densely flowered head of an inflorescence only one or a few flowers produce seed, and the majority do not possess a fertile ovary. There may be a tendency here for monoecism.

Psychotria steinii Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, summit, Camp 2, 2–8 km NE of Pico Phelps, 0°49′40″N, 65°59′W, 15 Apr. 1984, 2,100 m, *B. A. Stein & A. Gentry 1553* (holotype, MO; isotype, VEN). Figure 12.

Suffrutex vel subherbacea 0.35–1-metralis, caulibus plerumque glabris; foliorum laminis ovatis apice acuminatis basi acutis vel obtusis 2.5–4.5 cm longis 0.9–1.5 cm latis utrinque glabris marginibus valde ciliatis; petiolis 2–3 mm longis; inflorescentia terminali plerumque tribus simul, omnibus conspicue bracteatis, bracteis foliaceis 4–7 ovatis acutis vel acuminatis 8–13 mm longis 3–5 mm latis glabris vel basim versus sparsim hirtellis, marginibus ciliatis; pedunculo pubescenti; inflorescentiae axibus pubescentibus; corolla 11–11.5 mm longa, tubo intus minute papillato sed admodum glabro extus glabro.

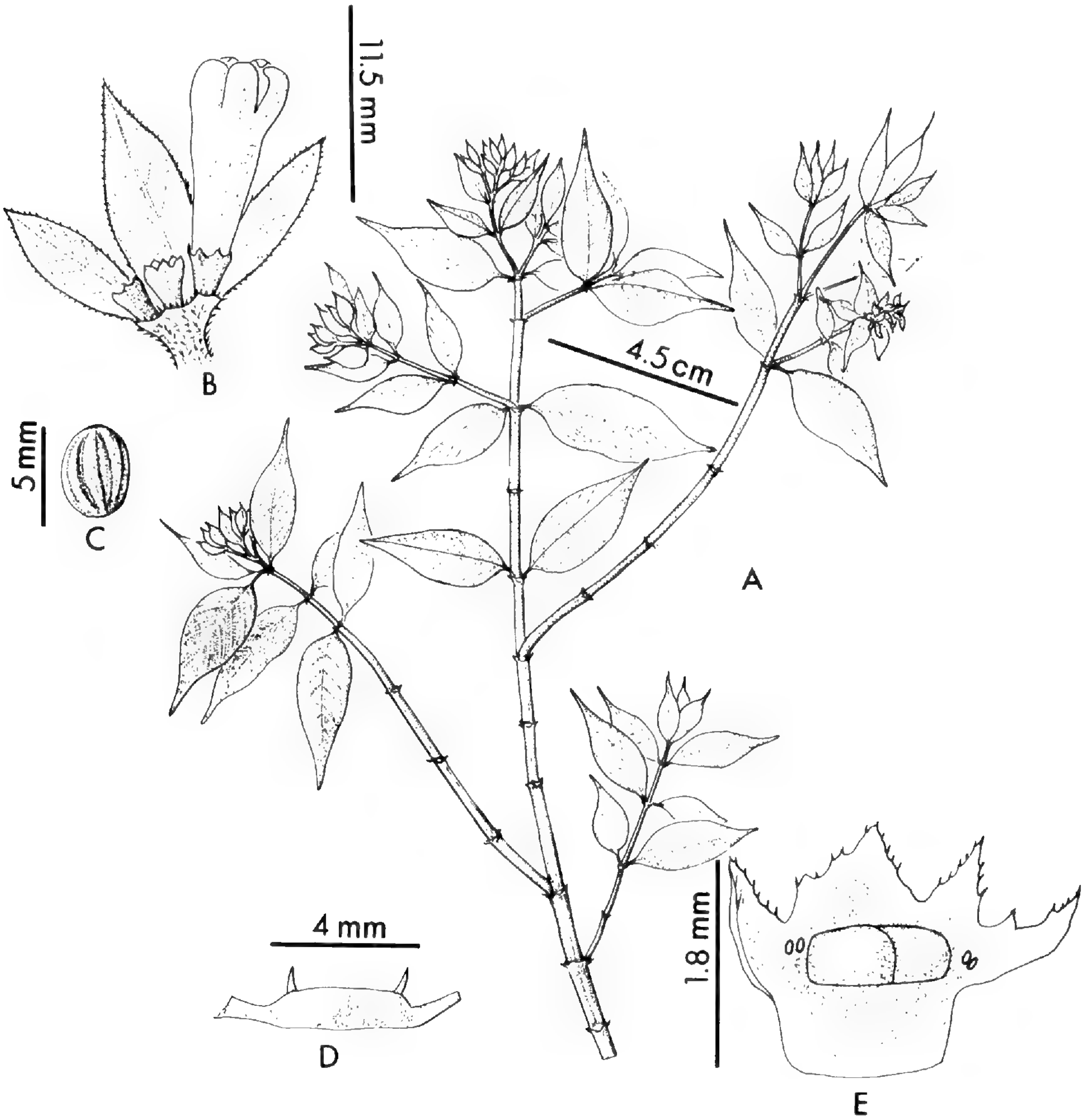

FIGURE 12. Psychotria steinii.—*A. Habit of flowering branch.—B. Portion of inflorescence.—C. Pyrene.—D. Stipule with bases of petioles.—E. Calyx, showing portion of interior with calycine glands and disk.*

Subherbaceous or suffruticose plant 0.35–1 m tall, the stems glabrous except at upper youngest nodes where hirtellous with spreading hairs. Stipule with a shallow sheath 0.2–0.5 mm high, 1–4 mm wide, glabrous, indurated with 2 teeth on each side, linear-lanceolate, acute, 0.5–0.8 mm long. Leaves shortly petiolate, leaf blades subcoriaceous, ovate, acuminate at apex, acute to obtuse at base, 2.5–4.5 cm long, 0.9–1.5 cm wide, glabrous on both surfaces, the margins strongly ciliate, the lower side with conspicuous cystoliths; midrib below glabrous to hirsutulous-ciliolate along margins; lateral nerves 6–8 on each side of the midrib, sulcate above, slightly elevated below, ascending at a 45° angle, ending near or at margins without anastomosing; tertiary venation inconspicuous; petioles 2–3 mm long. Inflorescence terminal, usually 3 together; each inflorescence with 4–7 conspicuous, foliaceous bracts arising at the summit of 2 short lateral axes 1–2 mm long and 1 central subsessile axis scarcely 1 mm long; bracts green, similar to leaves in shape but smaller, ovate to elliptic-oblanceolate, acute to acuminate, 8–13 mm long, 3–5 mm wide, glabrous or sparsely hirtellous toward base, the margins ciliolate, the narrower lateral bracts narrowed to a subpetiolate base, the broader bract subtending the inflorescence at a slightly lower level and not narrowed at base. Peduncle 3–10 mm long, 0.6–0.8 mm wide, densely hirtellous with spreading hairs 0.1 mm long. Flowers sessile, 2, or 2 on each axis. Calyx and hypanthium 1.5–1.8 mm long; hypanthium short columnar, 1 mm long, 1 mm wide at summit, glabrous; calyx 0.8–1 mm long, unequally 5-lobed, the tube 0.5–0.6 mm long, 1.5 mm wide, glabrous without; lobes broadly triangular, narrowed to a subacute apex, 0.5–0.7 mm long, ciliolate on margins, glabrous elsewhere, irregularly erose, glandular within at base of each of the 5 sinuses. Corolla white, tubular-infundibuliform, 11–11.5 mm long, the tube gradually enlarged upward, 7–8 mm long, 2 mm wide at base, 4 mm wide at orifice, glabrous without, within microscopically papillate but essentially glabrous; lobes 5, 4–4.5 mm long, 2 mm wide, ligulate-oblong, obtuse, glabrous without, microscopically papillate within but essentially glabrous. Stamens protruding slightly above orifice; anthers linear, 2.5 mm long, 0.4 mm wide at the orifice; filaments attached in upper half of tube, 2 mm long; disk shorter than calyx tube. Fruit blue, fleshy, subglobose, 11 mm long, 12 mm wide, 2-seeded; pyrenes broadly ovoid, dorsally 3-costate with 1 additional costa on each side, the inner face subconcave, 5 mm long, 3.5 mm wide.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro de la Neblina, Camp 12, Venezuelan-Brazilian frontier, 1,950 m, 26–27 Feb. 1985, *Boom et al. 5982* (MO, VEN, GH, INPA, NY).

This taxon is related to *Psychotria duidana* Standley of Cerro Duida and *P. oblata* of Mount Roraima. It is characterized by the essentially glabrous, although minutely papillate, interior of the corolla tube, much smaller, ciliolate leaves, densely pubescent peduncle, smaller corolla, and pubescent axes of the inflorescence above the peduncle.

Psychotria thesceloantha Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: upper Caño Baria, swampy area between Río Mawarinuma and headwaters of Río Baria, 0°52′N, 66°15′W, 130 m, 4 Dec. 1984, *R. Liesner 16963* (holotype, MO; isotype, VEN). Figure 13.

Suffrutex 1-metralis, caulibus glabris; stipulae vagina truncata 5 mm longa 9 mm lata glabra; foliorum laminis elliptico-ovatis apice acutis vel obtuse subacuminatis basi cuneatim acutis 21–24 cm longis 10–11 cm latis; inflorescentia axillari ut videtur monocephala 2 cm longa 4 cm lata brevipedunculata, petiolo 0.4 mm longo glabro; bracteis extimis quattuor capitulum cingentibus basi liberis, elliptico-ovatis, apice abrupte acuminatis basi rotundatis 2 cm longis 1.3–1.5 cm latis extus puberulentibus intus glabris; floribus omnibus a bracteolis duabus circumcinctis bracteolis lanceolato-linearibus acuminatis 13 mm longis 1.5 mm latis setuloso-serrulatis; calycis lobis aristatis 2.5–4 mm longis ciliato-plumosis.

Suffruticose plant 1 m tall, the stem glabrous, 4–5 mm diam. except 8–10 mm diam. at nodes. Leaves large, submembranous, leaf blades elliptic-ovate, the apex acute to obtusely subacuminate, the base cuneately acute, 21–24 cm long, 10–11 cm wide, glabrous below except minutely sparsely puberulent on midrib and nerves; lateral nerves 10–11 each side; tertiary venation not evident; petiole 4.5–5 cm long, glabrous to sparsely puberulent. Inflorescence axillary, subhemispheric, 2 cm long, 4 cm wide, appearing monocephalous on a short glabrous peduncle 0.4 mm long, not enveloped by the stipular sheath, consisting of 3–4 separate monocephalous heads in a compact mass appearing as monocephalous, each portion of the head hemispheric, 1.8–2 cm long, 2–2.8 cm wide, the complete head surrounded by 4 main outermost bracts separate to the base, elliptic-ovate, abruptly acuminate, rounded at base, carinate, 2 cm long, 1.3–1.5 cm wide, puberulent without, glabrous within; large bracts within the outermost bract broadly ovate, acute, ecarinate, 1.5 cm long, 1 cm wide, puberulent without, glabrous within; each of the 3–4 smaller heads consisting of multibracteate flowers, each surrounded by an obovate, abruptly acuminate bractlet 1.5 cm long, 0.5 cm wide, puberulent on both sides; each bractlet subtending 2 oblanceolate bracteoles rounded at apex, 1.2–1.3 cm long, 0.4 cm wide, puberulent without, sparsely puberulent within and subtending a group of 3 flowers; each pair of bracteoles subtending an ultimate pair of floral bracteoles, these lanceolate-linear, acumin-

FIGURE 13. Psychotria thesceloantha.—*A. Habit of flowering branch.—B. Individual flower without corolla, subtended by two bracteoles and a bract.—C. Inflorescence with bracts.—D. One of the inner bracts of the inflorescence.*

ate, 1.3 cm long, 1.5 mm wide, setulose-serrulate in the upper half of the margins. Hypanthium obconic-columnar, 2 mm long, 1 mm wide, glabrous; calyx lobes 5, setaceous, unequal, plumose-ciliate.

This unusual species has large, axillary, compound inflorescences that appear to be monocephalous but are composed of 3–4 condensed heads having the outermost and major bracts separate to the base. The ultimate three flowers are surrounded by narrowly oblanceolate, serrulate-ciliolate bractlets, with the large inner bracts acuminate and puberulent on both sides, while the calyx lobes are elongate, awnlike, and plumose-ciliate. In the present taxon the inflorescence is not enveloped by the stipular sheath as in *Psychotria celiae* Steyerm. of Cerro de la Neblina.

Psychotria yutajensis Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Atures, summit of east slope of unnamed peak, 8 km NW of Yutajé settlement, 4 km west of Río Coro Coro, west of Serranía Yutajé, 5°41′N, 66°10′W, 1,500–1,760 m, 4 Mar. 1987, *R. Liesner & B. Holst 21649* (holotype, MO; isotype, VEN).

Frutex 1.5-metralis glaber; stipulis leviter dentatis, vagina 1.5 mm alta 4–6 mm lata, utroque latere bidentatis, dentibus late ovato-lanceolatis acutis 1–2 mm longis intus sericeis; petiolis 9–20 mm longis; inflorescentia terminali multiflora subcorymboso-cymoso vel cymoso-subhemisphaerica pedunculo excluso sub anthesi 2–2.5 cm longa 3–4 cm lata, axibus 5–8 cum rhachidi minute puberulentibus sub anthesi 3–15 mm longis sub fructu 10–23 mm longo, supremis brevissimis; pedunculo 10–12 mm longo 2 mm lato glabro; bracteis sub axibus lanceolato-triangularibus apice attenuatis; floribus 5-meris pedicellatis, pedicellis articulatis 0.5–1.5 mm longis 0.5–0.8 mm latis; calyce hypanthioque 2.3 mm longo, hypanthio doliiformi vel breviter cylindrico 1.2 × 1.2 mm minute puberulenti; calyce 1.2 mm longo 1.5 mm lato minute puberulenti, tubo 1 mm longo intus ad medium infra sinus 1-glandulifero, calycis dentibus triangulari-lanceolatis acutis 0.2–0.3 mm longis; corolla doliiformi 3 mm longa ad medium 1.6 mm lata, tubo 2.5 mm longo extus dense papillato-puberulenti, lobis lineari-oblongis obtusis 0.7 mm longis 0.4 mm latis dorso conspicue corniculatis, corniculis incrassatis; staminibus prope basim corollae insertis; bacca subbilobata 4–5 mm longa 6 mm lata calyce persistenti coronata; pyrenis subglobosis 3.5 × 3.5 mm dorso convexis ventraliter concavis.

Glabrous shrub 1.5 m tall. Stipular sheath shallow, 1.5 mm high, 4–6 mm wide, laterally 2-toothed on each side with the teeth broadly ovate-lanceolate, acute, 1–2 mm long, sericeous within. Leaves chartaceous, lanceolate-elliptic, broadest at the middle, acute at base and apex, 8–13 cm long, 2.5–5 cm wide. Petioles 9–20 mm long. Inflorescence terminal, many-flowered, 2–2.5 cm high excluding the peduncle, 3–4 cm wide in anthesis, 2.5–3.5 cm high, 4–7 cm wide in fruit, the 5–8 axes irregularly and ± trichotomously branched at the apices, in anthesis 3–15 mm long, in fruit 10–23 mm long, 1–1.5 mm wide, the upper ones the shortest. Peduncle green, becoming purple, 10–12 mm long, 2 mm wide, glabrous. Bracts at the base of the axes lance-triangular with subulate tips, 0.6–1 mm long, glabrous. Flowers numerous, 5-merous, pedicellate, pedicels green becoming gray-purple, 0.5–1.5 mm long, articulate. Calyx and hypanthium 2.3 mm long, the hypanthium barrel-shaped or shortly cylindric, 1.2 × 1.2 mm, minutely puberulent; calyx 1.2 mm high, 1.5 mm wide, minutely puberulent, the tube longer than the teeth, these triangular-lanceolate, acute, 0.2–0.3 mm long; interior of tube bearing 1 gland at the middle beneath each sinus and alternating with each calyx tooth. Corolla white, barrel-shaped, 3 mm long, 1 mm wide at base, 1.6 mm wide at the middle, 1.2 mm wide at the summit, tube 2.5 mm long, densely papillate-puberulent without, glabrous within; 5 lobes linear-oblong, obtuse, 0.7 mm long, 0.4 mm wide, conspicuously dorsally corniculate with a thickened appendage. Stamens 5, inserted at the base of the corolla; anthers 2 mm long, 0.3 mm wide. Style 0.8–1 mm long; stigmas linear-lanceolate, acute. Disk cupular, 0.3 mm high. Fruit green to purplish black, ± bilobed, 4–5 mm high, 6 mm broad, shallowly crowned by the persistent calyx. Pyrenes 2, subglobose, 3.5 × 3.5 mm, convex dorsally, concave ventrally.

This species is related to *Psychotria ceratantha* Standley & Steyerm. of the Venezuelan Guayana, from which it differs in the smaller corollas with internally glabrous tubes with the stamens attached at the base.

RUDGEA

Rudgea corocoroensis Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: 5–8 km NW of Yutajé settlement, 3 km west of Río Coro Coro, along stream on south slope below plateau, E side of unnamed peak, W of Serranía Yutajé, 5°40′N, 66°9′W, 700–1,000 m, 10 Mar. 1987, *R. Liesner & B. Holst 21827* (holotype, MO; isotype, VEN).

Arbor 4-metralis; stipularum vaginis 2–3 mm longis glabris apice vel infra apicem aculeis 5–7 rigidis 2–4 mm longis munitis; foliis anguste oblongo-lanceolatis apice acutis vel subobtusis basi obtusis vel subobtusis glabris; nervis lateralibus utroque latere 10–11 valde adscendentibus; venatio tertiaria obsoleta vel inconspicua; petiolis 3–7 mm longis glabris. Inflorescentia terminali thyrsoideo-paniculata pedunculo excluso 2–3 cm longa 1.5–2 cm lata, seriebus verticalibus tribus principalibus ordinatis, axibus infimis 4–5-verticillatis 4–8 mm longis dense pilosulis, aliis brevioribus; pedunculo 2–2.5 cm longo pilosulo; bracteis quattuor sub verticillo infimo suborbicularibus 3 × 3 mm marginibus ciliolatis; quoque axe in flores 6–7 aggregatos sessiles desinenti; bractea involucrali ciliolata patenti sub basi florium; pedunculo 2–2.5 cm longo pilosulo; hypanthio brevicampanulato 1 mm longo 1.5 mm lato; calycis tubo 2 mm longo 1 mm lato glabro, lobis 4–5 inaequalibus lanceolatis subacutis vel obtusis majoribus 1.2–1.8 mm longis 0.7 mm latis, brevioribus 1 mm longis dense ciliolatis; corolla infundibuliformi, tubo 2 mm longo orificio deorsumque 1 mm dense pilosulo extus glabro; lobis quinque lanceolatis-oblongis acutis 4 mm longis 1.2 mm latis extus glabris intus dense minuteque papillatis; staminibus paullo exsertis, antheris 1.2 mm longis.

Tree 4 m tall. Branchlets glabrous. Stipular sheath 2–3 mm long, glabrous, with 5–7 rigid aculeae arising at or just below the sheath summit. Leaf blade subcoriaceous, narrowly oblong-lanceolate, acute or obtuse at apex, obtuse to subobtuse at base, 7–10 cm long, 2–4 cm wide, glabrous on both sides, slightly revolute; lateral nerves 10–11 on each side, strongly ascending, scarcely anastomosing; tertiary venation obsolete or inconpsicuous. Petiole 3–7 mm long, glabrous. Inflorescence terminal, pedunculate, thyrsoid-paniculate, 2–3 cm long excluding the peduncle, 1.5–2 cm wide, in 3 main verticillate tiers, the lowest tier 12–17 mm distant below the middle tier; lowest axes 4–5-verticillate, 4–8 mm long, densely pilosulous, the other verticels with shorter axes; each axis subtended by spreading, glabrous, ciliolate involucral bract, terminating in a congested group of 6–7 sessile flowers. Peduncle 2–2.5 cm long, pilosulous, 4 suborbicular bracts 3 × 3 mm subtending base of main lowest verticels. Hypanthium short-campanulate, 1 mm long, 1.5 mm wide, glabrous. Calyx tube 2 mm long, 1 mm wide, glabrous. Calyx lobes 4–5, unequal, lanceolate, subacute to obtuse, the longer lobes 1.2–1.8 mm long, 0.7 mm wide, the shorter 1 mm long, densely ciliolate. Corolla white, subinfundibuliform, the tube 2 mm long, 1.5 mm wide at base, 2 mm wide above, densely pilose at orifice and 1 mm downward; lobes 5, lanceolate-oblong, acute with involute tip, 4 mm long, 1.2 mm wide, glabrous without, densely minutely gray papillate within. Stamens 5, slightly exserted, anthers 1.2 mm long; filaments 0.8 mm long, glabrous. Style 8 mm long, scabridulous-papillate, stigmas 2, 0.8 mm long.

This taxon is related to *Rudgea morichensis* Steyerm. from which it differs in the glabrous hypanthium, conspicuously lobed calyx, much shorter corolla tube, and shorter anthers. From *R. bolivarensis* Steyerm. it is distinguished by the lanceolate, longer calyx lobes and by the narrower, oblong-lanceolate leaf blades with shorter petioles.

SABICEA

Sabicea bariensis Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: upper Río Baria, mostly non-inundated area along riverside, 0°55′N, 66°16′W, 140 m, 9 May 1984, *A. Gentry & B. Stein 47314* (holotype, MO; isotype, VEN).

Planta scandens, caulibus strigosis; foliorum laminis elliptico-ovatis apice subacuminatis basi acutis majoribus 11–13 cm longis 5.5–7 cm latis supra sparsim puberulis, costa media nervisque strigosis, subtus praeter costam mediam nervisque strigosis plerumque glabris; inflorescentia pedunculata 20–30-flora trichotome ramosa 2.3 cm longa 3.5 cm lata; floribus pedicellatis, pedicellis 3–5 mm longis; calycis lobis inaequalibus, majoribus ovatis acuminatis 3–4.5 mm longis 1.5–2.5 mm latis extus adpresso-pubescentibus intus glabris infra sinum squamellis duabus munitis.

Vine with strigose pubescent stems. Leaves firmly membranous, elliptic-ovate, subacuminate at apex, acute at base, the larger leaf blades 11–13 cm long, 5.5–7 cm wide, sparsely puberulous above, the midrib and lateral nerves strigose, the lower surface mainly glabrous except for strigillose midrib, the margins appressed-ciliolate; lateral nerves 10 each side, arcuate-ascending at 50–60° angle, impressed above, subelevated below; tertiary venation slightly evident, transversely connecting the secondary nerves; petioles 2–3.5 cm long, strigillose. Stipule reflexed, ovate, acute to acuminate, 10–12 mm long, 6–6.5 mm wide, strigose without, glabrous within. Inflorescence pedunculate, bracteate, 20–30-flowered, cymosely trichotomously branched, 2.3 cm long, 3.5 cm wide. Peduncle 4–5 mm long, densely antrorsely strigose. Lower axes of inflorescence 1.7 cm long with the flowers ca. 10-flowered. Lowest bracts subtending lowest axes of inflorescence 7–9 mm long, 3 mm wide, connate at their bases, divaricate, sparsely appressed-pubescent without, glabrous within; bracts subtending other axes paired, 7 mm long, 2 mm wide, appressed-pubescent without. Flowers on pedicels 3–5 mm long, these densely appressed pubescent. Calyx and hypanthium 5–7(–9.5) mm long, appressed-pubescent; hypanthium longer than the calyx lobes, 3.5–5.5 mm long, glabrous within; calyx lobes unequal, 4 larger and 1 smaller, the large ones erect-spreading, ovate, acuminate, 3–4.5 mm long, 1.5–2.5 mm toward the base, appressed-pubescent without, glabrous within, the smallest one 1.5 mm long, 1 mm wide, 2 unequal, elongate, dark squamellae situated below sinus of calyx lobes. Corolla narrowly cylindric, salverform, 14.5 mm long, the tube 10.5 mm long, 1.8 mm wide, densely antrorsely appressed pubescent without, glabrous within; 5 lobes lanceolate-ligulate, acute, 4 mm long, 1 mm wide at base, densely sericeous without, glabrous within. Anthers 2.8 mm long.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: 3–4 km upstream from Neblina Base Camp, gravel banks of main channel of Río Mawarinuma, 0°50′N, 66°10′W, 180 m, 4 Dec. 1984, *Kral 71981* (MO, VDB, VEN); upper Caño Baria, swampy area between Río Mawarinuma and headwaters of Río Baria, 0°52′N, 66°15′W, 130 m, 26 Mar. 1984, *Liesner 16967* (MO, VEN).

From other pedunculate species this differs from *Sabicea grandiflora* Steyerm. in the larger calyx lobes, nonarachnoid pubescence of the leaves, and divaricately spreading calyx lobes. From *S. morillorum* Steyerm. it is mainly distinguished by its nonarachnoid pubescence.

TEN NOVELTIES IN *XYRIS* (XYRIDACEAE) FROM THE PLANALTO OF BRAZIL

R. Kral[1] *and*
Maria das Graças de Lapa Wanderley[2]

ABSTRACT

Ten taxa of Xyris *(nine species and one variety), sent to the senior author for definitive treatment during the early 1980s, are herein described, figured, and proposed for addition to the flora of Brazil. All are from the Brazilian Planalto: five (*X. diaphanobracteata, X. jataiana, X. lutescens, X. pranceana, X. sceptrifera*) are from Goiás, four (*X. seubertii *var.* espinhacae, X. itambensis, X. obcordata, *and* X. villosicarinata*) are from Minas Gerais, and one (*X. dissitifolia*) is from Paraná. These new* Xyris *are presented alphabetically and each is contrasted with related species.*

Among the undetermined Xyridaceae from Brazil sent to the senior author for definitive treatment during the years 1980, 1981, and 1982 are ten that have long awaited publication as new taxa. They are arranged alphabetically.

1. **Xyris diaphanobracteata** Kral & Wanderley, sp. nov. TYPE: Brazil. Goiás: Rod. GO-12; km 5–10 ao sul de Alto Paraiso, campo arenoso, flor amarela, 24 May 1975, *G. Hatschbach 36815* (holotype, MBM; isotypes, US, VDB). Figure 1.

Planta perennis, caules breves, radices graciles. Folia ensiformi-linearia, 15–20 cm longa, disticha, flabellate expansa, solum basalia, vaginis scaporum longiora; laminae planae vel leviter tortae, 3–5 mm latae, compressae, flavovirentes, inconspicue multinervosae, papillosae, marginem versus crassinervae, ferrugineae; apices abrupte contracti, incurvato-acuti, incrassati; margines aciebus pallide villoso-ciliatis; vaginae carinatae, carinibus ciliatis, lateribus valde multicostatis, glabris, flavofuscatis, basin versus castaneis, rugulosis, marginibus in laminas gradatim convergentibus, infimis gradatim expansis, tum abrupte ad basim dilatatis, aciebus ad basim anguste scariosis, antrorse longiciliatis, pilis albidis. Vaginae scaporum basim versus ancipitae, pilosociliatae, glabrae, multicostatae, ferrugineae, nitidae, a medio ad apicem acute carinatae, carinibus rufis, ciliatis, laminis brevibus, obtusis. Scapi graciles, recti, 4.5–6 dm alti, leviter torti, anguste 2–3-costati, in sectione transversali elliptici, apicem versus ancipitii, costis longiciliatis, pilis albidis. Spicae late ovoideae, 1–1.5 cm longae, obtusae, multibracteatae, bracteis laxis, fere uniformis, spiraliter imbricatis, subscariosis, convexis, ecarinatis, late ovatis, 5–7 mm longis, rotundatis, testaceis, margine squarrosis, laceratis; area dorsalis indistincta; bracteae steriles plures. Sepala lateralia libera, valde curvata, leviter exserta, valde inaequilatera, oblanceolata, tenuia, 6–7 mm longa; ala carinalis lata, ciliato-fimbriolata. Laminae petalorum suborbiculatae vel reniformes, 7–8 mm longae, grosse erosae, flavidulae. Staminodia bibrachiata, brachiis complanatis, longipenicillatis. Antherae lanceolato-oblongae, sagittatae, ca. 2 mm longae. Capsula turgide obovoidea, ca. 3 mm longa, placenta basalis; semina numerosa, ellipsoidea, 0.5 mm longa, pallide vel profunde lampro-brunnea, prominente longitudine 12–14-costata.

Plants short-stemmed perennials with fine roots. Leaves ensiform-linear, 15–20 cm long, distichous, flabellately spreading, strictly basal, longer than the scape sheaths; blades flat to slightly twisted, 3–5 mm wide, flattened,

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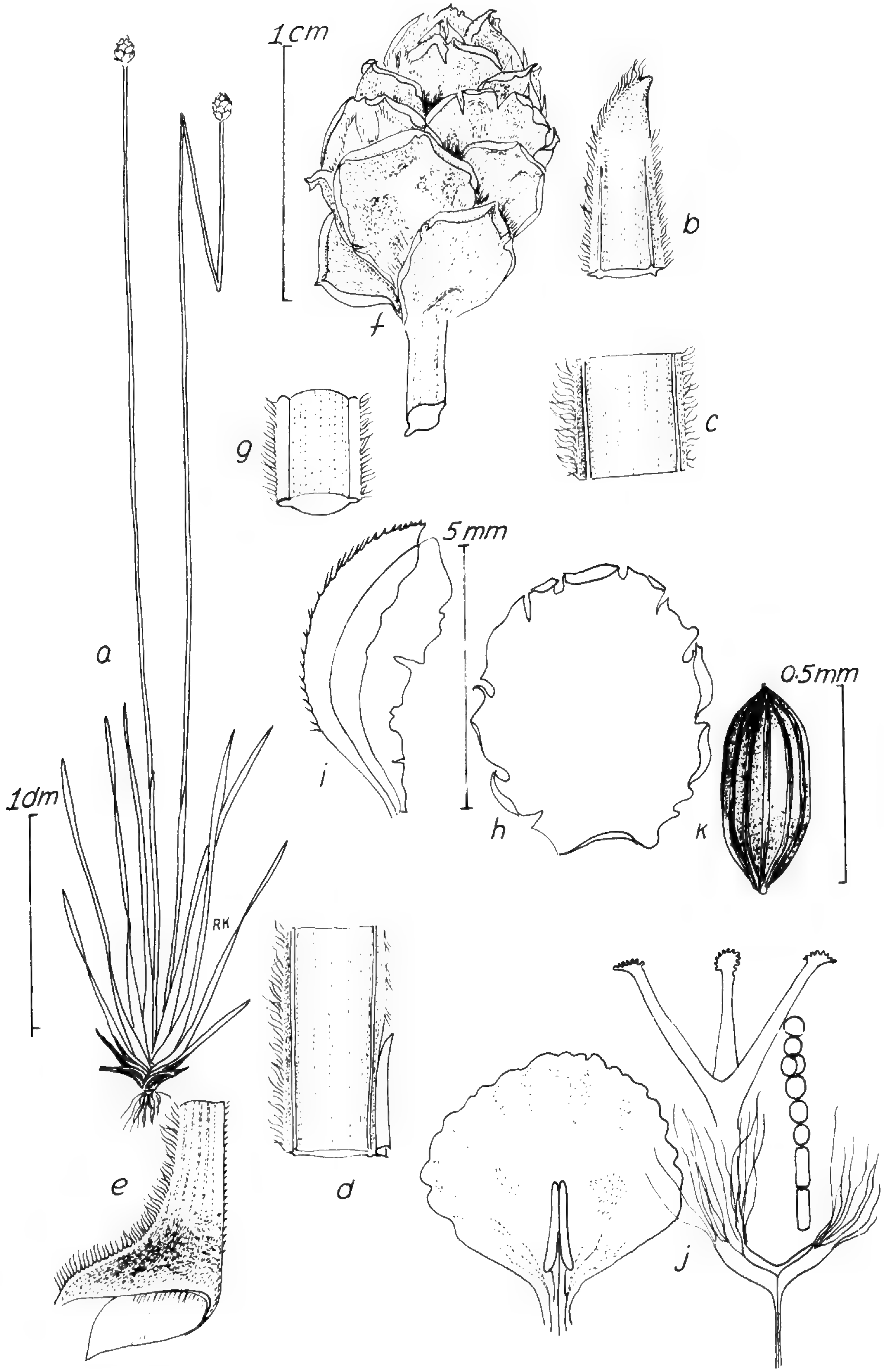
yellow-green, inconspicuously multinerved, papillose, thick-nerved toward margin, reddish brown; apices abruptly narrowed, incurved-acute, thickened; margins with edges pale villous-ciliate; sheaths ciliate-carinate, the sides strongly multicostate, smooth, yellowish-fuscous, castaneous toward the base, rugulose, with margins gradually narrowing into the blades, gradually expanding below, abruptly dilated at base, there the edges narrowly scarious, antrorsely long-ciliate with white hairs. Scape sheaths ancipital toward base, pilose-ciliate, smooth, multicostate, reddish brown, shining, acutely carinate from middle to apex, the carinae reddish, ciliate, the blades short, obtuse. Scapes slender, straight, 4.5–6 dm high, slightly twisted, narrowly 2–3-costate, elliptic in cross section, ancipital toward the apex, the costae long-ciliate with white hairs. Spikes broadly ovoid, 1–1.5 cm long, obtuse, the bracts numerous, loose, nearly uniform, spirally imbricate, subscarious, convex, ecarinate, broadly ovate, 5–7 mm long, rounded, brownish yellow, marginally squarrose, lacerate; dorsal area indistinct; sterile bracts many. Lateral sepals free, strongly curvate, slightly exserted, strongly inequilateral, broadly oblanceolate, thin, 6–7 mm long; keel wide, ciliate-fimbriolate. Petal blades suborbicular to reniform, 7–8 mm long, strongly erose, yellow. Staminodia bibrachiate, the branches flattened, long-penicillate. Anthers lanceolate-oblong, sagittate, ca. 2 mm long. Capsule turgidly obovoid, ca. 3 mm long, the placentation basal; seeds numerous, ellipsoid, 0.5 mm long, palely or deeply lustrous brown, prominently longitudinally 12–14-costate.

This novelty most resembles *X. pterygoblephara* Steudel, particularly by having long, pale ciliation on scape and leaf edges; distichous, flabellately spreading, flattened leaves; and concolorous bracts. *Xyris diaphanobracteata* differs conspicuously in its broader spikes and uniform bracts (sterile ones more numerous) with thin, translucent texture and squarrose edges. The lateral sepals are broader, more strongly curvate, blunter, exserted, very inequilateral (rather than equilateral), and more prominently ciliate.

2. **Xyris dissitifolia** Kral & Wanderley, sp. nov. TYPE: Brazil. Paraná: Mun. Campiná Gde. do Sul, campo umido encosta de morro, flor amarella, alt. 1,500–1,700 m s/mar, 15 Jan. 1969, *Hatschbach & Ckoczicki 20752* (holotype, MBM; isotypes, US, VDB). Figure 2.

Planta perennis, caespitosa, radicibus gracilibus. Caules breves vel elongati, per bases laxas foliorum obtecti. Folia laxa, anguste linearia, 2–5 dm longa, disticha, erecta vel leviter flabellate expansa, vaginis scaporum longiora; laminae vaginis 2–5-plo longiores, subteretes vel angulosae aut leviter compressae, tortae, valde mediane sulcatae et paucicostatae, olivaceae, a medio ad apicem glabrae, basin versus ruguloso-papillosae, subteretes; apices gradatim contracti, ad apicem anguste obtusi, erecti, persaepe incrassati et triangulati; vaginae laxae, latae, ecarinatae vel carinatae, pallide lamprobrunneolae, a basi ad apicem gradatim contractae, apicem versus ligulam oblongam obtusam scariosam 3–4 mm longam fascientes, marginibus latis integris nitidis, dorsis rotundato-plicatis, valde unicostatis, praeter basin papillosis aut rugulosis. Vaginae scaporum laxae, basin versus conduplicatae tubulosae multicostae, nitidae, tortae, apicem versus apertae, laminis similibus laminis foliorum sed brevioribus. Scapi graciles, 3–6 dm alti, subteretes aut (in sectione transversali) elliptici, ca. 1 mm crassi, olivacei, apicem versus 1–2-costati et subtiliter striatae, costis glabris, basin versus persaepe obtuse triangulati aut sulcati. Spicae cylindro-oblongae vel late ellipsoideae aut obovoideae, pauciflorae, ca. 1 cm longae; bracteae laxe spiraliter imbricatae, convexae, pallide ferrugineae, papillosae, rotundatae, marbinibus integris, tum erosis, ad apicem persaepe villoso-ciliatis, trichomatibus sordidis; bracteae steriles 4–6, obovatae, ca. 4–7 mm longae, inferiores breviores, prominente unicostatae; bracteae fertiles paucae, oblongae vel obovatae, usque ad 9 mm longae, carinatae, eis intimis navicularibus; area dorsalis inconspicua, brevis, anguste elliptica, pallide brunneola. Laminae petalorum late ovatae, ca. 1 cm longae, subacutae, leviter erosae, luteolae. Staminodia bibrachiata, brachiis oblongis complanatis, ad apicem longipenicillatis. Antherae late lanceolatae, ca. 2 mm longae, sagittatae; filamenta plana, ca. 3 mm longa. Capsula oblonga vel obovoidea, ca. 5 mm longa, apiculata, placenta basali. Semina matura non visa sed immatura lineari-fusiformia, 1.5 mm longa, bicaudata, brunneola, longitudine minute striata.

Plants perennial, cespitose, slender-rooted. Stems short or elongated, covered by the lax bases of leaves. Leaves loose, narrowly linear, 2–5 dm long, distichous, erect or slightly flabellately spreading, longer than the scape sheaths; blades 2–5 times longer than the sheaths, subterete to angulate or slightly com-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pressed, twisted, medially strongly sulcate and few-ribbed, olivaceous, smooth from middle to apex, rugulose-papillose and subterete toward base; apices gradually contracted, narrowly obtuse at tip, erect, usually thickened and triangulate; sheaths lax, wide, ecarinate or carinate, pale lustrous brown, gradually narrowing from base to tip, producing near the apex a scarious, oblong, obtuse ligule 3–4 mm long, the margins broad, entire, shining, the backs rounded-plicate, strongly unicostate, papillose or rugulose except for the base. Scape sheaths lax, conduplicate toward base, tubular, multicostate, shining, twisted, open toward apex, with blades similar to leaf blades but shorter. Scapes slender, 3–6 dm high, subterete, or elliptic in cross section, ca. 1 mm thick, olivaceous, toward apex 1–2-costate and finely striate, the costae smooth, toward base often obtusely triangulate or sulcate. Spikes oblong-cylindric or broadly ellipsoid to obovoid, few-flowered, ca. 1 cm long; bracts loosely spirally imbricate, convex, pale reddish brown, papillose, rounded, with margins entire, then erose, at apexes often villous-ciliate with sordid trichomes; sterile bracts 4–6, obovate, ca. 4–7 mm long, the lowest shortest, prominently unicostate; fertile bracts few, oblong to obovate, up to 9 mm long, the inner ones navicular, carinate; dorsal area inconspicuous, short, narrowly elliptic, pale brown. Petal blades broadly ovate, ca. 1 cm long, subacute, slightly erose, yellow. Staminodes bibrachiate, the branches oblong, flat, long-penicillate at apex. Anthers broadly lanceolate, ca. 2 mm long, sagittate; filaments flat, ca. 3 mm long. Capsule oblong to obovoid, ca. 5 mm long, apiculate, the placenta basal. Immature seeds linear-fusiform, 1.5 mm long, brownish, minutely longitudinally striate. Mature seeds not seen.

Additional specimens examined. BRAZIL. PARANÁ: Serra Ibitiraquire, Abrigo 1 (Mun. Campiná Gde. do Sul), campo umido encosta de morro, alt. 1,700 m, 23 Jan. 1970, *Hatschbach 23404* (MBM, US, VDB); Serra Capivari Grande (mun. Campiná Gde. do Sul), encostas graminosas umidas de morro, alt. 1,500 m, 8 Feb. 1971, *Hatschbach 26322* (MBM, US, VDB).

This species, with its slender, long leaf blades, loose and distichous leaf sheaths along definite stems, papillose-backed bracts with small, pale brown dorsal areas, and villous sepal tips, shows some characters of *Xyris filifolia* Nilsson but has more stem, hairier sepal keels, and less evident dorsal areas. On the other hand, the vestite sepals liken it to *X. rigida* Kunth, or *X. regnellii* Nilsson, but leaf characters do not agree, nor do characters of fertile bract or scape.

3. **Xyris itambensis** Kral & Wanderley, sp. nov.

TYPE: Brazil. Minas Gerais: Serra do Ispinhaco, sandy soil, eastern slopes of Pico do Itambe; elev. ca. 1,550 m; sandstone outcrops with shrubby vegetation, adjacent grassy slopes, and valley of small stream; mostly sandy soil but with overlying black humus in many places, 12 Feb. 1972, *W. R. Anderson, M. Stieber, J. H. Kirkbride, Jr. 35879* (holotype, UB; isotypes, NY, US). Figure 4.

Planta perennis, densicaespitosa, glabra; caules breves; radices graciles. Folia erecta vel leviter expansa, 1.5–3 dm longa, solum basalia, vaginis scaporum longiora, torta et flexuosa, lucida; laminae vaginis 3–6-plo longiores, teretes vel subteretes, filiformes, 0.5–0.6 mm crassae, virides, longitudine subtiliter striatae, basin versus minute rugulosae; apices gradatim contracti, anguste conici; vaginae ecarinatae, ad basim abrupte dilatatae, lamproferrugineae, fimbriociliatae, prominente longitudine costatae, superne gradatim contractae, lamprospadiceae, marginibus latis, tenuibus sed firmis, integris vel parce villoso-fimbriatis, in medio longitudine multicostatae, ad apicem ligulam erectam oblongam acutam 4–6 mm longam fascientes. Vaginae scaporum ad basim teretes, laxe conduplicatae, multicostatae, tortae et leviter flexuosae, purpureae vel pallide ferrugineae, apicem versus apertae, marginibus latis integris purpureis et ad apicem cuspidatis. Scapi gracillimi, 3.5–5.5 dm alti, torti et flexuosi, olivacei, subteretes, laeves, ecostati vel unicostati, costibus glabris. Spicae late ellipsoideae vel anguste obovoideae, 6–8 mm longae, 4–5 mm crassae, pauciflorae, pluribracteatae,

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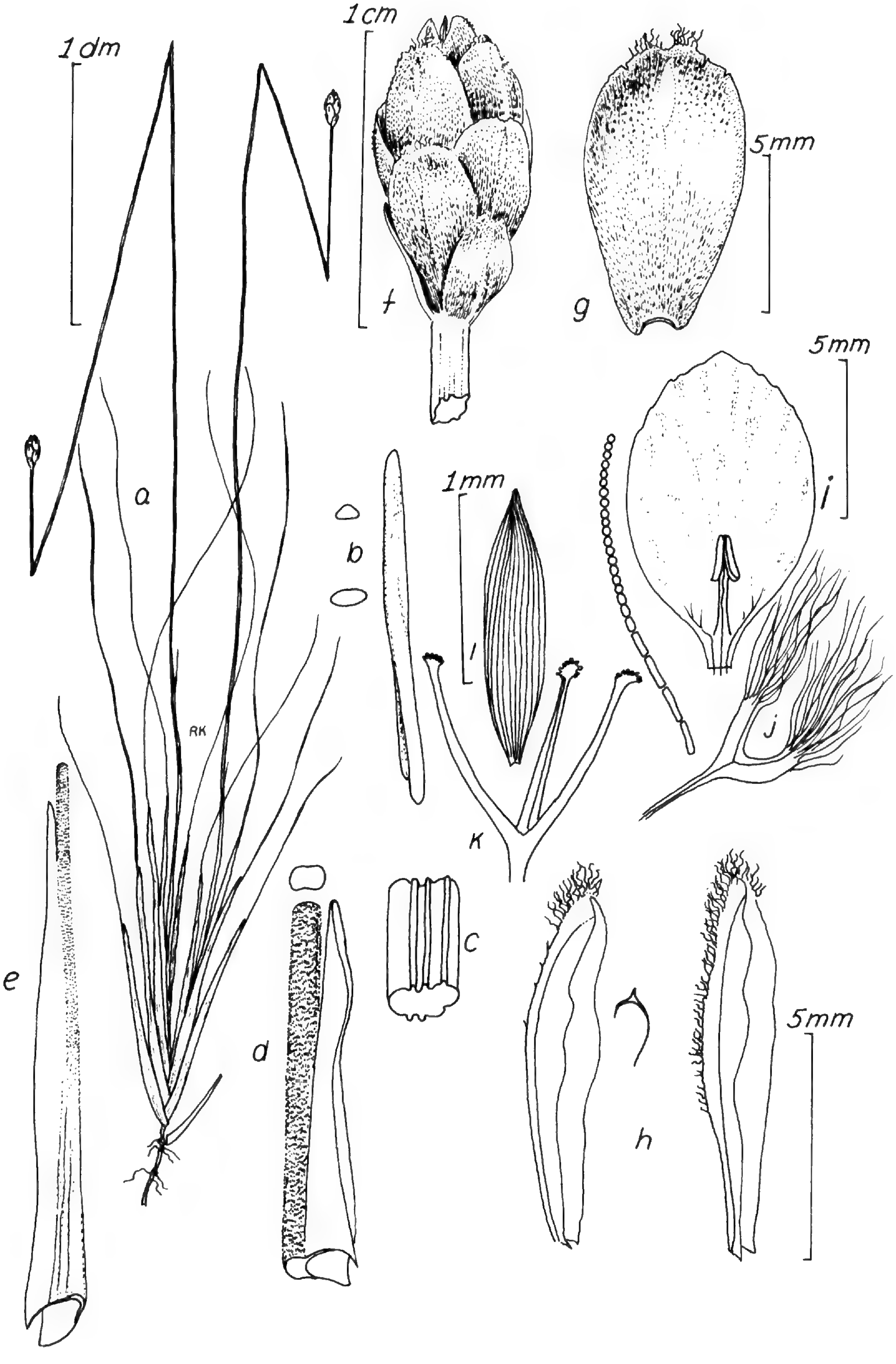
FIGURE 1. Xyris diaphanobracteata (Hatschbach 36815).—*a. Habit sketch.—b. Leaf tip.—c. Sector of mid blade.—d. Sector at leaf sheath–blade junction.—e. Leaf base.—f. Spike.—g. Sector of scape ca. 2 cm below apex.—h. Fertile bract.—i. Lateral sepal.—j. Petal and stamen, stylar apex, staminode, enlarged beard hair.—k. Seed.*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bracteis sterilibus pluribus, convexis, inferioribus suborbicularibus vel late ovatis, 2–3.5 mm longis, superioribus navicularibus usque ad 5 mm longis; bracteae fertiles late oblongae vel obovatae, ad 5–6 mm longae, marginibus tenuibus, laceratis, ad apicem parce rufovillosulis, intimis valde plicatis; area dorsalis elliptica, ca. 2 mm longa. Sepala lateralia libera, curvata, oblonga, ca. 5–6 mm longa, acuta, leviter inaequilatera, ala carinali angusta, a medio ad apicem rufofimbriolata. Laminae petalorum oblongae, 6–6.5 mm longae, late acutae, sed integrae, luteolae. Antherae lanceolato-oblongae, 1.5 mm longae, emarginatae et sagittatae, filamentis longiores. Staminodia bibrachiata, brachiis subteretibus, longipenicillatis. Placenta centralis. Semina matura non visa sed immatura cylindrico-fusiformia, 1.2 mm longa.

Plants perennial, densely cespitose, smooth; stems short; roots slender. Leaves erect to slightly spreading 1.5–3 dm long, strictly basal, longer than the scape sheaths, twisted and flexuous, lustrous; blades 3–6 times longer than sheaths, terete or subterete, filiform, 0.5–0.6 mm thick, green, longitudinally finely striate, minutely rugulose toward base; tips gradually narrowing, narrowly conic; sheaths ecarinate, abruptly dilated at base, shining red-brown, fimbrio-ciliate, prominently longitudinally costate, gradually narrowing above, lustrous brown, with margins broad, thin but firm, entire to sparsely villous-fimbriate, at middle longitudinally multicostate, at apex producing an erect, oblong, acute ligule 4–6 mm long. Scape sheaths terete at base, laxly conduplicate, multicostate, twisted and somewhat flexuous, purplish or pale red-brown, open toward apex, with margins broad, entire, purplish, and at apex cuspidate. Scapes very slender, 3.5–5.5 dm high, twisted and flexuous, olivaceous, subterete, smooth, ecostate to unicostate, with costae smooth. Spikes broadly ellipsoid to narrowly obovoid, 6–8 mm long, 4–5 mm thick, few-flowered, several-bracted, the sterile bracts several, convex, the lower ones suborbicular to broadly ovate, 2–3.5 mm long, the upper sterile bracts navicular, up to 5 mm long; fertile bracts broadly oblong to obovate, to 5–6 mm long, with thin, lacerate margins, sparsely red-villosulous at apex, the inner ones strongly plicate; dorsal area elliptic, ca. 2 mm long. Lateral sepals free, curvate, oblong, ca. 5–6 mm long, acute, slightly inequilateral, the keel narrow, red-fimbriolate from middle to tip. Petal blades oblong, 6–6.5 mm long, broadly acute, entire, yellow. Anthers lanceolate-oblong, 1.5 mm long, emarginate and sagittate, longer than the filaments. Staminodia bibrachiate, the branches subterete, long-penicillate. Placenta central. Immature seeds cylindric-fusiform, 1.2 mm long. Mature seeds not seen.

In habit the new species resembles *X. filifolia* Nilsson, a slender species which also has small but prominent dorsal areas and strongly ligulate leaves with very slender and terete blades. The scapes, unlike those of *X. filifolia*, are terete, the tips of the fertile bracts are villosulous with red hairs, and the lateral sepal keels are densely villosulous above the middle. *Xyris itambensis* relates also to the complex involving *X. rigida* Kunth, but is more slender, has fewer flowers, and has subequilateral (rather than strongly inequilateral) sepals.

4. **Xyris jataiana** Kral & Wanderley, sp. nov. TYPE: Brazil. Goiás: Mun. Jatai Rod. Jatai–Caiapenia, km 50 (mun. Jatai), Goiás; flor amarela, do brejo, 24 July 1977, *G. Hatschbach 40060* (holotype, MBM; isotypes, US, VDB). Figure 5.

Planta perennis, glabra, densicaespitosa; radices graciles, fibrosae; rhizomata ascendentia, per bases persistentes veternas foliorum obtecta. Caules elongati vel breves. Folia rhizomatum et caulium subdisticha, rigida, torta et flexuosa, 2–4 dm longa, vaginis scaporum longiora; laminae vaginis 5–8-plo longiores, tortae, anguste lineares, 0.8–1.5 mm latae, compressae, flavovirentes, longitudine 4–5-nervosae, inferne sulcatae; apices leviter contracti, asymmetrice anguste rotundati callosi; margines filo metalico similes, luteoli vel brunneoli, persaepe nitidi, quam in centro laminae crassiores; vaginae ecarinatae, anguste plicatae, atrocastaneae, nitidae, marginibus tenuibus, integris, gradatim convergentibus, ad apicem ligulam erectam acutam plene 10 mm longam fascientes, et hic quam laminis distincte latiores, infime gradatim dilatatae. Vaginae scaporum laxae, plerumque apertae, tortae, basin

←

FIGURE 2. Xyris dissitifolia *(*Hatschbach & Ckoczicki 20752*).—a. Habit sketch.—b. Leaf apex.—c. Sector of leaf at mid blade.—d. Leaf blade–sheath junction.—e. Leaf base.—f. Spike.—g. Fertile bract.—h. Two lateral sepals.—i. Petal blade, stamen.—j. Staminode and enlarged beard hair.—k. Stylar apex.—l. Seed.*

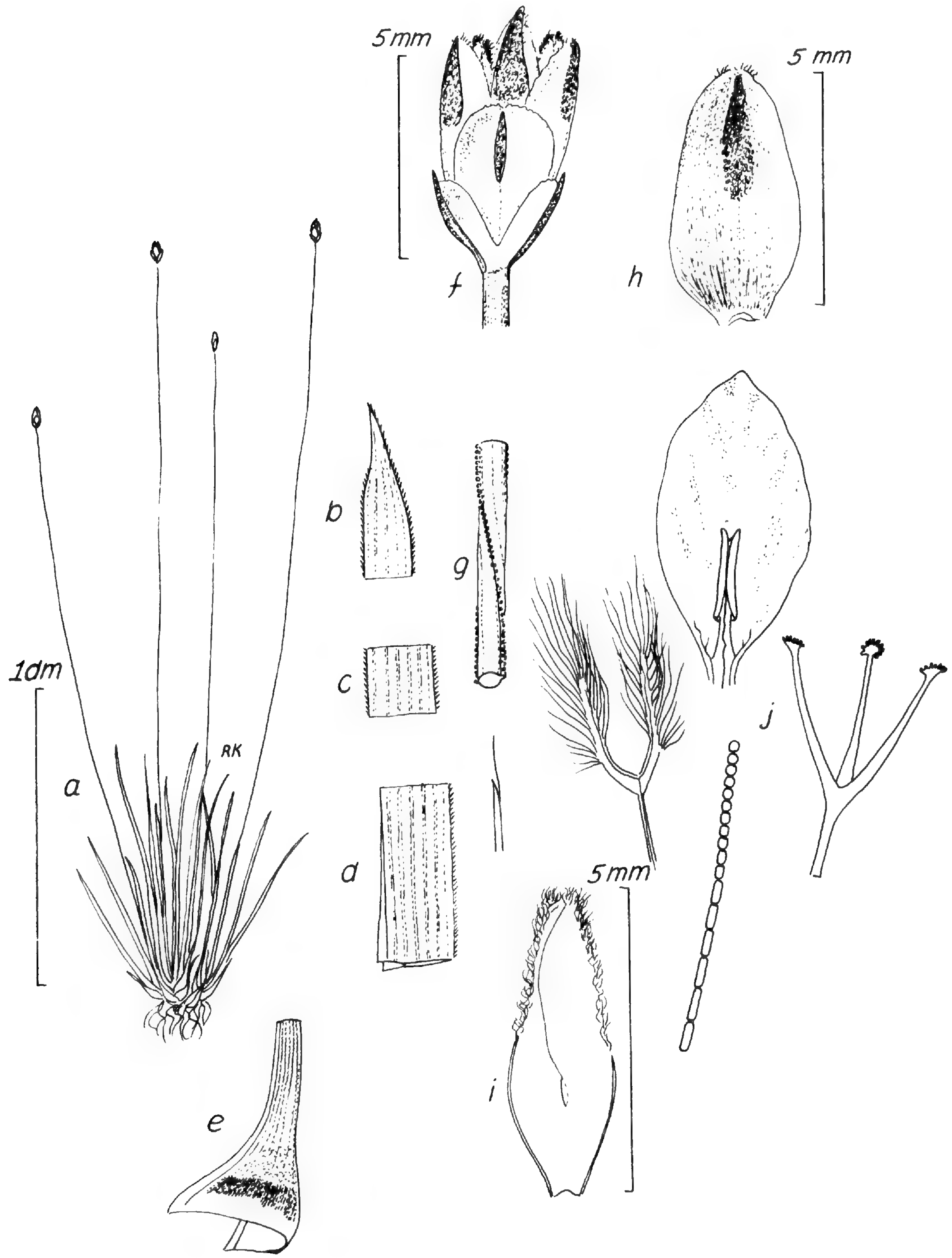

Figure 3. Xyris seubertii *var.* espinhacae (Irwin et al. 32667).—*a. Habit sketch.—b. Leaf apex.—c. Sector of mid blade.—d. Sheath-blade junction.—e. Leaf base.—f. Spike.—g. Sector of scape.—h. Fertile bract.—i. Lateral sepals.—j. Petal and stamen, staminode with enlarged view of beard hair, stylar apex.*

versus paucicostatae, castaneae, apicem versus carinatae, laminis brevibus erectis compressis vel triangulatis, obtusis. Scapi erecti, leviter torti, teretes, 5–6 dm alti, inferne fusci, compressi, apicem versus teretes, ecostati, luteovirides. Spicae multiflorae, multibracteatae, anguste obovoideae, 1–1.5 cm longae, attenuatae; bracteis convexis, ecarinatis, ferrugineofuscis, spiraliter imbricatis, rotundatis, integris vel minute erosis; bracteae steriles plures, anguste obovatae, 2–4 mm longae, fertilibus breviores et in eas gradatim transientes; bracteae fertiles late obovatae, ca. 4.5–5 mm longae, apice rotundatae; area dorsalis distincta, ovata vel elliptica, ca. 1.5–2 mm longa, olivacea vel atroferruginea. Sepala lateralia libera, leviter inaequilatera, anguste oblanceolata, ca. 5 mm longa, acuta; ala carinalis ciliata, basin versus angusta, apicem versus lata, firma. Laminae petalorum late ellipticae, 5–5.5 mm longae, luteolae, apice anguste rotundatae, erosae. Staminodia bibrachiata, brachiis longipenicillatis. Antherae oblongae, ca. 2 mm longae. Capsula matura non visa.

Plants perennial, glabrous, densely cespitose from slender roots. Rhizomes ascending, their bases covered by persistent old leaves. Stems short or elongated. Leaves of rhizomes and stems subdistichous, rigid, twisted and flexuous, 2–4 dm long, longer than the sheaths of the scapes; blades 5–8 times longer than sheaths, twisted, narrowly linear, 0.8–1.5 mm wide, flattened, yellowish green, longitudinally 4–5-nerved, sulcate below; apices somewhat contracted, asymmetrically narrowly rounded, callused; margins wirelike, yellowish to brown, often shining, thicker than the central part of the blade; sheaths ecarinate, narrowly folded, deeply castaneous, lustrous, with thin, entire margins, these gradually converging, at the apex forming an erect, acute ligule 10 mm long, this distinctly wider than the blade, gradually dilating below. Sheaths of scapes lax, largely open, twisted, few-ribbed toward the base, castaneous, carinate toward the apex, with blades short, erect, compressed or triangulate, obtuse. Scapes erect, slightly twisted, 5–6 dm long, brown below, compressed, terete toward the apex, ecostate, yellow-green. Spikes many-flowered, many-bracteate, narrowly obovoid, 1–1.5 cm long, attenuate; bracts convex, ecarinate, reddish brown, spirally imbricate, rounded, entire to minutely erose; sterile bracts several, narrowly obovate, 2–4 mm long, shorter than the fertile bracts and grading into them; fertile bracts broadly obovate, ca. 4.5–5 mm long, apically rounded; dorsal area distinct, ovate to elliptic, ca. 1.5–2 mm long, olivaceous to dark reddish brown. Lateral sepals free, slightly inequilateral, narrowly oblanceolate, ca. 5 mm long, acute; carinal keel ciliate, toward the base narrow, toward the apex wide, firm. Petal blades broadly elliptic, 5–5.5 mm long, yellow, narrowly rounded, erose. Staminodia bibrachiate, the branches long-hairy. Anthers oblong, ca. 2 mm long. Mature capsule not seen; placentation basal. Seeds not seen.

This species, with its distinct, elongate ligule broader than the leaf blade base, multiflowered spikes with (often) reddish brown dorsal areas, and free lateral sepals with ciliate keels, shows affinities to the rare *X. downsiana* Smith, a species thus far known only from Pará. However, *X. jataiana* has a longer ligule; its leaf blade margins are more broadly incrassate; the leaf apecies are bluntly callus tipped; the flowers are larger; and the lateral sepals are more nearly equal. Mature fruit and seeds of either of these species are unavailable.

5. **Xyris lutescens** Kral & Wanderley, sp. nov. TYPE: Brazil. Goiás: Mun. Posse, Nova Vista, brejo da borda de chapada, 8 Oct. 1976, *G. Hatschbach 39021* (holotype, MBM; isotypes, US, VDB). Figure 6.

Planta perennis, solitaria vel cespitosa, basibus bulbosis, atrocastaneis. Radices graciles. Caules breves. Folia ensiformi-linearia, 10–20 cm longa, torta, erecta vel leviter expansa, vaginis scaporum longiora; laminae planae vel leviter tortae, 3–4-plo vaginis longiores, 1.2–2.2 mm latae, valde compressae, flavovirentes, punctatae, inconspicue longitudine multinervosae; apices abrupte contracti, incurvato-acuti, incrassati; margines angusti, leviter incrassati, nitidi, luteoli; vaginae ecarinatae vel asymmetrice carinatae, multicostatae, lateribus stramineis, transversim rugulosis, marginibus pallide longiciliatis, in laminas gradatim convergentibus, infime gradatim expansae tum abrupte ad basim dilatatae, acies scariosae. Vaginae scaporum laxae, luteo-carinatae, tortae, acute 2–multi-costatae, laminis laminis foliorum similibus sed brevibus. Scapi graciles, flexuosi, torti, subteretes, glandacei, 4–6 dm alti, valde 2–pluricostati et angulosi, apicem versus ca. 1 mm crassi, costis papillosis vel tuberculatis aut glabris, intervala punctata. Spica multiflora, cylindro-ovoidea vel anguste ellipsoidea, 1–2 cm longa, 5–8 mm crassa, attenuata, bracteis spiraliter imbricatis, tenuibus, pallide luteobrunneolis, ecarinatis, marginibus tenuissimis

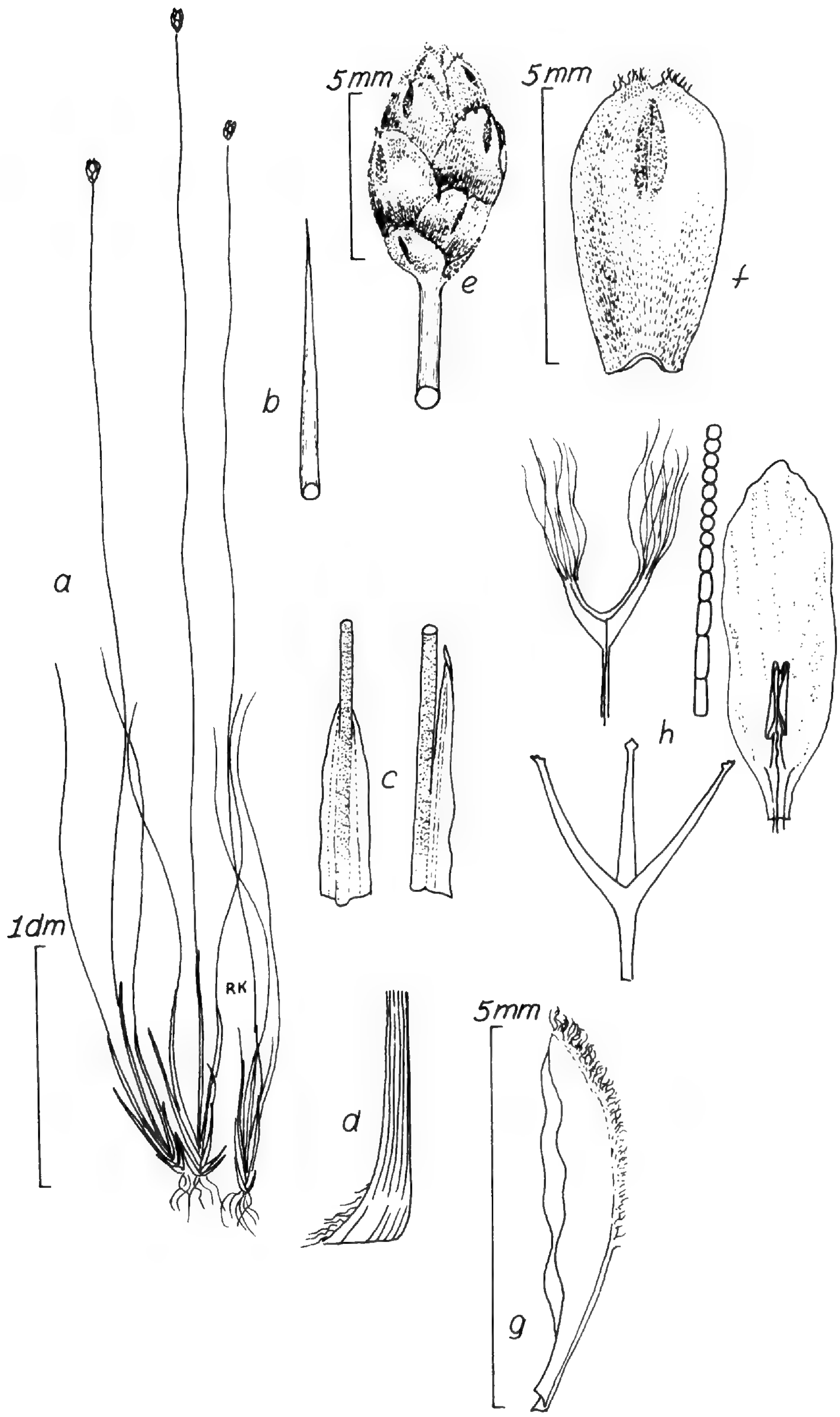

FIGURE 4. Xyris itambensis (Anderson et al. 35879).—*a. Habit sketch.*—*b. Leaf apex.*—*c. Dorsal (left) and side (right) views of leaf-sheath junction.*—*d. Leaf base.*—*e. Spike.*—*f. Fertile bract.*—*g. Lateral sepal.*—*h. Petal blade and stamen, staminode, enlarged version of beard hair, stylar apex.*

et profunde laceratis; bracteae steriles ovatae vel suborbiculatae, 2.5–3.5 mm longae, fertilibus breviores et in eas gradatim transientes; bracteae fertiles late obovatae vel suborbiculatae, usque 5 mm longae; area dorsalis indistincta. Sepala lateralia libera, valde inaequilatera, oblanceolata, ca. 5 mm longa, acuta, tenuissima; ala carinalis lata, supra medium irregulariter ciliatolacerata. Laminae petalorum late obovatae, ca. 5 mm longae, late rotundatae, leviter erosae, luteolae. Staminodia bibrachiatis, brachiis longipenicillatis, erectis, pilis clavatis. Antherae late oblongae, ca. 1 mm longae, retusae et sagittatae, filamentis ca. 2-plo breviores. Capsula ellipsoidea, leviter compressa, ca. 2.5 mm longa, acuta; placenta basalis. Semina cylindrico-ellipsoidea, 0.8–0.9 mm longa, translucida, pallide ferruginea, longitudinaliter et prominente 16–18-costata.

Plants perennial, solitary, with bulbous, deep chestnut bases. Roots slender. Stems contracted. Leaves ensiform-linear, 10–20 cm long, twisted, erect to slightly spreading, longer than the scape sheaths; blades flat or slightly twisted, 3–4 times longer than the sheaths, 1.2–2.2 mm wide, strongly flattened, yellow-green, punctate, inconspicuously longitudinally multinerved; apices rather abruptly contracted, incurved-acute, thickened; margins narrow, slightly incrassate, shining, yellowish; sheaths ecarinate or asymmetrically carinate, multicostate, with sides stramineous, transversely rugulose, the margins long-ciliate with pale hairs, narrowing gradually into the blades, gradually spreading below, then abruptly dilating at the base, the edges scarious. Sheaths of scapes loose, yellowish-carinate, twisted, sharply 2–many-ribbed; blades similar to blades of leaves but short. Scapes slender, flexuous, twisted, subterete, yellow with tints of brown, 4–6 dm high, strongly 2–many-costate and angulate, ca. 1 mm thick toward the apex, the costae papillose to tuberculate or glabrous, the intervals punctate. Spikes many-flowered, cylindro-ovoid to narrowly ellipsoid, 1–2 cm long, 5–8 mm thick, attenuate, the bracts spirally imbricate, thin, pale yellow-brown, ecarinate, the margins very thin and deeply lacerate; sterile bracts ovate to suborbicular, 2.5–3.5 mm long, shorter than the fertile bracts and grading into them; fertile bracts broadly obovate to suborbicular, to 5 mm long; dorsal areas indistinct. Lateral sepals free, strongly inequilateral, oblanceolate, ca. 5 mm long, acute, very thin; keel wide, irregularly ciliate-lacerate from the middle to the apex. Blades of petals broadly obovate, ca. 5 mm long, broadly rounded, slightly erose, yellowish. Staminodia bibrachiate, the branches pubescent with long, clavate trichomes. Anthers broadly oblong, ca. 1 mm long, emarginate or sagittate, half as long as the filaments. Capsule ellipsoid, slightly compressed, ca. 2.5 mm long, acute; placentation basal. Seeds cylindro-ellipsoid, 0.8–0.9 mm long, translucent, pale red-brown, longitudinally and strongly 16–18-ribbed.

This species, with sheath edges gradually converging to blade bases, and lacking dorsal areas on its thin, pale-margined, broad, ragged bracts, appears to blend characteristics of the species complex around *X. ciliata* Thunb. The yellow tints of both spike and complanate foliage are distinctive, together with the strongly and sharply multicostate scape. In most xyrids the anthers are longer than the free portions of the filaments, or at least these are equal; in *X. lutescens* the anthers are considerably shorter than the filaments.

6. **Xyris obcordata** Kral & Wanderley, sp. nov. TYPE: Brazil. Minas Gerais: Serra do Espinhaço, wet sand among outcrops, cut-over gallery forest and adjacent outcrops, Rio Jequití, ca. 25 km E of Diamantina, elev. 790 m, 17 Mar. 1970, *H. S. Irwin, S. F. da Fonseca, R. Souza, R. Reis dos Santos & J. Ramos 27763* (holotype, UB; isotypes, NY, US). Figure 7.

Planta perennis, densicaespitosa, basibus infirmis. Caules breves. Radices graciles. Folia laxa, 1–2 dm longa, indistincte disticha, glabra, vaginis scaporum longiora; laminae planae, valde compressae, vaginis 1–2-plo longiores, 2–3.5 mm latae, longitudine indistincte multinervosae, virides; apices abrupte contracti, anguste acuti, leviter incrassati, incurvati; margines tenues, uniforme subtiliter albociliati; vaginae carinatae (carinibus integris), stramineae, marginibus scariosis, integris, in laminas gradatim convergentibus, basin versus gradatim dilatatae. Vaginae scaporum laxae, tortae, humile costatae, ad folia in coloribus, laminis apiceque similes. Scapi graciles, 2.5–4 dm alti, ca. 1 mm lati, virides, in sectio transversali elliptici vel anguste elliptici, longitudine subtiliter acute striatonervosae, a medio ad apicem valde bicostati et vulgo ancipiti, costis compressis, latis, subtiliter antrorse albo-

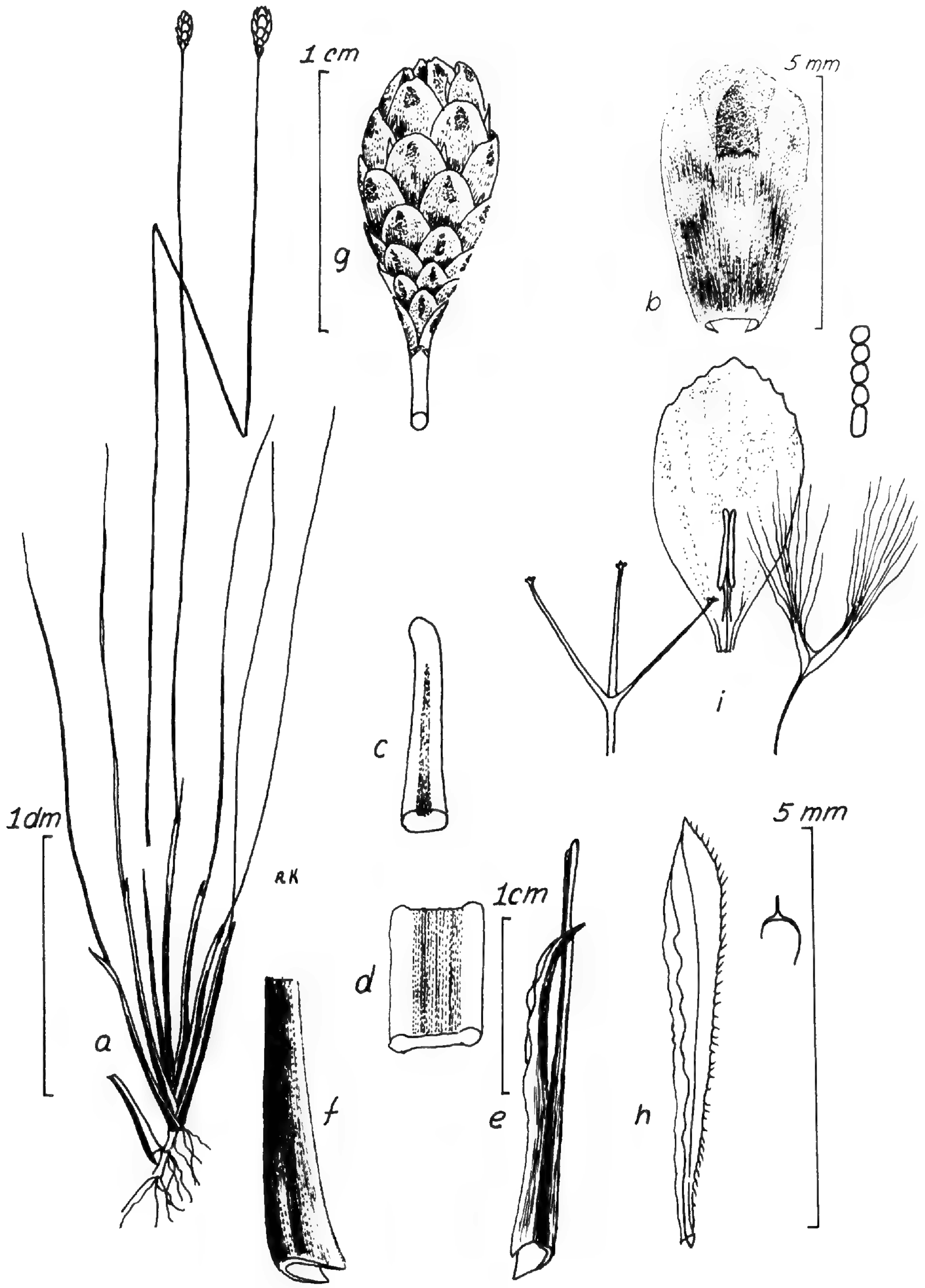

FIGURE 5. Xyris jataiana (Hatschbach 40060).—*a. Habit sketch.—b. Bract.—c. Leaf apex.—d. Sector of leaf at mid blade.—e. Upper part of leaf sheath at blade base.—f. Leaf base.—g. Spike.—h. Lateral sepal.—i. Petal blade, staminode, enlarged cells of staminode beard, stylar apex.*

ciliatis. Spicae multiflorae, late ovoideae, 7–9 mm longae, laxae, si prementes nunc compressae, 6–7 mm latae; bracteae ecarinatae, ovatae vel late obovatae aut suborbiculatae, obcordatae, laxe spiraliter imbricatae, tenues, pallide fulvae, marginibus amplis tenuissimis, friabilibus, ad apicem ferrugineis; bracteae steriles 5–6, 2–2.5 mm longae; bracteae fertiles usque ad 4.5 mm longae; area dorsalis late vel anguste elliptica, ca. ⅔ bracteis breviori, viridis. Sepala lateralia libera, spathulata, acuta, ca. 4 mm longa, tenuia, ala carinali tenuissima, subintegra.

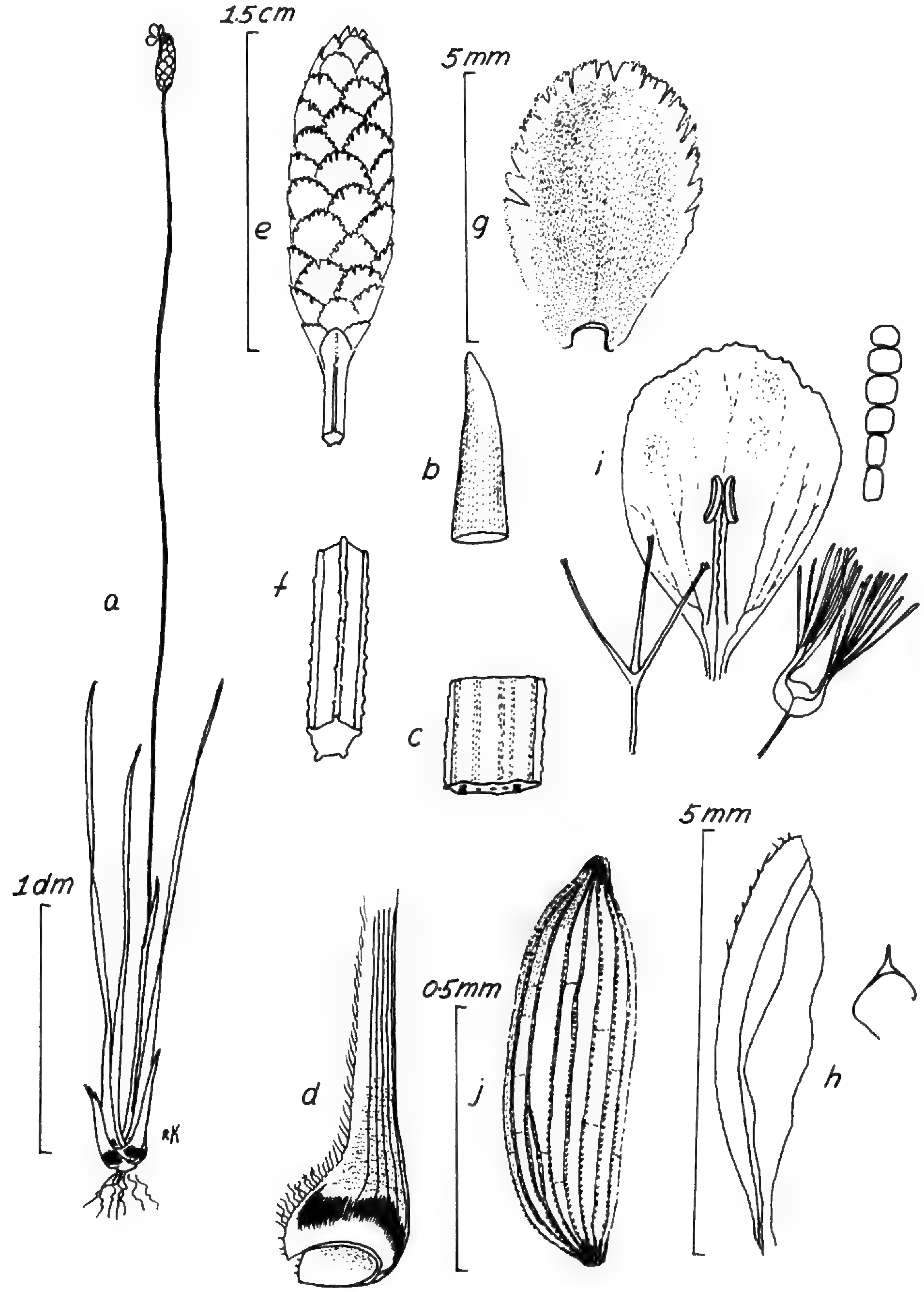

FIGURE 6. Xyris lutescens (Hatschbach 39021).—*a. Habit sketch.—b. Leaf tip.—c. Sector of mid blade.—d. Leaf sheath.—e. Spike.—f. Sector of mid scape.—g. Fertile bract.—h. Lateral sepal.—i. Floral parts.—j. Seed.*

Laminae petalorum obovatae, ca. 3 mm longae, rotundatae, luteolae. Staminodia bibrachiata, brachiis compressis, longipenicillatis. Antherae oblongo-lanceolatae, ca. 1.5 mm longae, valde emarginatae et sagittatae, filamentis longiores. Capsula obovoidea, ca. 2 mm longa, placenta centralis. Semina numerosa, turgide et late asymmetrice ovoidea, ca. 0.3 mm longa, atroferruginea, nitida, prominente longitudinaliter 14–16-costata.

Plants perennial, densely cespitose, the bases soft. Stems short. Roots slender. Leaves lax, 1–2 dm long, indistinctly distichous, smooth, longer than the scape sheaths; blades flat, strongly compressed, 1–2 times longer than the sheaths, 2–3.5 mm wide, longitudinally indistinctly multinerved, green; apices abruptly narrowed, narrowly acute, slightly thickened, incurved; margins thin, uniformly finely white ciliate; sheaths carinate (carinae entire), stramineous, the margins scarious and entire, narrowing gradually into the blades, gradually dilating toward base. Scape sheaths lax, twisted, low-costate, like leaves in color and with similar tips. Scapes slender, 2.5–4 dm high, ca. 1 mm broad, greenish, in cross section elliptic or narrowly elliptic, longitudinally finely and sharply striate-nerved, from middle to apex strongly bicostate and commonly ancipital, the costae compressed, wide, finely antrorsely white ciliate. Spikes many-flowered, broadly ovoid, 7–9 mm long, soft, if pressed then flattened, 6–7 mm wide; bracts ecarinate, ovate to broadly obovate or suborbicular, obcordate, loosely spirally imbricate, thin, pale tan except ferruginous apex, the ample margins very thin, friable; sterile bracts 5–6, 2–2.5 mm long; fertile bracts up to 4.5 mm long; dorsal area broadly to narrowly elliptic, about ⅔ as long as the bracts, green. Lateral sepals free, spathulate, acute, ca. 4 mm long, thin, the keel very thin, subentire. Petal blades obovate, ca. 3 mm long, rounded, yellowish. Staminodia bibrachiate, with branches flattened, long-penicillate. Anthers oblong-lanceolate, ca. 1.5 mm long, strongly emarginate and sagittate, longer than the filaments. Capsule obovoid, ca. 2 mm long, placentation central. Seeds numerous, turgidly and broadly asymmetrically ovoid, ca. 0.3 mm long, deep reddish brown, shining, prominently longitudinally 14–16-ribbed.

This soft-based, lax-leaved plant appears to be in the same complex as *X. mima* Smith & Downs and *X. moraesii* Smith & Downs; it is most similar in habit to the latter, differing mainly in the broader leaf blades, slightly narrower spikes, coloration of bract apex, and subentire sepal keels. *Xyris obcordata* is taller than the former and has broader spikes and entire (vs. ciliate) sepal keels. It is unlike either in its ancipital, broadly bicostate scape and reddish coloration of the thin, friable apex of the obcordate bracts.

7. **Xyris pranceana** Kral & Wanderley, sp. nov. TYPE: Brazil. Goiás: Chapada dos Veadeiros, 2 km from Veadeiros, Cerrado, common, 18 July 1964, *G. T. Prance & N. T. Silva 58195* (holotype, UB; isotypes, NY, US, VDB). Figure 8.

Planta perennis, densicaespitosa, glabra, basibus bulbosis, castaneis, rhizomate nullo vel brevi horizontali, per bases persistentes veternas foliorum obtecto. Radices graciles. Folia rigida, 1.5–3 dm longa, erecta, torta et leviter flexuosa, vaginis scaporum longiora; laminae teretes vel subteretes, vaginis 4–5-plo longiores, 0.3–0.5 mm crassae, vade multicostatae, saepe 1–2-sulcatae, ferrugineae vel brunneolae aut olivaceae; apices valde contracti, conice subulati; vaginae nitidae, integrae, ad basin ecarinatae, apicem versus carinatae, ferrugineae vel brunneolae, quam laminis multomagis latiores, valde ligulatae; ligula firma, plana, oblonga, 4–5 mm longa, ad apicem obtusa; margines tenues, integrae, infime gradatim expansae, tum abrupte ad basin dilatatae. Vaginae scaporum tortae, leviter multicostatae, lamproferrugineae, laminis brevibus, subulatis. Scapi vulgo 2.5–4.5 dm longi, recti, leviter torti, teretes, 0.5 mm crassi, inconspicue longitudine striati, olivacei. Spicae ellipsoideae, 8–10 mm longae, attenuatae, pluriflorae, bracteae convexae, ecarinatae, pallide ferrugineae vel brunneolae, nitidae, tenues, integrae, laxe spiraliter imbricatae; bracteae steriles 5–7, ellipticae vel ovatae, infimae ellipticae, fertilibus multo breviores et in eas gradatim transientes; bracteae fertiles ovatae vel late oblongae, ca. 5 mm longae, supernae magis plicatae et infernis tenuiores, ad apicem brevicarinatae; area dorsalis brevilinearis, ferruginea, apicalis. Sepala lateralia libera, valde inaequilatera, lineari-elliptica, curvata, 5–5.5 mm longa, acuta; ala carinali firma, a basi integra, a medio ad apicem ciliata, ad apicem alis et pilis ferrugineis. Laminae petalorum anguste obovatae, ca. 5.5 mm longae, luteolae, acutae, sparse erosae, cuneatae. Staminodia bibrachiata, brachiis longipenicillatis. Antherae lanceolato-oblongae, ca. 1.5 mm longae, sagittatae. Capsula lanceolata, ca. 4 mm longa, subulata; placenta centralis. Semina ovoidea vel ellipsoidea, ca. 0.5 mm longa, atroferruginea, minute sed acute multicostata.

Plants perennial, densely cespitose, smooth, the bases bulbous, castaneous, the rhizome none or short and horizontal, covered by chaffy bases of old leaves. Roots slender. Leaves stiff, 1.5–3 dm long, erect, twisted and somewhat flexuous, longer than the scape sheaths; blades terete or subterete, 4–5 times longer than the sheaths, 0.3–0.5 mm thick, shallowly several-ribbed, often 1–2-sulcate, reddish brown, or brownish, or greenish-brown; apices

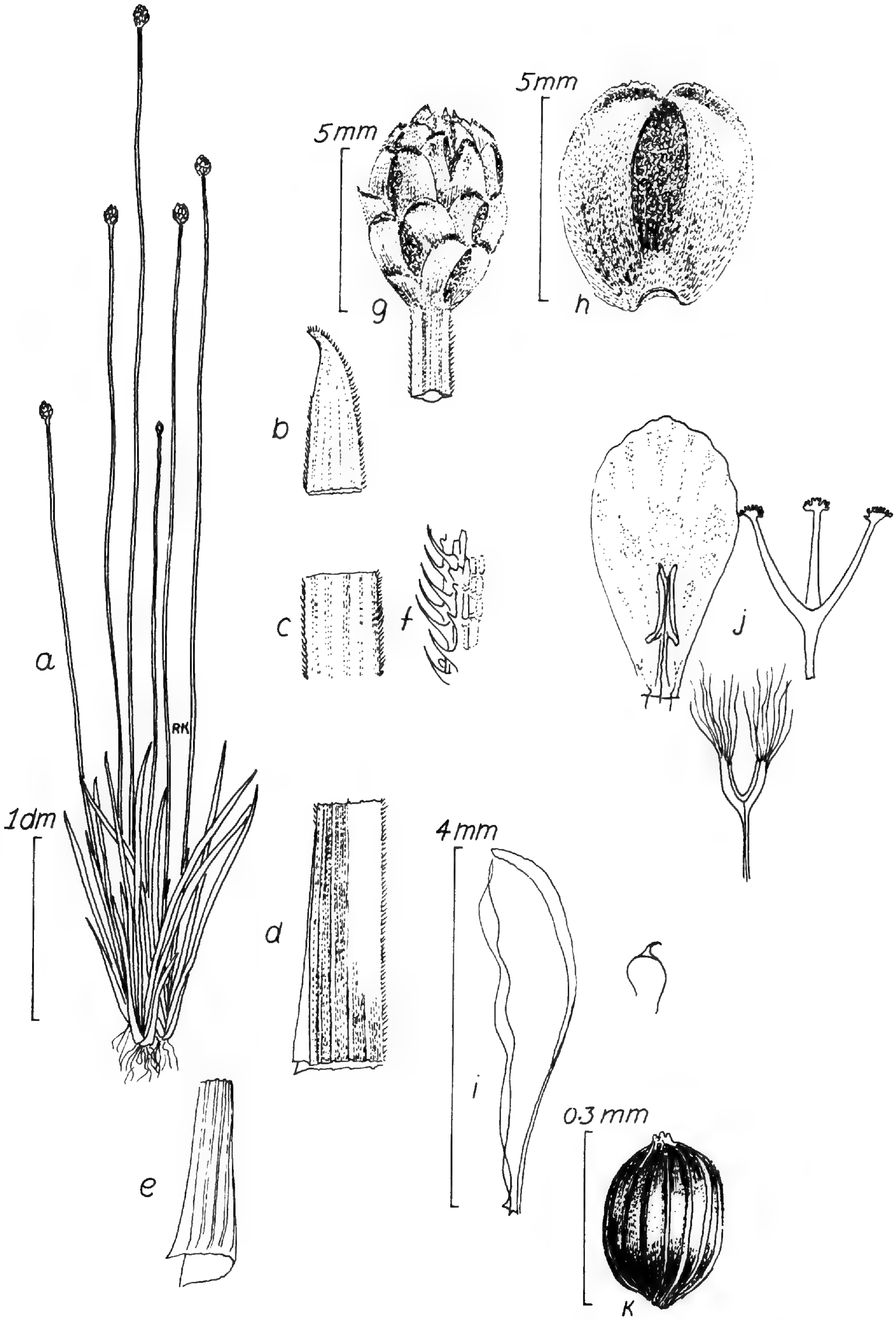

FIGURE 7. Xyris obcordata (Irwin et al. 27763).—*a. Habit sketch.—b. Leaf apex.—c. Sector of leaf at mid blade.—d. Sector of leaf at blade-sheath junction.—e. Leaf base.—f. Very enlarged small sector of leaf blade edge.—g. Spike.—h. Fertile bract.—i. Lateral sepal.—j. Petal blade and stamen, staminode, stylar apex.—k. Seed.*

strongly narrowed, conic-subulate; sheaths shining, ecarinate at base, carinate toward apex, reddish brown to brown, much wider than the blades, strongly ligulate, the ligule firm, flat, oblong, 4–5 mm long, apically obtuse, the margins thin, entire, gradually expanding downward, then abruptly dilating at base. Scape sheaths twisted, low-multicostate, lustrous reddish brown, with short, subulate blades. Scapes commonly 2.5–4.5 dm long, erect, somewhat twisted, terete, 0.5 mm thick, inconspicuously longitudinally striate, olivaceous. Spikes ellipsoid, 8–10 mm long, attenuate, many-flowered, the bracts convex, ecarinate, pale reddish brown or brownish, shining, thin, entire, loosely spirally imbricate; sterile bracts 5–7, elliptic to ovate, the lowest elliptic, much shorter than the fertile bracts and grading gradually into them; fertile bracts ovate to broadly oblong, ca. 5 mm long, the upper ones more folded and thinner than the lower ones, all short-carinate at apex; dorsal area short-linear, reddish brown, apical. Lateral sepals free, strongly inequilateral, linear-elliptic, curvate, 5–5.5 mm long, acute; keel firm, entire at base, sparsely (deciduously) ciliate from middle to apex, the keel and hairs at the sepal apex reddish brown. Petal blades narrowly obovate, ca. 5.5 mm long, yellow, acute, sparsely erose, the base cuneate. Staminodia bibrachiate, the branches long-penicillate. Anthers oblong-lanceolate, ca. 1.5 mm long, sagittate. Capsule ca. 4 mm long, lanceoloid, the tip subulate; placenta central. Seeds ovoid to ellipsoid, ca. 0.5 mm long, reddish brown, minutely but sharply multicostate.

While the dorsal areas of the bracts of this distinctive species are small, they are dark in contrast to the rest of the bract and are thus evident. The slender, terete leaf blades are much narrower than the dilated, strongly ligulate sheaths. The only hairs on the plant are those found scattered along the keel apex of the lateral sepals.

8. Xyris sceptrifera Kral & Wanderley, sp. nov. TYPE: Brazil. Goiás: Serra dos Cristais, 17°S, 48'W, creek margin ca. 5 km S. of Cristalina, Goiás, elev. 1,200 m, 3 Mar. 1966, *H. S. Irwin, J. W. Grear, Jr., R. Souza & R. Reis dos Santos 13410* (holotype, UB; isotypes, NY, US). Figure 9.

Planta perennis, caespitosa, basibus bulbosis castaneis; radices graciles. Folia rigida, glabra, solum basalia, valde torta et flexuosa, 5–6 dm longa, erecta vel leviter expansa aut excurvata, vaginis scaporum longiora; laminae subteretes vel angulatae, paucinervosae et sulcatae, 1–2 mm latae, flavovirentes, 3–4-plo vaginis longiores, glabrae; apices erecti, gradatim contracti, aristati, pagina superiore concava; margines (si evidentes) incrassati, glabri; vaginae basin versus rotundatae, longitudine multicostatae, atrocastaneae, nitidae, marginibus integris, in laminam gradatim convergentibus et ad apicem conduplicatis, infime gradatim expanse tum abrupte ad basin dilatatae. Vaginae scaporum laxe conduplicatae vel apertae, leviter carinatae, laminis subteretibus, erectis, acutis. Scapi lineares, recti, vade multicostati, valde torti et flexuosi, ca. 7–10 dm alti, teretes, 1–2 mm crassi, glabri, dilute virides. Spicae ovoideae, ellipsoideae, aut cylindricae, 1–2.5 cm longae, multibracteatae, bracteis spiraliter imbricatis, convexis ecarinatis, oblongis vel obovatis, brunneolis, vadose erosis vel integris; bracteae infimae paucae, oblongae, fertilibus leviter breviores et in eas transientes; bracteae fertiles 5–5.5 mm longae, convexe rotundatae, apicale late rotundatae vel truncatae, area dorsali anguste elliptica, pallide viridis. Sepala lateralia libera, valde inaequilatera, elliptica, ca. 5.5 mm longa, valde incurvata, leviter exserta; ala carinalis angusta, a basi ad medium integra, a medio retrorse fimbriata, ad apicem expanse vel antrorse dense fimbriata, trichomatibus ferrugineis. Laminae petalorum obovatae, ca. 4 mm longae, ad apicem anguste rotundatae, dentatae, luteolae. Staminodia bibrachiata, brachiis elongatis longipenicillatis. Antherae oblongae, ca. 2 mm longae, profunde sagittatae et retusae, filamentis longiores. Capsula cylindrica, ca. 2.5 mm longa; placenta centralis. Semina anguste oblongo-fusiformia, 1.2–1.3 mm longa, ferruginea, longitudine valde multicostata.

Plants perennial, cespitose, with castaneous bases, bulbous; roots slender. Leaves rigid, smooth, strictly basal, strongly twisted and flexuous, 5–6 dm long, erect or slightly spreading or excurved, longer than the scape sheaths; blades subterete or angulate, few-nerved and sulcate, 1–2 mm wide, yellow-green, 3–4 times longer than the sheaths; apices erect, gradually narrowed, aristate, with upper surface concave; margins (if evident) thickened, smooth; sheaths rounded toward base, longitudinally multicostate, dark castaneous, lustrous, entire-margined, narrowing gradually into the blade, conduplicate at apex, toward base gradually widening then abruptly dilating. Scape sheaths loosely conduplicate

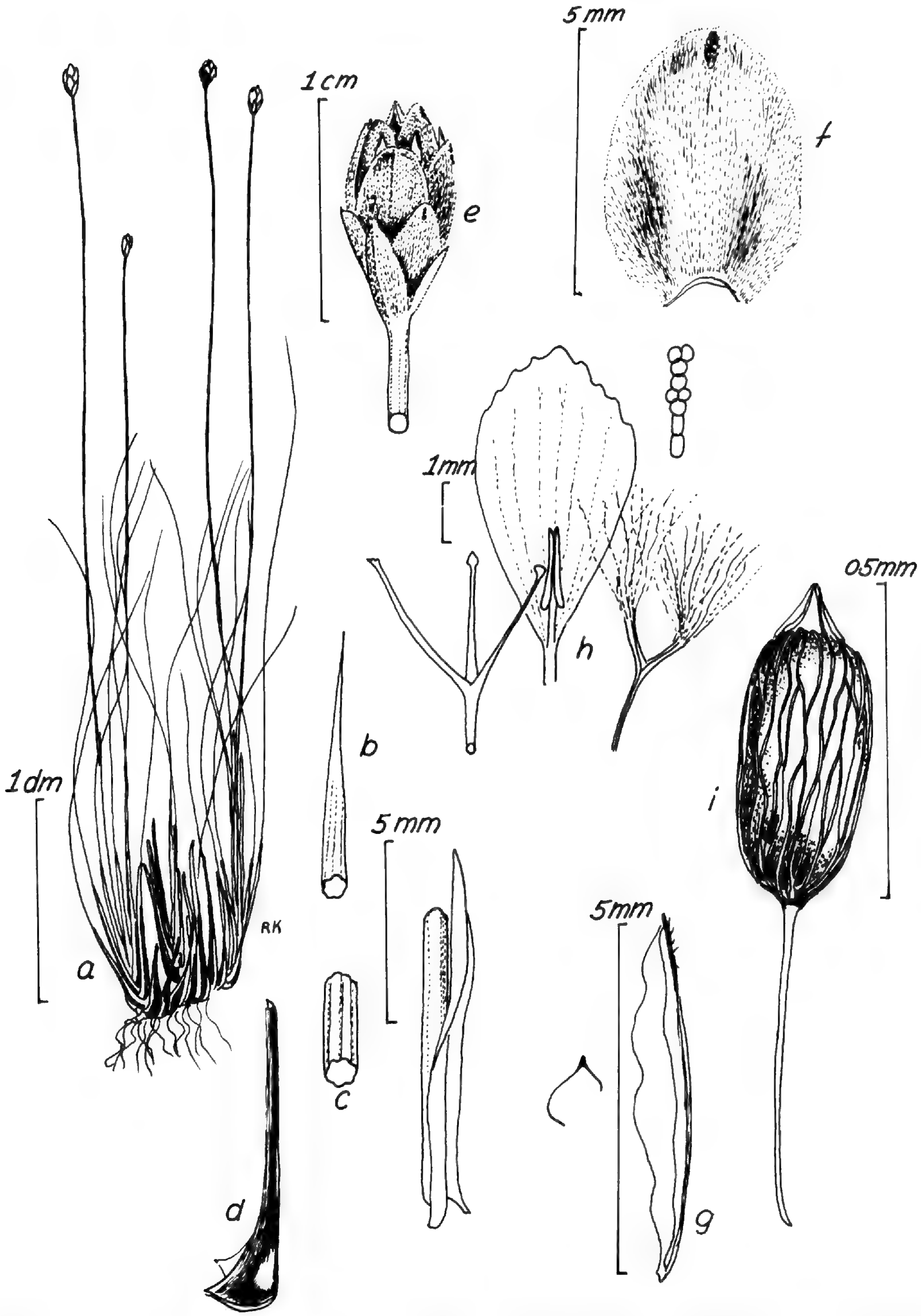

FIGURE 8. Xyris pranceana (Prance & Silva 58195).—*a. Habit sketch.—b. Leaf apex.—c. Sector of mid blade.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Flower parts.—i. Seed with attached funicle.*

or open, slightly carinate, the blades subterete, erect, acute, short. Scapes linear, shallowly multicostate, strongly twisted and flexuous, ca. 7–10 dm high, terete, 1–2 mm thick, smooth, pale green. Spikes ovoid, ellipsoid or cylindric, 1–2.5 cm long, 5–7 mm thick, with many spirally imbricate bracts, convex-backed, oblong to obovate, brown, shallowly erose or entire; sterile bracts few, oblong, slightly shorter than the fertile bracts and grading into them; fertile bracts 5–5.5 mm long, convexly rounded, broadly rounded to truncate apically, the dorsal area elliptic, pale green. Lateral sepals free, strongly inequilateral, elliptic, ca. 5.5 mm long, strongly curvate; carinal keel narrow, entire from base to middle, retrorsely fimbriate at middle, spreadingly or antrorsely densely fimbriate at apex, the trichomes ferrugineous. Petal blades obovate, ca. 4 mm long, yellow, at apex narrowly rounded, toothed. Staminodia bibrachiate, the branches elongate, long-penicillate. Anthers oblong, ca. 2 mm long, deeply sagittate and retuse, longer than the filaments. Capsule cylindric, ca. 2.5 mm long; placentation central. Seeds narrowly oblong-fusiform, 1.2–1.3 mm long, reddish-brown, longitudinally strongly multiribbed.

Additional specimens examined. BRAZIL. GOIÁS: creek bank, ca. 6 mi. S of Cristalina, el. 1,175 m, 5 Nov. 1965, *H. S. Irwin, R. Souza & R. Reis dos Santos 9947* (NY, US). MINAS GERAIS: Morro das Pedras, wet campo, red clay, ca. 35 km NE of Patrocino, elev. 1,000 m, 29 Jan. 1970, *H. S. Irwin, E. Onishi, S. F. da Fonseca, R. Souza, R. Reis dos Santos & J. Ramos 25625* (NY, US).

This tall, bulbous-based species with twisted and flexuous leaves and scapes plainly relates to *Xyris goyazensis* Malme, and a full study may later reveal a varietal relationship. However, the fertile bracts, in addition to being more numerous in a larger spike, lack an apical tuft of villous hairs, and the lateral sepals, while fimbriate, have narrower keels which are entire toward the base. The apex of the leaf, unlike that of *X. goyazensis*, is spinulose. *Xyris sceptrifera* differs from the closely related *X. veruina* Malme by having fertile bracts with more obtuse tips, smaller and narrower dorsal areas, and narrower sepal keels which are less copiously fimbriate.

9. **Xyris seubertii** Nilsson var. **espinhacae** Kral & Wanderley, var. nov. TYPE: Brazil. Minas Gerais: Serra do Espinhaco, wet sand, sandstone precipices and adjacent cerrado, ca. 18 km west of Grão Mogol, elev. 950 m, 21 Feb. 1969, *H. S. Irwin, R. Reis dos Santos, R. Souza & S. F. da Fonseca 23667* (holotype, UB; isotypes, NY, US). Figure 3.

Planta perennis, caespitosa, basibus subbulbosis; caules breves; radices graciles. Folia flabellate expansa, anguste linearia, vulgo 5–7 cm longa, vaginis scaporum plerumque longiora; laminae 1–3-plo vaginis longiores, planae, 0.8–1.2 mm latae, glabrae, valde compressae, olivaceae, longitudine indistincte nervosae; apices gradatim tum abrupte contracti, anguste acuminati, scabri, erecti; margines tenues, antrorse scabrosi; vaginae praeter bases carinatae, carinis glabris, lateribus purpureis vel ferrugineis, glabris, valde multicostatis, basim versus papillosis, marginibus integris, in laminas gradatim convergentibus, infime gradatim expansis, tum abrupte ad basim dilatatis castaneis vel atroferrugineis. Scapi graciles, recti vel aliquantum torti, 2–3 dm alti, subteretes, olivacei, ecostati vel subtiliter 1–3-costati, costis glabris vel subtiliter scabrosis. Spicae pauciflorae, ovoideae vel ellipsoideae aut obovoideae, 5–7 mm longae, bracteae convexae, ecarinatae vel carinatae, subdecussatae, pallide brunneolae, marginibus scariosis, latis, integris, rotundatis, ad apicem ferrugineo-fimbriolatis; bracteae steriles 4, pari infimo oblongo vel anguste obovato, ca. 3 mm longo, carinato, areis dorsalibus linearibus, breviter excurrentibus, pari intimo latiores, obovato, ca. 3.5 mm longo; bracteae fertiles 4, oblongae, ca. 4.5–5 mm longae, rotundatae, plicatae, area dorsalis lanceolata, viridis, 3–4 mm longa. Sepala lateralia ⅓-connata, inaequilatera, curvata, ca. 5 mm longa, lobis oblongis, ala carinali angusta sed forte, a medio ad apicem dense ferrugineo-fimbriolata. Laminae petalorum ellipticae, ca. 5 mm longae, acutae, subintegrae, luteolae. Staminodia bibrachiata, brachiis linearibus compressis apicibus et lateribus longipenicillatis. Antherae lineari-oblongae, ca. 2 mm longae, refusae et sagittatae, filamentis 2-plo longiores. Capsula anguste ellipsoidea, ca. 3.5 mm longa; placenta centralis. Semina matura non visa.

Plants perennial, cespitose, with subbulbous base; stems short, the roots slender. Leaves flabellately spreading, narrowly linear, commonly 5–7 cm long, mostly longer than scape sheaths; blades 1–3 times longer than sheaths, flat, 0.8–1.2 mm wide, smooth, strongly flattened, olivaceous, longitudinally indistinctly nerved; apices gradually, then abruptly, narrowed, narrowly acuminate, scabrous, erect; margins thin, antrorsely scabrid; sheaths except for bases smooth-carinate, the

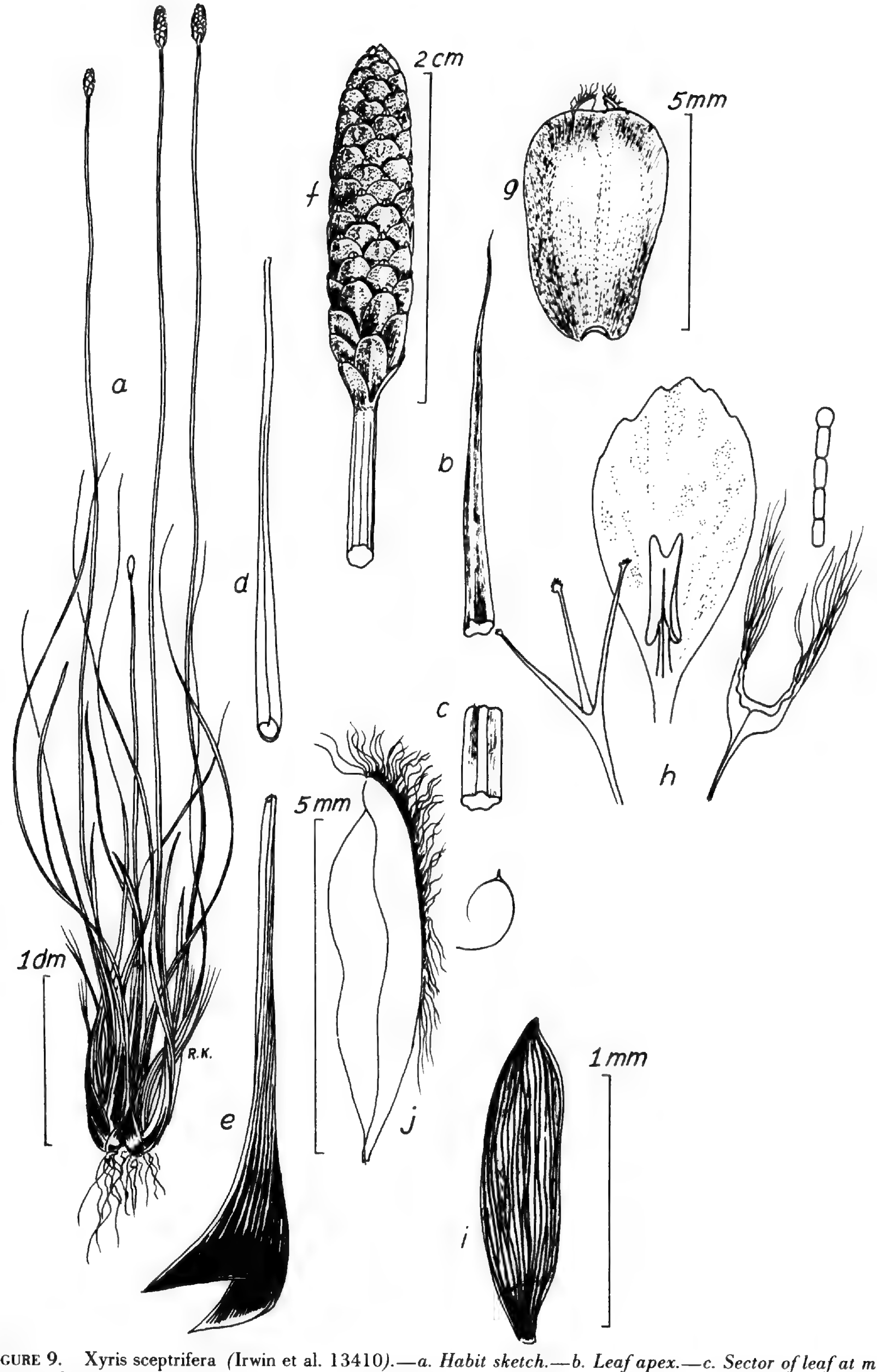

FIGURE 9. Xyris sceptrifera (Irwin et al. 13410).—*a. Habit sketch.—b. Leaf apex.—c. Sector of leaf at mid blade.—d. Sector of leaf showing sheath and blade junction.—e. Leaf base.—f. Spike.—g. Fertile bract showing exserted lateral sepal tips.—h. Petal, stamen, stylar apex, staminode.—i. Seed.—j. Lateral sepal.*

sides purplish or ferruginous, smooth, strongly multicostate, papillose toward base, the margins gradually narrowing into the blades, below gradually widening then dilating abruptly at base, castaneous or deep red-brown. Sheaths of scapes lax, twisted toward base, multicostate, brown, toward apex open, green, with margins broadly scarious, with blades as on foliage leaves but short. Scapes slender, straight or somewhat twisted, 2–3 dm high, subterete, olivaceous, ecostate or finely 1–3-costate, the costae smooth or finely scabrid. Spikes few-flowered, ovoid or ellipsoid or obovoid, 5–7 mm long, the bracts convex, ecarinate or carinate, subdecussate, pale brown, the margins broad, entire, scarious, rusty fimbriolate at apex; sterile bracts 4, the lower pair oblong or narrowly obovate, ca. 3 mm long, carinate, with linear, short-excurrent dorsal areas; inner pair wider, obovate, ca. 3.5 mm long; fertile bracts 4, oblong, ca. 4.5–5 mm long, rounded-plicate, the dorsal area lanceolate, greenish, 3–4 mm long. Lateral sepals ca. ⅓ connate, inequilateral, curvate, ca. 5 mm long with lobes oblong, acute, the keel narrow but strong, densely rusty fimbriolate from middle to apex. Petal blades elliptic, ca. 5 mm long, acute, subentire, yellow. Staminodia bibrachiate, the branches linear, flattened, apically and laterally long-penicillate. Anthers linear-oblong, ca. 2 mm long, retuse and sagittate, 2 times as long as filaments. Capsule narrowly ellipsoid, ca. 3.5 mm long, the placentas central. Mature seeds not seen.

The new variety appears to be a small variant of *X. seubertii,* agreeing with that species by having greenish, excurrent dorsal areas and connate lateral sepals with densely rusty-pubescent keels. The bracts are sparsely but definitely villosulous (vs. glabrous) apically; the placentation is definitely free-central rather than basal as in the type variety.

10. Xyris villosicarinata Kral & Wanderley, sp. nov. TYPE: Brazil. Minas Gerais: wet depression near creek, grazed campo and cerrado, upland valley, Serro do Itabirito, Minas Gerais, ca. 45 km SE of Belo Horizonte, ca. 1,500 m elev., 8 Feb. 1968, *H. S. Irwin, H. Maxwell & D. C. Wasshausen 19570.* (holotype, UB; isotypes, NY, US). Figure 10.

Planta perennis, caespitosa, basibus leviter bulbosis, fuscis. Caules breves, per bases persistentes veternas foliorum obtecti. Radices graciles. Folia rigida, erecta, 0.8–1.5 dm longa, solum basalia, vaginis scaporum longiora; laminae vaginis 4–5-plo longiora, tortae, 1–1.3 mm latae, compressae, flavovirentes vel ferrugineofuscae, transverse rugulosae, distincte longitudine 3–4-nervosae; apices anguste acuti, interdum aristulati; aciebus crassiusculi; vaginae ad basim leviter dilatatae, ecarinatae, in laminas gradatim decrescentes, transverse rugulosae, apicem versus carinatae, lateribus fuscis, aciebus pallide longiciliatis. Vaginae scaporum fuscae vel ferrugineae, transverse rugulosae, multicostatae, apicem versus carinatae, laminis brevibus incurvatis. Scapi teretes vel subteretes, plus minus spiraliter torti, flexuosi, 2–3 dm alti, ca. 1 mm crassi, transverse rugulosae, virides, bicostati vel ecostati. Spicae anguste ovoideae vel ellipsoidales, 0.7–1 cm longae, pauciflorae, bracteae convexae, leviter carinatae, costales, pallide lamproferrugineae, integrae vel leviter laceratae, dorsis papillosis; bracteae steriles 4, subdecussatae, pari infimo oblongo, ca. 3 mm longo, pari intimo obovato, ca. 5 mm longo; bracteae fertiles obovatae, rotundatae, plicatae, usque ad 7 mm longae, tenues, area dorsali indistincta. Sepala lateralia libera, subaequilateralia, lineari-oblonga, ca. 6 mm longa, obtusa; ala carinali apicem versus irregulariter ciliata vel fimbriolata, lateribus villosulis. Laminae petalorum ellipticae, 6–7 mm longae, acutae, integrae, flavae. Staminodia bibrachiata, brachiis compressis, longipenicillatis. Antherae lanceolatae, ca. 2 mm longae, sagittatae, filamentis longiores. Placenta basalis. Semina non visa.

Plants perennial, cespitose, with bases slightly bulbous, brown. Stems short, covered by bases of old foliage leaves. Roots slender. Leaves rigid, erect, 0.8–1.5 dm long, strictly basal, longer than the scape sheaths; blades 4–5 times longer than sheaths, twisted, 1–1.3 mm wide, flattened, yellow-green to reddish brown, transversely rugulose, distinctly longitudinally 3–4-nerved; apices narrowly acute, sometimes aristulate; edges thickened; sheaths slightly dilated toward base, ecarinate, gradually narrowing above into blades, transversely rugulose, carinate toward apex, the sides brownish, the edges ciliate with long pale hairs. Scape sheaths brownish to reddish brown, transversely rugulose, multicostate, carinate toward apex, with short, incurved blades. Scapes terete or subterete, ± spirally twisted, flexuous, 2–3 dm high, ca. 1 mm

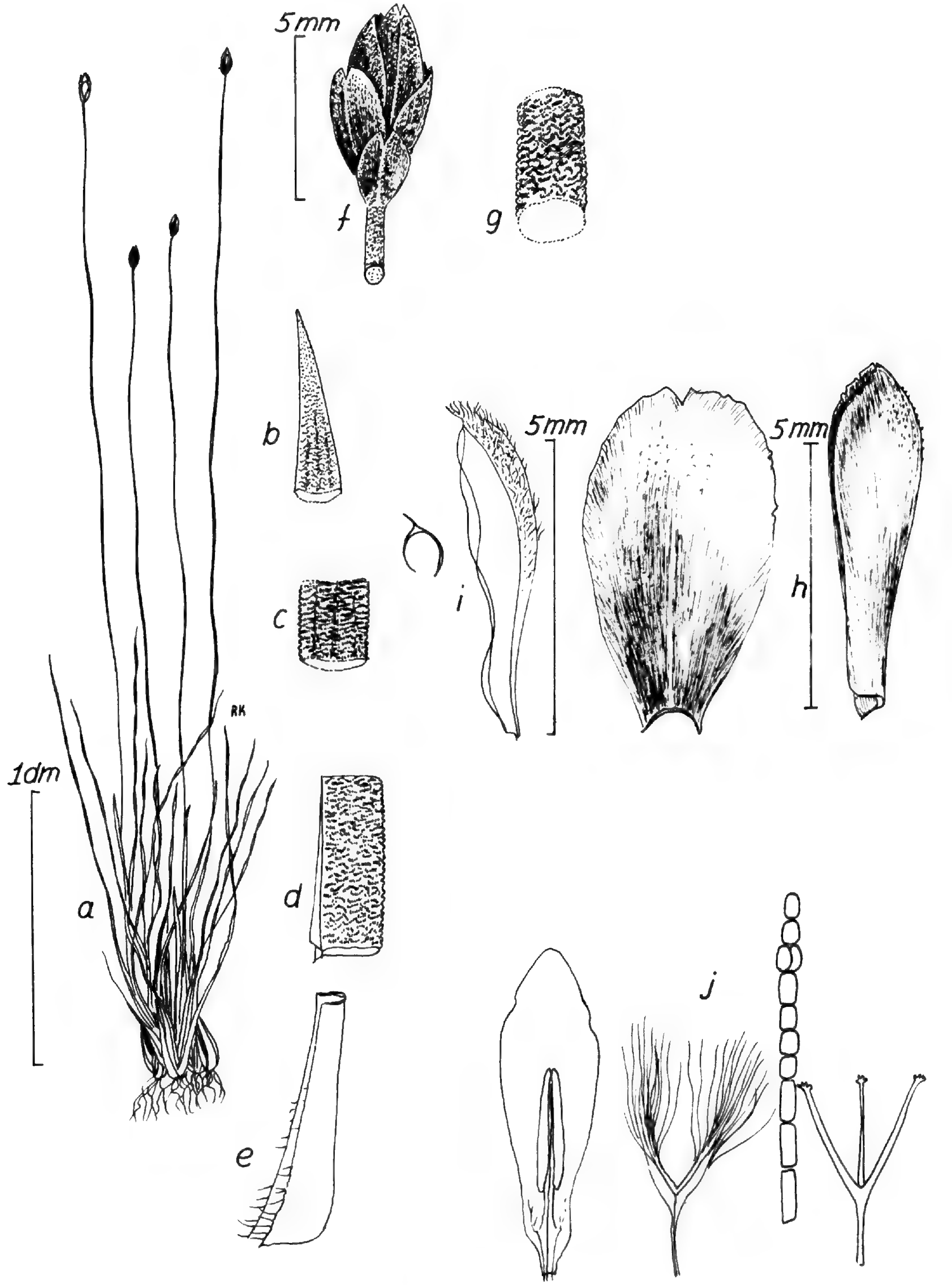

FIGURE 10. Xyris villosicarinata (Irwin et al. 19570).—*a. Habit sketch.—b. Leaf apex.—c. Sector of mid blade.—d. Sector at leaf blade–sheath junction.—e. Leaf base.—f. Spike.—g. Sector of scape at mid scape.—h. Two views of fertile bract.—i. Lateral sepal.—j. Petal and stamen, staminode, staminodial beard hair, stylar apex.*

thick, transversely rugulose, green, bicostate to ecostate. Spikes narrowly ovoid or ellipsoid, 0.7–1 cm long, few-flowered, the bracts convex, slightly carinate, with midrib, pale shining reddish brown, entire or slightly lacerate, the backs papillose; sterile bracts 4, subdecussate, the lowest pair oblong, ca. 3 mm long, the inner pair obovate, ca. 5 mm long; fertile bracts obovate, rounded, plicate, up to 7 mm long, thin, the dorsal area indistinct. Lateral sepals free, subequilateral, linear-oblong, ca. 6 mm long, obtuse; keel irregularly ciliate or fimbriolate toward apex, the sides villosulous. Petal blades elliptic, 6–7 mm long, acute, entire, yellow. Staminodia bibrachiate, the branches flattened, long-penicillate. Anthers lanceolate, ca. 2 mm long, sagittate, longer than the filaments. Placenta basal. Seeds not seen.

This bears several of the characters of *Xyris tortula* Martius, but the foliage is rugulose throughout (not smooth), the margins of the narrow, twisted leaf blades are not cartilaginous as in *X. tortula*, and the sides of the lateral sepal keel toward its apex are densely villosulous with pale hairs, rather than confined to the keel only as in *X. tortula*.

NEW AND NOTEWORTHY TAXA FROM PANAMA[1]

Gordon McPherson[2]

ABSTRACT

Three new species, Prunus fortunensis *(Rosaceae),* Symplocos panamensis *(Symplocaceae) and* Angostura kunorum *(Rutaceae), as well as four new generic records for Panama are described.*

Botanical exploration of Panama has been going on for decades and yet many species still remain undiscovered. Collecting trips made in 1986 to such western Panamanian sites as the Fortuna Dam area, the Bocas del Toro slope above Chiriquí Grande, and Cerro Colorado could be counted on to yield new species as well as new records, some of them generic, for the Panamanian flora. Moreover, other rich but long-accessible areas such as the El Llano to Carti strip, Santa Rita Ridge, and Cerro Jefe continue to yield novelties. For the most part these are not fully appreciated until they reach the hands of appropriate specialists and then, typically, are published only after some delay. In some cases, however, it is possible to readily evaluate the collections of special interest, and the following three species are here described as new.

Prunus fortunensis McPherson, sp. nov. (Rosaceae). TYPE: Panama. Bocas del Toro: Fortuna Dam region, 1,250–1,300 m, 11 Feb. 1986, *McPherson 8404* (holotype, PMA; isotypes, CAS, CR, DUKE, K, MEXU, MICH, MO, US, UTD). Figure 1.

Species combinatione foliorum parvorum integrorum glabrorum cum inflorescentia racemosa et floribus parvis circa 10-stamineis a congeneribus regionis diversa.

Tree 14 m; branchlets glabrous, somewhat longitudinally striate in older portions, the slightly raised lenticels 0.5–1 mm long; nodes marked by raised leaf scars, these pubescent along their adaxial margin when newly exposed, glabrescent. Leaf blades elliptic to slightly ovate, 3.5–6 cm long, 1.4–3 cm wide; base obtuse; apex acuminate, ultimately narrowly obtuse; margin entire; both surfaces glabrous, the laminar glands usually 1 pair, intramarginal, basal; secondary veins 5–6(–7) on each side of the midrib, all of the venation slightly impressed on the upper surface, the midrib alone raised on the lower surface. Petioles 5–8 mm long, caniculate, glabrous. Stipules triangular, 1.5–2 mm long, 1 mm wide at base, caducous. Inflorescences in the axils of leaves of the current season, racemose, 3–5.5 cm long, glabrous; peduncle 6–10 mm long, bearing 14–20 flowers; pedicels 2–4 mm long; bracts small, absent at anthesis. Hypanthium campanulate at anthesis, glabrous, 1–1.5 mm long from base to rim; lobes

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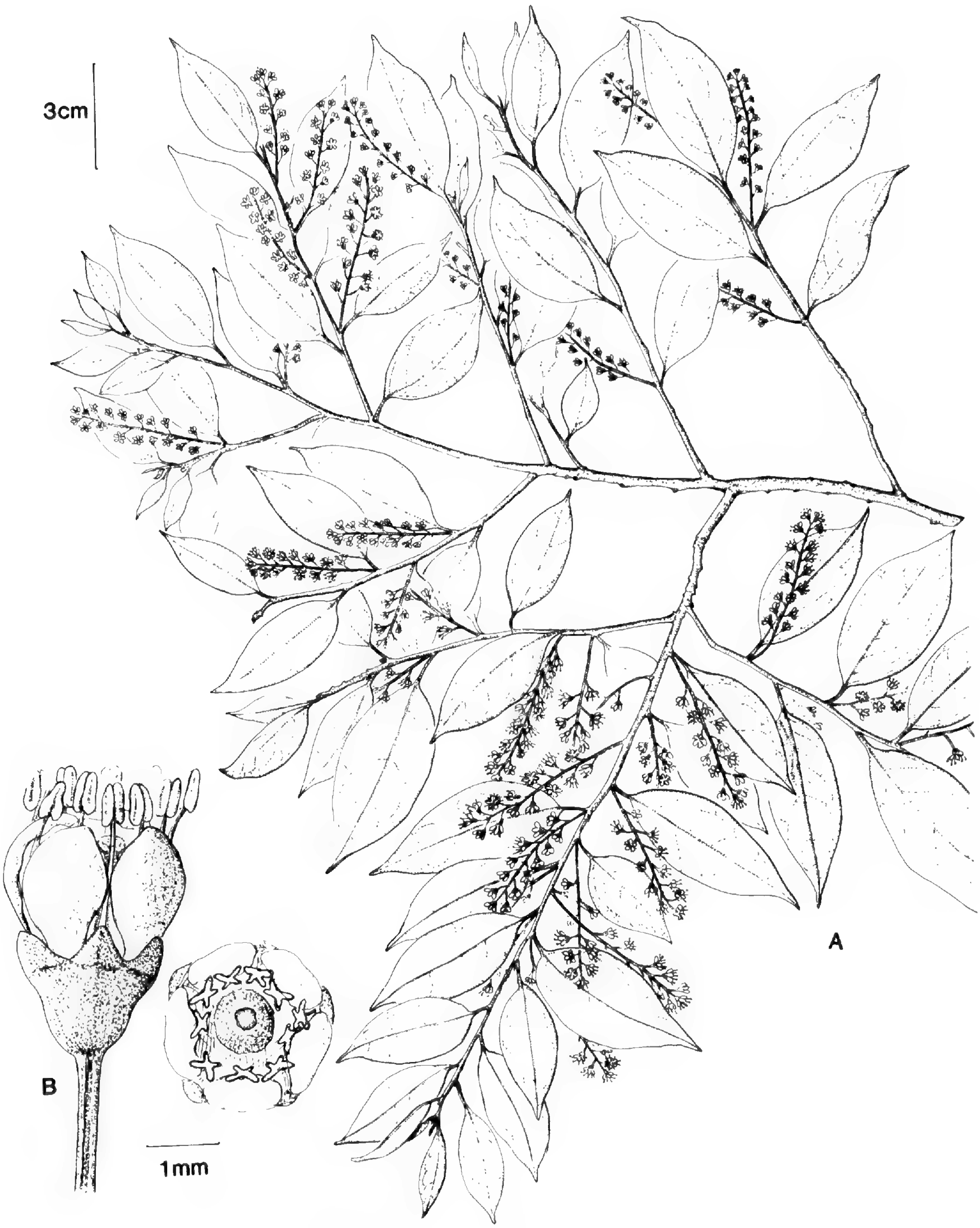

FIGURE 1. Prunus fortunensis (McPherson 8404).—*A. Flowering branchlet.—B. Flower, lateral and top views.*

ca. 0.6 mm long, 1 mm wide at the base, obtuse, somewhat cucullate. Petals white, roughly circular, 1–1.5 mm diam., entire. Stamens 9–11(–15), 1.8–2 mm long, the anthers ca. 0.5 mm long. Ovary ca. 1 mm diam., glabrous; style 1.5–2 mm long, glabrous; stigma flattened, 0.5–0.8 mm wide. Fruit unknown.

This species is distinguished from its congeners in the region (*P. annularis* Koehne, *P. brachybotrya* Zucc.) by its combination of small, entire, glabrous leaves, racemose inflorescence, and small flowers with ca. 10 stamens.

Symplocos panamensis McPherson, sp. nov. (Symplocaceae). TYPE: Panama. Colón: Santa Rita Ridge, ca. 500 m, 16 Feb. 1986, *McPherson 8447* (holotype, PMA; isotypes, BM, CAS, COL, CR, DUKE, K, L, MEXU, MICH, MO, NYBG, US, UTD). Figure 2.

Species pilis appressis, foliis chartaceis fere glabris dentatis a paucis nervis, petiolis brevibus, sepalis partim pubescentibus, corollis 11–16 mm fere glabris, floris 40–45-stamineis, stylis aliquantum pubescentibus omnino a congeneribus regionis diversa.

Tree 10–12 m; twigs pale in color, somewhat flattened, the youngest often channeled (at least on drying); young stems and buds white pubescent, the buds densely so, the hairs strongly appressed, those of the stem not dense, ± persistent but becoming sparse on older stems. Leaf blades obovate-elliptic to elliptic, 7–21 cm long, 2.7–7.2 cm wide, thinly chartaceous; base usually somewhat attenuate and narrowly obtuse, sometimes acute; apex acuminate; margin entire proximally, denticulate to dentate distally, often pubescent; upper surface glabrous, the lower surface pubescent while immature but glabrous or nearly so at maturity, a few hairs sometimes remaining near the base; midrib adaxially sunken over most of its length, raised abaxially, pubescent with white, appressed hairs; secondaries 5–6(–8) on each side of the midrib, somewhat arcuate, puberulent. Petiole 2–5(–7) mm long, channeled and glabrous adaxially, appressed-pubescent abaxially. Inflorescences axillary, the subtending leaf often fallen; axis 1–5 mm long, pubescent, bearing (1–)3–7 flowers; bracts several, the peduncular bracts densely pubescent abaxially, the pedicellar bracts less so, all glabrous adaxially. Hypanthium 1 mm long, glabrous or sparsely pubescent. Calyx lobes white, 5, 1.5–2 mm long, 1.5–2 mm wide at the base, obtuse, pubescent abaxially along the midline with white, appressed, somewhat flexuous hairs; margins pubescent. Corolla white, of 4–6 partly fused petals 11–16 mm in length and connate near the base, adnate to androecium about halfway up, the spreading portion of the lobes typically ca. 4 mm long, 2–5 mm wide, glabrous or sparsely puberulent with appressed hairs, occasionally bearing a misshapen anther apically. Stamens 40–45, exserted, the filaments straplike, the free portions of the outer ones up to 5 mm long, 0.7 mm wide, the inner stamens shorter, narrower, and somewhat inflexed. Ovary 3-locular; ovules 4 per locule, the superior portion of the ovary ca. 1 mm long, pubescent; style 9–11 mm long, at least sparsely pubescent over its entire length; stigma capitate, ca. 1 mm diam. Fruit unknown.

This species differs from other *Symplocos* species of the region (*S. austin-smithii* Standley, *S. chiriquensis* Pittier, *S. serrulata* Humb. & Bonpl., *inter alia*) in its appressed hairs, thin, nearly glabrous, distally dentate leaf blades with few secondaries, short petioles, only partially pubescent sepals, nearly or quite glabrous, rather long corolla, 40–45 stamens, and styles pubescent their entire length.

Additional specimen examined. PANAMA. DARIÉN: Cuasi-Cana trail on Cerro Campamineto, east of Tres Bocas, headwaters of Río Cuasi, 29 Apr. 1968, *Kirkbride & Duke 1246* (MO).

Angostura kunorum McPherson, sp. nov. (Rutaceae). TYPE: Panama. San Blas: along El Llano–Carti road, ca. 14.5 mi. from Interamerican Highway, ca. 350 m, 17 June 1986, *McPherson 9525* (holotype, PMA). Figure 3.

Species 5–7-foliolatis, foliolis grandibus latis, inflorescentia anguste paniculata, alabastris rectis petalis valvatis, androeciis omnino fertilibus a congeneribus diversa.

Slender tree 4 m tall; young, leaf-bearing stems ca. 1 cm diam., roughened by many small ridges (at least on drying), conspicuously lenticellate, brown puberulent with a mixture of erect, curved, whitish hairs and minute,

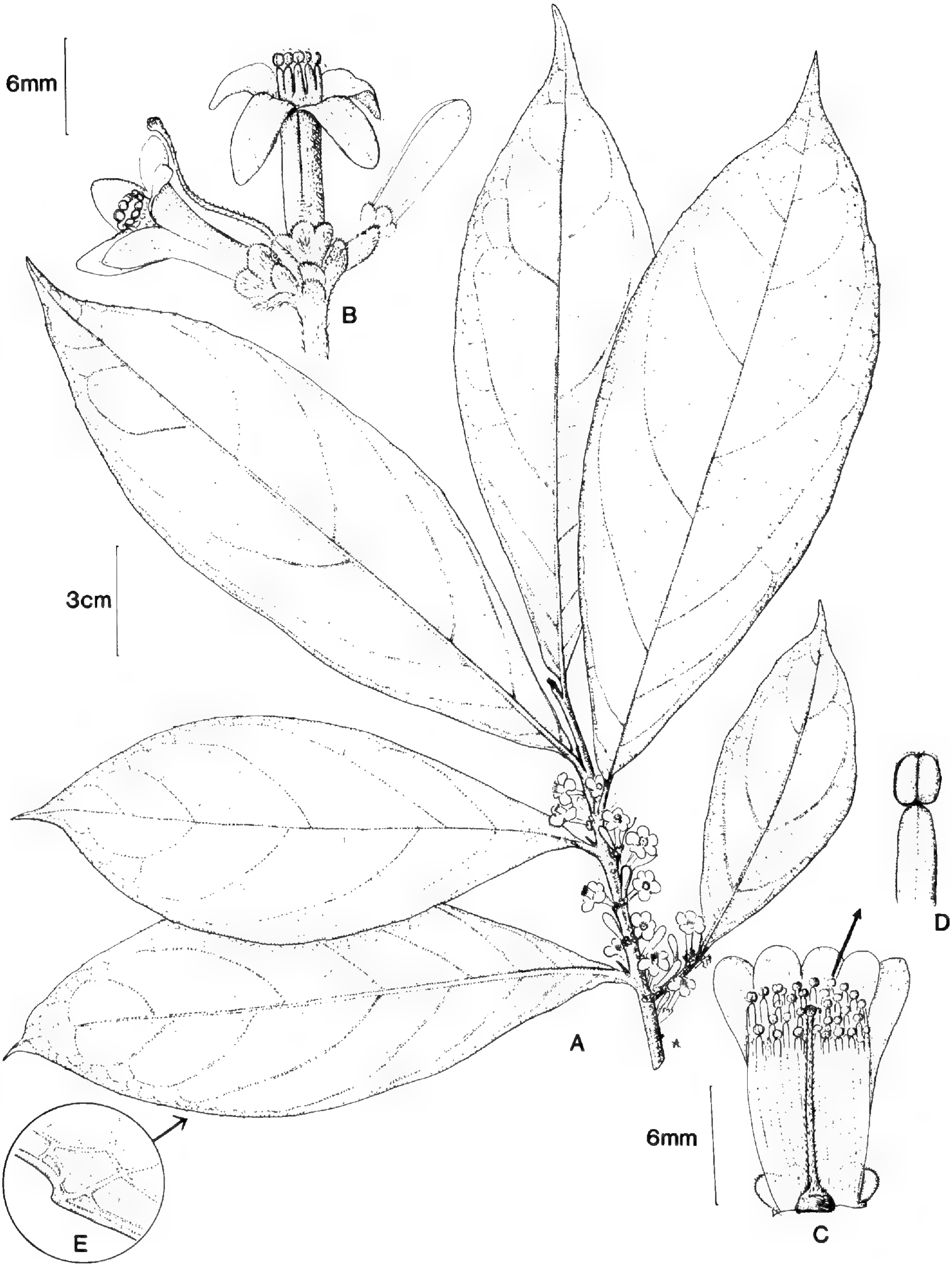

FIGURE 2. Symplocos panamensis (McPherson 8447).—*A. Flowering branchlet.—B. Inflorescence.—C. Opened flower.—D. Stamen.—E. Detail of leaf margin.*

brown, spherical, sessile granulations as well as with intermediates; leaf buds with a similar but denser indument; leaf scars ca. 1 cm long, ca. 1 cm wide. Leaves alternate; blades palmately compound, 5- or 7-foliolate, the leaflets diverging through ½–⅔ of a circle, elliptic, the central and largest leaflet ca. 37 cm long, 12–13 cm wide, the outermost and

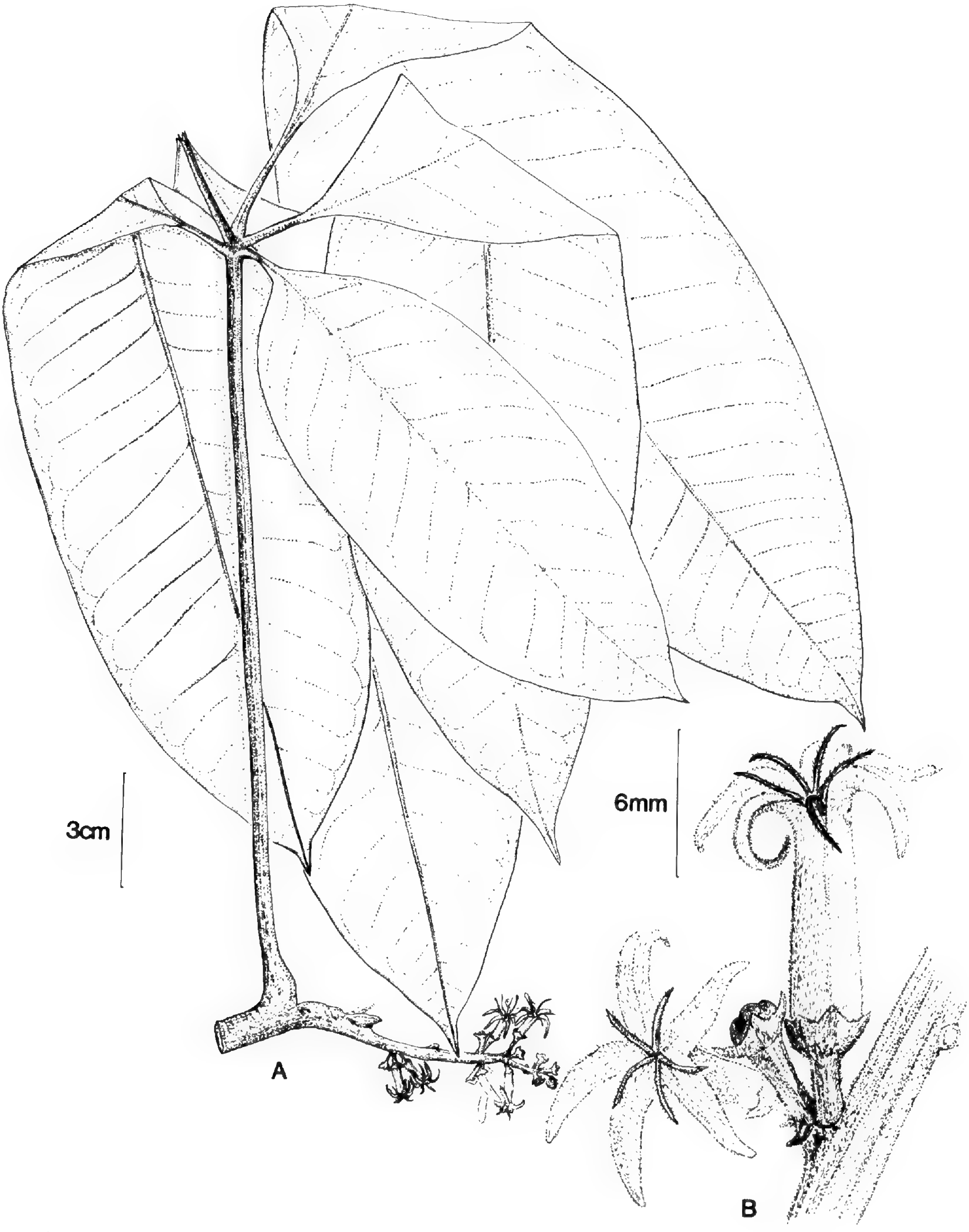

FIGURE 3. Angostura kunorum (McPherson 9525).—*A. Flowering branchlet.*—*B. Flowers.*

smallest 19–29 cm long, 7–11.5 cm wide, attenuate at base, shortly and sharply acuminate at apex, chartaceous, the margins entire, the surfaces densely punctate, glabrous at least at maturity (except for the midrib, this puberulent like the stem and reddish brown when dry), the secondaries slightly impressed on the adaxial surface, ca. 27–30 in number on each side of the largest leaflets and ca. 18 on each side of the smallest leaflets; petiolules canaliculate, puberulent like the stem but glabrescent, pulvinate basally, the central one ca. 3.5 cm long, the outermost 0.8–1.5 cm long, all ca. 3 mm diam.; petiole ca. 28–31.5 cm long, ca. 5 mm diam. near mid length, broadly caniculate, conspicuously lenticellate, pubescent like the stem but partially glabrescent, pulvinate basally, the apex of the petiole flattened, ca. 1 cm diam. Inflorescence appearing pseudoterminal but perhaps truly terminal, very narrowly paniculate (the lateral dichasia subsessile), the axis of the single known inflorescence 8 cm long (further collections may be significantly longer), ca. 4 mm diam. near mid length, puberulent like the stem; stalks of the lateral dichasia 1–2 mm long; bracts triangular, ca. 2 mm long, 2 mm wide at base, stout, acute, puberulent; pedicels 3–5 mm long, puberulent. Buds straight. Calyx cupular, white, 5–6-lobed, 2 mm long, 4–5 mm diam.; lobes shallow, acute, densely puberulent, densely beset with swollen surficial glands ca. 0.2 mm diam. Corolla of 4–6 petals, white, valvate (or very nearly so) in bud, up to 2 cm long in bud, 1.2–1.5 cm long when open (the recurved portion not included); petals linear, connate by marginal tomentum, separating and recurving at anthesis and eventually ¾ to completely unattached to one another, tomentose on both surfaces, the hairs longer and curlier than those of the calyx and unaccompanied by brown granulations, the swollen surficial glands obvious, clear to brownish (at least on drying). Stamens all fertile, 5 or 6; filaments adnate to petal bases, 8–9 mm long, ca. 1.5 mm wide near base, somewhat flattened, tomentose; anthers 11–13 mm long, ca. 0.8 mm wide, introrse, pubescent with long, straight, ± erect hairs, abaxially densely beset with swollen surficial glands. Disk cupular, sometimes bearing impressions of the petal bases and hence ridged, 1 mm high, 2–3 mm diam. Ovary 5-carpellate, 1 mm long, glabrous; style ca. 2 mm long, glabrous; stigma ca. 2 mm long, cylindric, slightly thicker than style, glandular. Fruit unknown.

Angostura kunorum differs from other species of this varied genus in its 5–7 large, broad leaflets, narrowly paniculate inflorescence, straight buds with essentially valvately arranged petals, and entirely fertile androecium.

Among the genera recently added to the known flora of Panama are *Sparattanthelium* of the Hernandiaceae (*S. amazonum* Mart., *McPherson 9643*), *Etaballia* of the Leguminosae (*E.* cf. *guianensis* Benth., *McPherson 9513*), *Metteniusa* of the Icacinaceae (*M. tessmanniana* (Sleumer) Sleumer, *Gentry 13829A*, *McPherson 7364*), and *Plinia* of the Myrtaceae (*P.* spp.; *McPherson 7341*, *9089*). These four genera are primarily South American in their distributions.

NOTES

TWO NEW RUSHES (*JUNCUS*, JUNCACEAE) FROM CHIAPAS, MEXICO

This note describes a new species and a new variety of *Juncus* from the state of Chiapas in Mexico.

Juncus chiapasensis Balslev, sp. nov. TYPE: Mexico. Chiapas: Lagunas de Montebello near Guatemala border, 30 km (air) E of La Trinitaria, 1,200 m, *Roe, Roe & Mori 966* (holotype, DS-584358; isotypes, F, WIS). Figure 1A, B.

Planta perennis, caespitosa; folia linearia, teretia, septata; inflorescentia anthela, 10–20 × 5–12 cm, 8–17-capitulata; capitula 10–35-flora; tepala 2.5–3 mm longa, castanea; stamina 3, 1.8–2.5 mm longa; capsula 4–4.5 × 1–1.2 mm, obclavata, castanea, tepalis longior.

Perennial, caespitose herbs 60–90 cm tall. Rhizome 3 mm diam. Culms erect, 2–3 mm diam., terete, smooth or finely striate. Basal sheathing bladeless leaves absent or one to each culm, up to 7 cm long. Foliar leaves 1–2 basal and 1–2 cauline to each culm, 10–45 cm long; sheaths 4–8 cm long with membranaceous margins, terminally biauriculate, the auricles 2–3 mm long and rounded; blades 1.5–3 mm diam., round in cross section, conspicuously cross septate. Inflorescence a decompound anthela, 10–20 × 5–12 cm, of 8–17 flower heads, these globose, 10–13 mm diam., 10–35 flowered, castaneous, the ultimate head-bearing branches ca. 0.5 mm thick. Lower inflorescence bract 3–7 cm long, much shorter than the inflorescence, resembling basal and cauline leaves; upper bracts progressively shorter, the floral bracts acuminate, ca. 0.2 mm long, membranaceous. Tepals subequal, 2.5–3 mm long, lanceolate, acute, the outer ones V-shaped in cross section, the inner ones flat. Stamens three, 1.8–2.5 mm long; filaments linear; anthers oblong, 0.6–0.8 mm long, about half as long as the filaments. Capsule 4–4.5 × 1–1.2 mm, conspicuously longer than the tepals, obclavate, trigonous, acute, gradually tapering towards the apex, castaneous, unilocular. Seeds 1 × 0.2 mm, ellipsoid, apiculate, reticulate, yellow-brown, with a thick, hyaline outer seed coat.

This new species is known only from a few localities in the state of Chiapas, Mexico, near the Guatemalan border. It has been collected at elevations of 1,200–2,200 meters in marshes along lake shores. It belongs to *Juncus* subg. *Septati* Buchenau (1875), as evidenced by its terete, hollow, and cross-septate leaf blades. This subgenus, with some 80 species distributed worldwide, is the largest in the genus. In the neotropical region, some 15 species belong to subg. *Septati.* The inflorescence of this new species is also typical of that subgenus: the flowers are congested into heads arranged in an anthela of which the proximal branches overtop the distal branches. *Juncus chiapasensis* differs from the closely related *J. guadeloupensis* Buchenau by having globose flower heads and obclavate, castaneous capsules much longer than the tepals. *Juncus guadeloupensis* has golden brown capsules and is endemic to the Caribbean island of Guadeloupe. *Juncus debilis* A. Gray likewise occurs in Chiapas and has longer capsules than tepals, but it is much smaller than *J. chiapasensis* in all dimensions.

Additional specimens examined. MEXICO. CHIAPAS: La Trinitaria, Lagunas de Montebello, 1,300 m, *Breedlove & Thorne 21247* (DS); San Cristóbal valley, 2,200 m, *Breedlove & Thorne 21285* (DS, mixed with *J. ebracteatus* E. Meyer; MICH).

FIGURE 1. A, B. Juncus chiapasensis (Roe, Roe & Mori 966).—*A. Habit.—B. Flower with protruding capsule. C, D.* Juncus liebmannii *var.* polycephalus (Breedlove 15065).—*C. Habit.—D. Flower with capsule and floral bract.*

Juncus liebmannii Macbride, Field Mus. Nat. Hist., Bot. Ser. 11(1): 9. 1931 (as *J. liebmannii*). Replaced synonym: *Juncus brevifolius* Liebm. (1850), non Hoffsgg. & Link in Rostkov (1801).

This species has one variety in the Andes of Ecuador and Colombia (var. *quitensis* (Buchenau) Balslev, 1979), and two varieties in Mexico and Central America, one of which is described here as new. *Juncus liebmannii* was first collected in Puebla, Mexico by Liebmann in 1841 and described as *J. brevifolius* (Liebmann, 1850). Liebmann was aware that Hoffmannsegg & Link in Rostkov (1801) had used the name *J. brevifolius* before, but since the entity bearing the first application of the name was a synonym of a species of *Luzula*, he felt free to use the name again for a species of *Juncus*. This was accepted by Buchenau (1873, 1886, 1890, 1906), who called the typical variety *J. brevifolius* var. *mexicanus*. Macbride (1931) renamed the species according to current nomenclatural rules.

Juncus liebmannii Macbride var. **polycephalus** Balslev, var. nov. TYPE: Mexico. Chiapas: southern city limits of Tepisca, 1,800 m, *Breedlove 15065* (holotype, DS-609015; isotypes, MICH, NY). Figure 1C, D.

Planta perennis; rhizoma repens, internodiis 1 cm longis. Folia linearia, teretia vel aliquantum compressa, septata; auriculae involutae; inflorescentia anthela 3–8 × 2–4 cm, 10–30-capitulata; capitula 4–6 mm lata, 10–15-flora.

Perennial herbs 60–70 cm tall. Rhizome horizontally creeping, 2–3 mm diam. Culms erect, 1–2 mm diam., terete, finely striate. Cataphylls 1–2 to each culm, up to 12 cm long. Foliar leaves 2–3 to each culm, inserted along the whole culm, 10–25 cm long, the basal and upper foliar leaves with shorter blades than the middle ones; sheaths 5–15 cm long, with a distinct membranaceous margin terminating in two involute auricles; blades 1–1.5 mm diam., round or slightly flattened in cross section, hollow and cross septate. Inflorescence a decompound anthela, 3–8 × 2–4 cm, of 10–30 flower heads, these semiglobose or conical, 4–6 mm diam., 10–15 flowered, castaneous, the ultimate head-bearing branches 0.2–0.3 mm thick. Lower inflorescence bract up to 8 cm long, with a foliar blade, this round in cross section and with transverse septa, or only 3–4 cm long and with the blade reduced to a small acicular appendage; upper bracts much smaller; floral bracts 1–2 mm long, membranaceous. Tepals subequal, 2–2.5 mm long, lanceolate, acute, the outer ones V-shaped in cross section, inner ones flat. Stamens six, 1–1.5 mm long; filaments linear; anthers oblong, ca. 0.3 mm long, about ⅓ as long as the filaments. Capsules 2–2.5 × 1–1.5 mm, obovoid, acuminate to short-beaked, about as long as the tepals, keeled along the sutures, castaneous, unilocular. Seeds 0.4 × 0.2 mm, ellipsoid, apiculate, reticulate, yellow-brown.

This new variety agrees with *J. liebmannii* var. *liebmannii* in all characters except for the inflorescence, which is divided into 10–30 distinct flower heads. In the typical variety the inflorescence is divided in two subequal parts with the flowers arranged diffusely in 2–3-flowered glomerules but not in distinct heads.

I thank Kirsten Tind for the beautiful and illustrative plate and Rupert Barneby for linguistic assistance.

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A NEW SPECIES OF *STRYCHNOS* (LOGANIACEAE) FROM NICARAGUA

While preparing treatments of Loganiaceae for the forthcoming *Flora de Nicaragua* and *Flora Mesoamericana*, I encountered a new species of *Strychnos* from the Caribbean lowlands of Nicaragua. *Strychnos* is a pantropical genus of some 200 species. Of the approximately 90 species of the American tropics, only nine, including the one described here, occur in Mexico or Central America. In the most recent treatments of the American species of *Strychnos* (Krukoff & Barneby, 1969; Krukoff, 1972), *S. nicaraguensis* would be assigned to sect. *Breviflorae* Progel subsect. *Eriospermae* Krukoff & Barneby on the basis of its recurved spines, terminal inflorescences, short styles, and seeds with testa composed of soft fibers. Unfortunately, the corolla of *S. nicaraguensis* remains unknown, so that the length of the corolla tube in relation to the calyx, one of the important sectional characters in *Strychnos* (equaling or shorter than the calyx in sect. *Breviflorae*, much longer in the other sections), cannot be positively ascertained. Nevertheless, other characters, principally the recurved spines and fibrous testa, assure its placement in subsect. *Eriospermae* of sect. *Breviflorae*.

Strychnos nicaraguensis Huft, sp. nov. TYPE: Nicaragua. Zelaya: N of Talolinga in gallery forest, 19 Aug. 1983, *J. C. Sandino 4509* (holotype, F-1988116, F neg. no. 62188; isotype, MO, not seen).

Frutex volubilis; caules non conspicue lenticellis praediti, spinis recurvatis. Folia glabra rhombeo-ovata, apice longiacuminata, basi acuta vel acuminata, costa supra non impressa, nervis lateralibus obscuris. Flores 4–7, cymis terminalibus compactis; sepala 5 discreta deltato-lanceolata ciliata aliter glabra; corolla staminaque non visa. Fructus laevis, ca. 1.5 mm diametro, luteus, pericarpio tenui; semina 1 vel 2, depresso-globosa, testa fibrosa.

Liana; stems not conspicuously lenticellate, with recurved spines to 2 cm long; branchlets wandlike, flexuous, densely puberulous, soon glabrate. *Leaves* with petioles 1–2 mm long, puberulous; blades rhombic-ovate, 3–5(–5.5) cm long, 1.4–2.2 cm wide, (1.7–)2–2.9(–3.2) times as long as wide, glabrous, dull green above, pale below, triplinerved, the midvein scarcely or not at all impressed above, the secondary veins obscure; apex long-acuminate; base acute to acuminate; margin entire. *Flowers* 4–7 in compact, terminal, slender-pedunculate cymes 5–7 cm diam., the peduncles 1–1.5 cm long; bracts lanceolate, 1.5–3 mm long, ciliate; pedicels 1–2 mm long; calyx segments 5, free, slightly unequal, deltate-lanceolate, navicular, long-acuminate, ciliate, otherwise glabrous, 1.2–1.8(–2) mm long; corolla not seen; stamens not seen; style ca. 0.8 mm long. *Fruits* globose, smooth, ca. 1.5 cm diam., the shell ca. 0.5 mm thick, yellow; seeds 1 or 2, depressed globose, ca. 5 mm long, ca. 7 mm diam., the testa fibrous.

Subsection *Eriospermae* is distinguished from subsect. *Breviflorae* Krukoff & Barneby, which comprises the rest of sect. *Breviflorae*, solely by the characteristic soft fibrous testa of the seeds, which breaks away from the dry, shrunken endosperm of old seeds and encloses the endosperm like a sac. *Strychnos nicaraguensis* belongs to a group of species of subsect. *Eriospermae* that are characterized by conspicuously lenticellate branchlets, recurved spines, midveins impressed above, faint or obscure foliar reticulations, distinctly pedicellate flowers, and sparingly ciliate calyx lobes. It is distinguished from all species in this group by the absence of conspicuous lenticels and by its distinctive small rhombic-ovate leaves without an impressed midvein. The only other species of this group in Central America, *S. brachi-*

ANN. MISSOURI BOT. GARD. 75: 383–384. 1988.

stantha Standley, further differs by its much larger fruits (to 9 cm in diameter) with thick shells, as does *S. nigricans* Progel of southeastern Brazil. The species most closely related to *S. nicaraguensis* appears to be *S. mattogrossensis* S. Moore, a species widely distributed in the Amazon basin. Both species have small fruits with thin shells ca. 0.5 mm thick, but *S. mattogrossensis* differs in having ovate, obovate, or elliptic leaves that are not at all rhombic-ovate and larger, more highly branched cymes 7–25 mm in diameter. Other species in this group include *S. cerradoensis* Krukoff & Barneby, native to the state of Minas Gerais, Brazil, which differs from *S. nicaraguensis* by its thick-shelled fruit, and *S. alvimiana* Krukoff & Barneby (Phytologia 27: 105. 1973), of the state of Bahia, Brazil, which has larger leaves that are dull on both surfaces and rounded or obtuse at the base.

Additional specimens examined. NICARAGUA. ZELAYA: Municipio de Siuna, Comarca El Hormiguero, Trocha El Hormiguero, 7 Jan. 1983, *Ortiz 586* (F); Municipio de Siuna, "Calera," 13°46′N, 84°46′W, 300–345 m, 12 Mar. 1984, *Ortiz 1790* (F).

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TWO NEW SPECIES OF *INGA* (LEGUMINOSAE) FROM PANAMA

This paper describes two species of *Inga* from Panama, bringing the total number of *Inga* species known from that country to 29 (D'Arcy, 1987). The two species are unrelated within the genus, apparently belonging to different sections. Both are from areas where endemism is reported in other groups.

Inga jefensis Liesner & D'Arcy, sp nov. TYPE: Panama. Panamá: 1 mi. upstream from Frizzel's Finca Indio, slopes of Cerro Jefe, flower & fruit, 9 Sep., *Foster & Kennedy 1828* (holotype, PMA; isotype, MO). Figure 1.

Arbor parva, differt Ingis aliis panamensibus foliolis glabris concoloribus, rhachibus non alatis, inflorescentia umbellata, pedicellis gracilibus longioribus, fructibus longioribus.

Tree 15 m tall, the branchlets copiously lenticellate, nearly glabrous but with occasional minute trichomes. Leaves with petiole 5–10 cm long, terete, slender, unwinged, drying olive green; rachis ca. 15 cm long, resembling the petiole, the glands ca. 2 mm across; petiolules (*Gentry 8854*) ca. 6 mm long, thick, drying olive green; leaflets 4–5 pairs, elliptic to obovate, acuminate, basally obtuse, 6.3–19 cm long, drying concolorous, olive green (emerging growth drying reddish brown), glabrous, the lateral veins 9–10 on each side; stipules oblong or obovate, ca. 15 mm long, 6 mm wide, drying enervate, membranaceous. Inflorescence umbellate; peduncle ca. 7 cm long, slender; pedicels slender, 7–12 mm long. Flowers ca. 23; calyx tubular, ca. 2 mm long, glabrate, the lobes short, rounded; corolla tubular, 13–14 mm long, lobed $\frac{1}{5}$–$\frac{1}{3}$ its length, the lobes ca. 3 mm long, ca. 3 mm wide at the base; stamens ca. 3 cm long, exserted ca. 1.5 cm, the exserted portion longer than the corolla. Fruit linear, compressed around the seeds, the margins slightly sinuate between the seeds, ca. 30 cm long, 18–25 mm wide, 8 mm thick (dried).

The fruit of this species is similar to but longer than that of *Inga portobellensis* Beurling (sect. *Leptinga* fide León, 1966) from the Caribbean coast north of the localities for the new species. *Inga jefensis* differs in its smaller calyx (2 mm vs. 20–25 mm long) and notably in having an unwinged leaf rachis. This species is also somewhat similar to *Inga paterno* Harms (also in sect. *Leptinga*), which ranges from Costa Rica to Mexico, but *I. paterno* has sessile florets and a short, massive fruit 4–7 mm wide and 2–3 cm thick.

Inga jefensis is known only from Central Panama. The two locations, Cerro Jefe, a mountain ridge behind Panama City with elevations up to 900 m, and Santa Rita Ridge, another mountain ridge paralleling the Caribbean coast, are both areas known to have many endemic species. The collection from Cerro Jefe was taken in flower and fruit in September, and the collection from Santa Rita Ridge was taken in December in flower.

Paratypes. PANAMA. COLÓN: Santa Rita Ridge road 4 mi. from Transisthmian Highway to Agua Clara weather station, 500 m, flower, 11 Dec., *Gentry et al. 8854* (MO).

Inga spiralis Liesner & D'Arcy. TYPE: Panama. Panamá: 23.4 km from Panamerican Highway, fruiting, 13 Apr., *Mori & Kallunki 5577* (holotype, PMA; isotype, MO). Figure 2.

Arbor parva, differt Ingis aliis panamensibus foliis grandibus, foliolis grandibus discoloribus rigidis, rhachibus non alatis, calyce lato, fructu solido spiraliter 1½-plo superposito puberulenti.

Tree 15 m tall (*Dressler 4325*), the branchlets drying reddish with scattered minute simple hairs, prominently lenticellulate when young, glabrescent, becoming grayish.

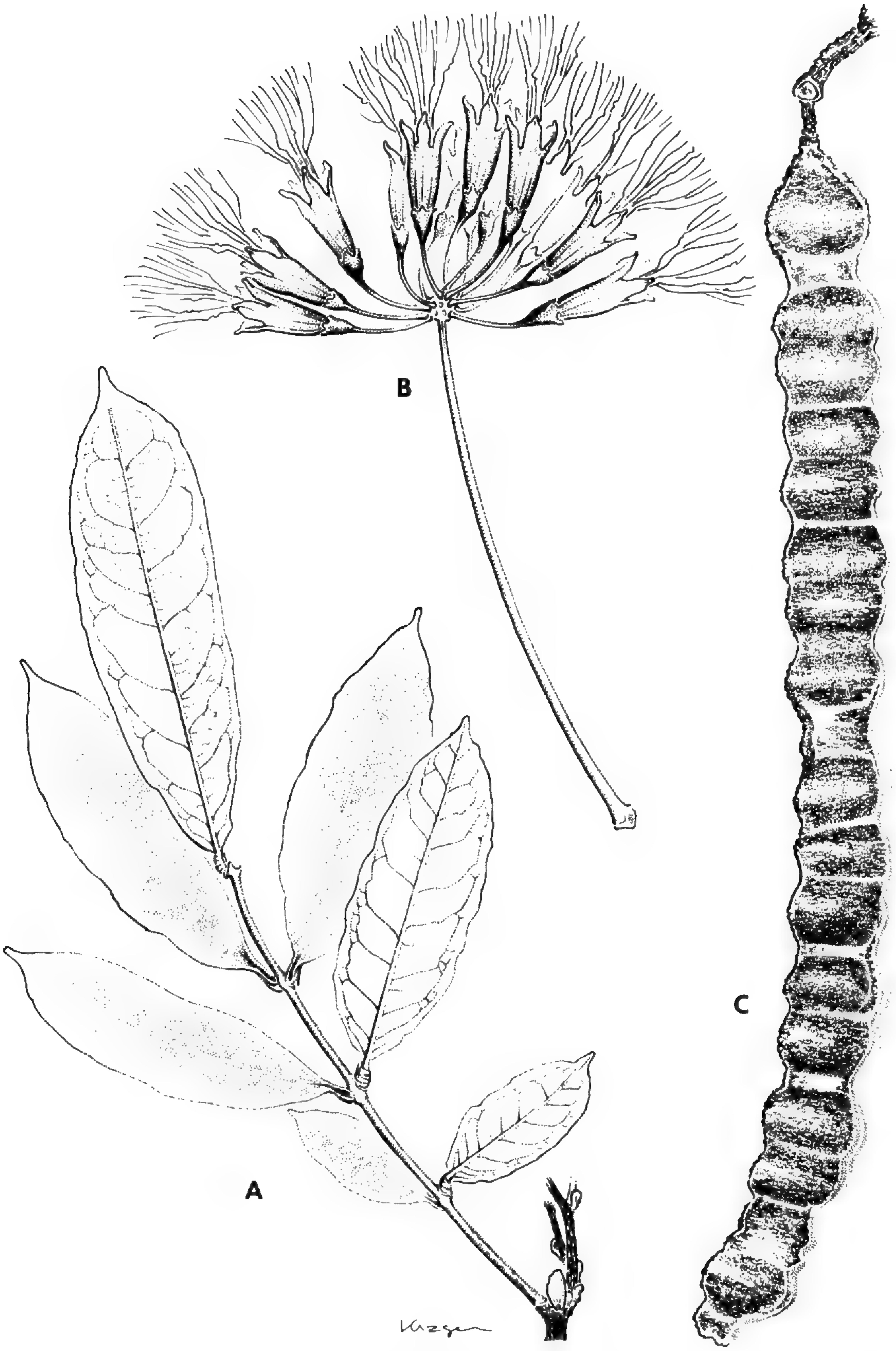

FIGURE 1. Inga jefensis (Foster & Kennedy 1828 *(MO)).—A. Leaf and twig with stipule (×0.5).—B. Inflorescence (×1).—C. Fruit (×0.5).*

Leaves with the petiole 10–21 cm long, subterete, slightly angled basally, unwinged, drying reddish, with sparse minute simple hairs; rachis 15–30 cm long, nonwinged, resembling the petiole, the glands subcupulate, ca. 3 mm across; petiolules ca. 4 mm long, stout; leaflets elliptic to obovate, apically rounded and short apiculate, basally obtuse, 20–30 cm long, 16 cm broad, drying discolorous, slate-colored above, reddish be-

FIGURE 2. Inga spiralis.—*A. Flower (× ⅓).—B. Fruit and pedicel borne on branch (× 0.5).—C. Leaf (× ⅓).—D. Stipule and old inflorescence (× 0.5). (A, C, from* Dressler 4325 *(MO); B, from* Mori & Kallunki 5577 *(MO); D, from* Liesner 1314 *(MO).)*

neath, glabrous above, softly puberulent beneath with short hairs; lateral veins 16–18 on each side; stipules conspicuous, subfoliaceous, subcircular, ca. 5 cm long, drying prominently nerved, persistent. Inflorescence (*Dressler 4325*) umbellate, the peduncle 7 cm long, straight, ca. 4 mm thick, borne "on branches ca. 3 cm diam.," pedicels 3–4 mm long, broadening upwards. Flowers 40–50; calyx 1 cm long, lobed ⅓–½ way down, the lobes oblong, 5–6 mm long, 4–5 mm wide at the base; corolla 2 cm long, deeply lobed, the lobes ca. 10 mm long, 4 mm wide, apically acute; filaments 3–4 cm long, exserted 2–3 cm. Fruit flattened, circinnate, coiled 1½ times, 3–4 cm across, conspicuously rugose nervate, forming a massive spiral 7–9 cm diam., softly puberulent with dense, short, whitish hairs.

This species is distinct in its massive, tightly coiled fruit. It is known only from the El Llano–Carti road in Panamá Province, not far south of Nusigandi. The fruit somewhat resembles that of *Inga davidsoniae* Standl. (sect. *Inga* ser. *Densiflorae* according to León, 1966) of Chiriquí Province, which is also short and thick, but that fruit is not coiled, and the leaflets of *Inga davidsoniae* are small in contrast to the unusually large leaves of the new species. Specimens in flower were collected in March and April and fruiting specimens in April.

Paratypes. PANAMA. PANAMÁ: El Llano–Carti highway ca. 20 km N of El Llano, 300–350 m, flowering, 6 Apr. *Dressler 4325* (MO). SAN BLAS: El Llano–Carti road, continental divide to 1 km N of divide, flowering, 30 Mar., *Liesner 1314* (MO).

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NOTES ON THE FIJIAN ENDEMIC *MERYTA TENUIFOLIA* (ARALIACEAE)

Meryta J. R. & G. Forst. comprises about 30 species of dioecious, simple-leaved araliaceous trees and shrubs, nearly all of which are endemic to one or a few Pacific islands. The genus is centered in New Caledonia, where 11 species occur (Lowry, unpubl. data), and four species are recognized in Samoa and Tonga (Cox, 1985), one of which also appears to have been collected recently on Alofi (Morat & Veillon, 1985). *Meryta* reaches its western limit in Micronesia on Yap and has one species each in Vanuatu (formerly New Hebrides), Norfolk Island, New Zealand, and Rarotonga (Cook Islands). In Polynesia, perhaps three to five species occur on Tahiti, where they form a polymorphic and taxonomically difficult complex; two species have been described from Raiatea, and one species, *M. brachypoda* Harms, occurs on Raiavavae and on Tubuai. One endemic species of *Meryta* is found on Rapa to the south, and an undescribed species has been collected in the Marquesas.

Until recently, *Meryta* was thought to be lacking from Fiji (Smith & Stone, 1968). In December 1968, however, a single pistillate collection with mature fruit was made in the mountainous interior of Viti Levu and was described as *M. tenuifolia* by Smith (1971). This material is somewhat fragmentary and the descriptive notes that accompany it are sketchy. Nevertheless, it is clear that *M. tenuifolia* is very distinctive within the genus and is remarkable in being a large, highly branched canopy tree to nearly 25 m tall.

During a visit to Fiji in November 1985, I was able to re-collect *Meryta tenuifolia* near the village of Vanualevu, at the edge of the Rairaimatuku Plateau. A small population comprising several individuals of this tree, known locally as "lutulutu," was found on a gentle slope in dense, undisturbed forest at 980 m elevation, less than one km to the east of Vanualevu, perhaps two km to the north-northeast of the type locality. We located staminate plants in bud and flower as well as pistillate individuals with flowers and nearly mature fruits. Pressed specimens supplemented with FAA-preserved material and color photographs permit the following amended description.

Meryta tenuifolia A. C. Smith, Pacific Sci. 25: 499. 1971, *emend.* Lowry. TYPE: Fiji. Viti Levu: Nandronga & Navosa (now Navosa) Prov., rocky bank of Nggalivava Creek, a northward flowing stream joining Lumunda Creek (Singatoka River tributary), ca. 1.5 km S of Vanualevu, 750–800 m, 4 Dec. 1968 (fr), *M. J. Berry* (coll. *E. Damanu*) *97* (holotype, BISH; isotype, K). Figure 1.

Dioecious, branched, glabrous trees to ca. 25 m tall; trunk to ca. 70 cm dbh, fluted to ca. 1 m; stems robust, covered with numerous leaf scars. Leaves simple, alternate, clustered at the ends of branches; blades medium green above, lighter below, chartaceous, broadly elliptic, (9–)11–22 × (5–)7–12(–13) cm, the venation light yellow green, the midvein raised but without prominent bulges below, the secondary veins 8–11, diverging from the midvein at 50–60° angles, arcuate at the ends, the higher-order veins evidently raised above and below, forming a dense network, the apex rounded to obtuse or broadly acute, the margin entire, minutely thickened and revolute, the base obtuse to rounded and often shortly decurrent; petiole slender, 1.5–2 mm diam., with an expanded, clasping, brownish base with scarious margins. Inflorescence a panicle of racemules (or sometimes umbellules), terminal, erect, light green, occasionally tinged

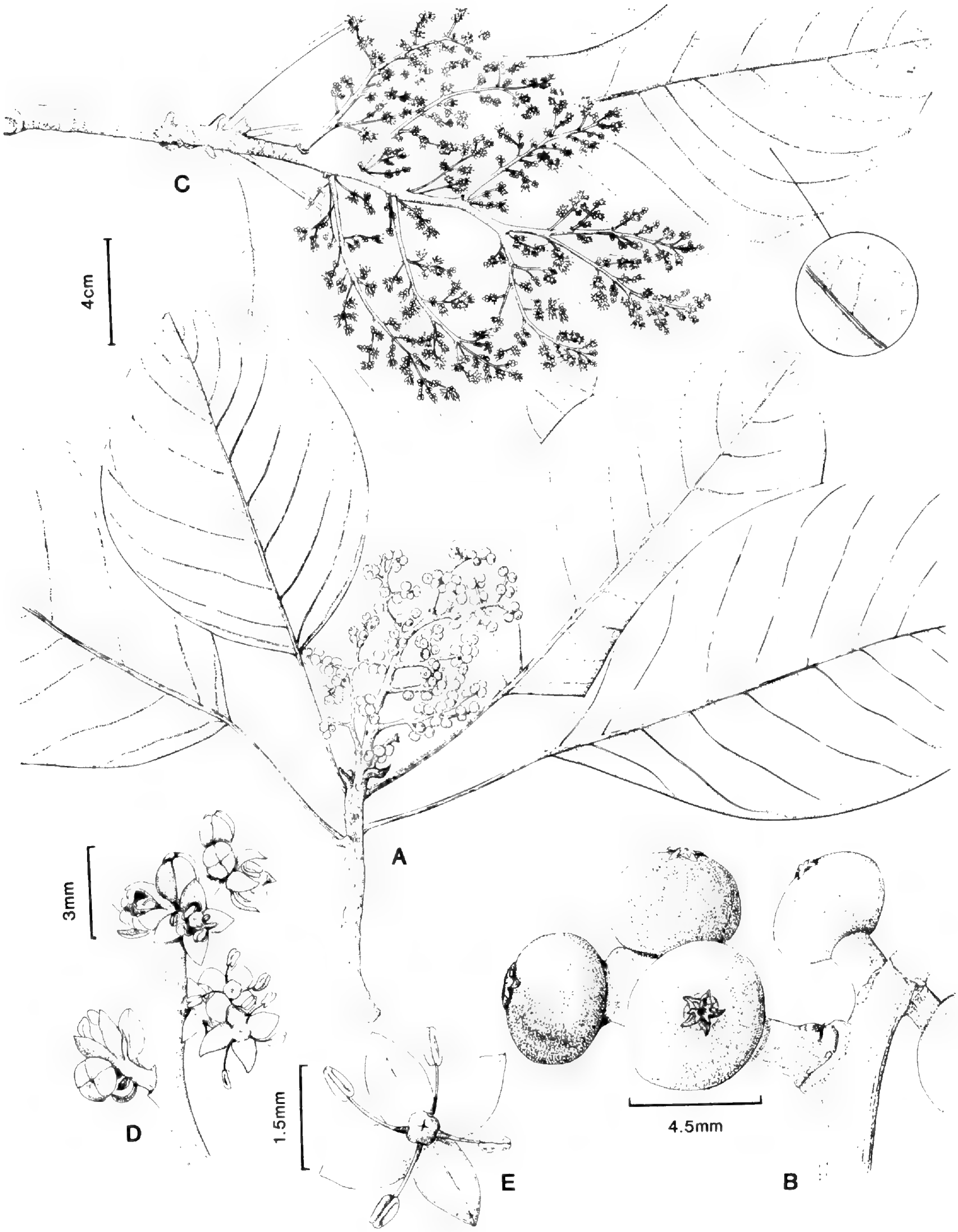

FIGURE 1. Meryta tenuifolia.—*A. Branch of pistillate plant with infructescence.—B. Nearly mature fruit.—C. Branch of staminate plant with inflorescence.—D. Tertiary axis with staminate flowers.—E. Staminate flower at anthesis (top view).*

orangish; primary axis slender, in staminate plants to 20 cm long, in pistillate plants to 10 cm long; the secondary axes 6–8, scattered, ascending, on staminate plants 6–9 cm long, on pistillate plants 3–4 cm long, each subtended by an early-caducous, ovate, cupulate, scarious, strongly adaxially concave cataphyll 12–15 mm long; tertiary axes subtended by small, scarious, caducous bractlets, the axes on staminate plants 6–12, ascending, 12–25 mm long, each with 3–6 racemules (sometimes reduced to umbellules) of (3–)4–6 sessile flowers, the axes on pistillate plants 4–6, ascending to spreading, 4–12 mm long, each with 4–6(–7) racemosely arranged sessile flowers. Staminate flowers ovate in bud; sepals wanting; petals 4, ovate, spreading at anthesis, ca. 1.5 mm long; stamens 4, inflexed in bud, ascending at anthesis, cream white, the filaments slender, 1.5–2 mm long, the anthers with 4 thecae, dorsifixed; the rounded nectar disk yellowish, weakly 4-sided. Pistillate flowers ovate-pyriform in bud; sepals wanting; petals 4 or 5, narrowly deltoid, subacute, recurved after anthesis, ca. 0.5 mm long, expanding to 0.6–0.9 × 0.9–1.3 mm in fruit; stamens vestigial, 0.5–0.8 mm long, caducous, the anthers sterile; ovary inferior, (5–)6–10-carpellate, ca. 1.5–2 mm high at anthesis, the flattened nectar disk 1–1.5 mm diam., expanding to ca. 2 mm in fruit; styles (5–)6–10, united basally, the free arms erect to ascending at anthesis, 0.3–0.6 mm long, in fruit expanding to 0.5–1 mm long, becoming divergent. Fruit a drupe, olive green when nearly mature, subglobose-oblate, 2–3.5(–4.5) × (3.5–)4–5.5 mm, smooth and plump when fresh, turning strongly and acutely (5–)6–10-costate when dry.

Additional specimens examined. FIJI. VITI LEVU: Navosa Prov., edge of Rairaimatuku Plateau, E and above Vanualevu village, dense forest on slight slope, 980 m, 18 Nov. 1985 (staminate bud, fl), *P. P. Lowry 3838* (BISH, MO (3 sheets), P, US); (pistillate fl, fr), *3839* (BISH, MO (3 sheets), P, US).

As Smith (1985) indicated, *Meryta tenuifolia* does not appear to be closely related to the very distinctive species occurring in Vanuatu and Samoa. Furthermore, it does not show strong affinities with species of *Meryta* on Rarotonga, Norfolk Island, and New Zealand. However, until my upcoming detailed revision of the genus has been completed, it will not be possible to determine whether *M. tenuifolia* is closest to Polynesian species such as *M. choristantha* Harms of Rapa, as suggested by Smith (1985), or to New Caledonian species such as *M. balansae* Baill.

I am grateful to A. C. Smith for providing locality information and a map of the original collection, and for valuable suggestions on the manuscript. Thanks are also due to J. M. Miller and S. Vodonaivalu for assistance in the field, to C. A. Todzia and B. C. Stone for additional comments, and to J. K. Myers for preparing the illustration. This work was supported in part by NSF Doctoral Dissertation Improvement Grant BSR83-14691, the Missouri Botanical Garden, the W. Alton Jones Foundation, and the Division of Biology and Biomedical Sciences of Washington University, St. Louis, Missouri.

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PASSIFLORA PUSILLA (PASSIFLORACEAE), A NEW SPECIES FROM CENTRAL AMERICA

During the course of an ongoing study of Central American Passifloraceae, the following distinctive new species has been found in collections generated by the *Flora de Nicaragua* project and from older Costa Rican collections.

Passiflora pusilla MacDougal, sp. nov. TYPE: Nicaragua. Chontales: Hacienda Corpus, W of Juigalpa, ca. 100 m, 12°07′N, 85°28′W, 14 June 1984, *Stevens 22968* (holotype, MO; isotype, HMNH). Figure 1.

Passiflora hirsuta nana, scandens vel decumbens; caulis 12–55 cm longus, triqueter vel subtriqueter; petioli eglandulosi; folia trilobata, basi cordati, lobis obtusis vel truncatis, marginibus integris; pedunculi singulares uniflori; bracteae nulli; coronae filamenta biseriata, filamentis interioribus submicroscopicis, 0.2–1.5 mm longis; operculum plicatum; ovarium dense puberulum; fructus 3.5–4 cm longus, 0.5–0.7 cm latus, anguste fusiformis, sexangularis; semina dentibus seriebus 2 longitudinalis dispositus.

Diminutive, weakly climbing or often decumbent herb, 12–55 cm long, often fertile within 10–15 cm of its base. Roots perennial, the primary root 2.5–4 mm diam.; 1–5 annual stems arising from axillary buds at base of stem. Plant hirsutellous throughout with cylindrical, straight or slightly antrorsely bent, unicellular but often many-septate pelucid trichomes (0.1–)0.4–1.4(–1.8) mm long, these generally intermixed with microscopic, appressed trichomes 0.06–0.08(–0.1) mm long. Stem triangular or subtriangular (drying sulcate), 3-carinate, nearly glabrous below, becoming puberulent above with microscopic, appressed trichomes, and conspicuously hirsute on the carinae with trichomes (0.1–)0.4–0.6(–0.8) mm long. Stipules (2.5–)3–4(–5) × 0.4–0.5 mm, narrowly lanceolate to linear-triangular, subfalcate, hirsute, greenish, the apices not necrescent. Petioles 1–2.5(–3.6) cm, eglandular, canaliculate, sometimes tinged purplish. Laminae 1–2.4 × 2–4.5 cm at fertile nodes, depressed obovate in general outline, cordate at base, very shallowly 3-lobed (and in one collection, very rarely the lateral lobes shallowly and obscurely lobed at base), the lateral lobes obtuse, ± rounded, the central lobe broadly obtuse or nearly truncate, the angle between lateral lobes (80–)85–100(–108)°, ratio of lateral to central lobe lengths 1.1–1.4, ratio of laminar width to length 1.6–2.2, the margins entire and minutely setose to strigose; laminar nectaries absent. Tendrils absent, or present at distal nodes and then capillary and nonlignified; posture of developing tendrils and shoot apex unknown. Prophyll of vegetative ramifying bud 1, narrowly ovate, caudate. Peduncles solitary at nodes, 4.5–15(–21) mm, uniflorous, ebracteate. Flower ca. 1 cm diam., with 1–1.7 mm stipe (elongating to 1.7–3 mm in fruit), the hypanthium 3.5–4 mm diam., hirsute, the longer trichomes often borne 0.1–0.2 mm above the surface of the epidermis on cylindrical, slightly raised bases; sepals 7 × 1.8–2.2 mm, lanceolate, pale yellowish green; petals 2.7–3.5 × 1–1.3 mm, narrowly ovate or oblong, pale yellowish green; filamentous corona in 2 series, the outer 5–6 mm long, yellow toward apex, yellowish green to greenish below and sometimes with 1–3 narrow purplish bands at base or in lower half; inner series rudimentary, the members few, borne at base of operculum, 0.2–1.5 mm, capillary, slightly clavate; operculum 0.7–1 mm, membranous, the margin erose, plicate; nectary with annulus or nectar ring adjacent to limen; limen (disk) cupuliform, closely surrounding base of androgynophore, its edge ± erect and 0.7–0.8 mm high; staminal filaments connate

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4.2–6 mm along androgynophore, the free portions ca. 2 mm long; anthers 1.8–2.1 mm long, ovary 1.4–1.8 × 0.7–1 mm, narrowly obovoid or ellipsoid, 6-ridged or hexagonal in cross section, densely puberulent with appressed trichomes 0.05–0.1 mm long; styles ca. 3 mm?; stigmas capitellate. Fruit 3.5–4 × 0.5–0.7 cm, narrowly fusiform or fusiform, the stipe often indistinct, distally caudate, hexagonal and 6-carinate, sparsely and minutely puberulent, dehiscent; arils whitish, scanty, shorter than seed; seeds 3.1–3.4 × 1.7–1.8 mm, obovate, obliquely beaked at chalazal end, the short beak sharply angled toward the raphe, with 2 longitudinal rows of teeth (or 5–6 transversely sulcate, the ridges traversed by a broad longitudinal furrow).

Phenology. This is a species of strongly seasonally dry habitats, and it apparently dies back to the ground each dry season. The small size of the plant suggests that it may flower and set seed within only a few months of germination; nevertheless, nearly all of the specimens studied were collected with roots intact and show remnants of dead shoots from previous seasons. The short herbaceous shoots may be expected to emerge after the spring rains in April. Flowering from May through the summer and into the end of the rainy season, *Passiflora pusilla* has been found in fruit from late June to November.

Habitat and distribution. In the low tropical dry and gallery forests in the general vicinity of Lake Nicaragua, this passionflower is associated with the distinctive soil type called "sonsocuite" in Nahuatl. This sticky black soil is alkaline, poorly drained, and is seasonally inundated. It supports a forest of low stature, with *Crescentia*, *Cordia*, and mimosoids like *Acacia*, but has been mostly converted to pasture or intensive cultivation of cotton, rice, or sesame. This small passionflower has been found mainly below 300 m elevation in partial shade at the edges of the "sonsocuite," on banks at the edges of roads and pastures, or in the shade of associated gallery forest. There are two records from a disturbed area at 800 m on the Meseta Central of Costa Rica.

The specific epithet refers to the very small size of this plant.

Paratypes. COSTA RICA. GUANACASTE: Santa Rosa National Park, 30 km W of Liberia, 0–320 m, 10°50′N, 85°35′W, 18 Aug. 1984 (fr), *Janzen 12412* (MO); 5 km NE of Bagaces, 95 m, 22 July 1964 (fl, fr), *Jiménez M. 2136* (F); W of airport, 10 km W of Liberia, 0–100 m, 10°30′N, 85°34′W, 25 June 1977 (fl), *Liesner & Rockwood 2516* (MO); 23 km SW of Liberia, 10°24′N, 85°34′W, 1–200 m, 23 July 1964 (fl, fr), *Tessene 1424* (WIS). SAN JOSÉ: Santa Ana [9°56′N, 84°11′W], 800 m, 25 Nov. 1963 (fl, fr), *Jiménez M. 1319* (F); Brasil de Santa Ana [9°56′N, 84°13′W], 800 m, 2 June 1957 (fl), *Rodríguez C. 464* (UC). NICARAGUA. CHONTALES: Hacienda Corpus, W of Juigalpa, ca. 100 m, 12°07′N, 85°28′W, 20 May 1984 (fl), *Stevens 22898* (MO, HMNH).

Passiflora pusilla is referred to subg. *Plectostemma* Masters sect. *Xerogona* (Rafinesque) Killip on account of the small flower with a plicate operculum, subtriangular carinate stem, absence of either floral bracts or extrafloral nectaries, dehiscent fusiform fruit, and testal architecture of a chalazal beak sharply angled towards the raphe with a fundamentally transversely grooved sclerotesta. The dehiscent, hexagonal, fusiform fruit of *P. pusilla*, characteristic of sect. *Xerogona*, is known in its fully mature state only from *Jiménez M. 2136*.

Passiflora pusilla is perhaps most similar vegetatively to *P. tenella* Killip. *Passiflora tenella* is endemic to the Pacific tropical deciduous forests of Ecuador and Peru (Holm-Nielsen et al., in press). The two species share a very reduced size, similar eglandular leaves, and solitary peduncles. The laminae of *P. tenella* differ, however, in being less pubescent (especially abaxially), with the apices of the lateral lobes acute and the angle between them broader. The ovary of *P. tenella* is nearly glabrous. Its fruit, although also fusiform, is shorter and relatively broader, lacking the caudate apex seen in *P. pusilla*; whether it dehisces is unknown. The seed of the South American species differs greatly by being transversely sulcate with five rugulose ridges. Killip (1938) placed *P. tenella* in sect.

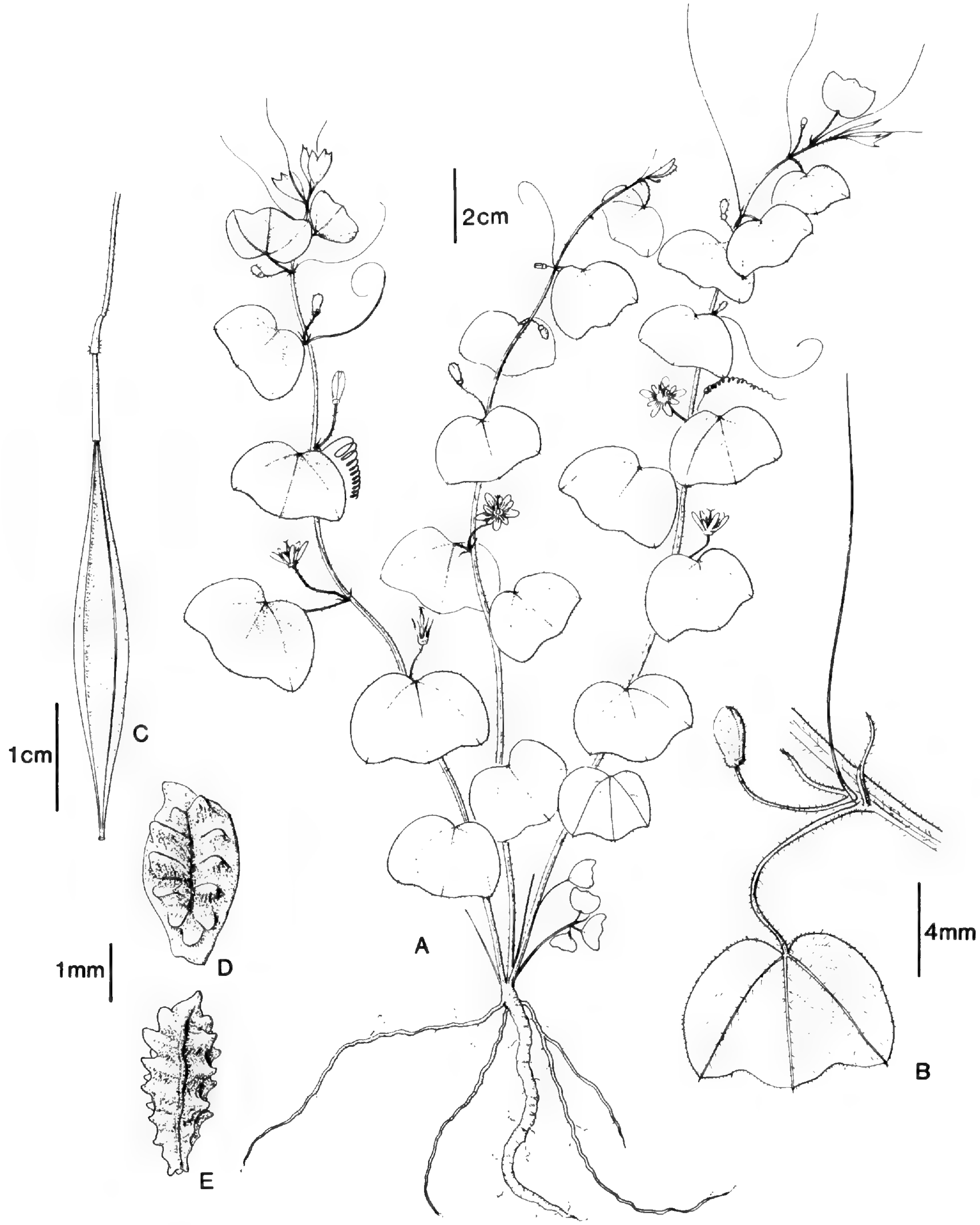

FIGURE 1. —Passiflora pusilla.—*A. Habit.—B. Detail of leaf, node, stipules, and peduncle.—C. Nearly mature fruit.—D, E. Seed.*

Decaloba (DC.) Mast., rather than in sect. *Xerogona*, based on the rugulose testal ridges and the presence of floral bracts. A close kinship between *P. pusilla* and *P. tenella*, phytogeographically plausible due to the close relationship of their respective habitats and vegetation types (Gentry, 1982), cannot be confirmed without further study of the poorly understood South American species.

Passiflora pusilla is also similar to both

P. conzattiana Killip and *P. goniosperma* Killip of Mexico. *Passiflora conzattiana* is a small, low-growing, often prostrate vine of wet montane or *Liquidambar* cloud forests in eastern Mexico. It has similar leaves, small flowers, and very similar fruits, but is a larger plant having apically truncate to lunately bilobed laminae with acute to acuminate lateral lobes, generally less pubescence, and seeds with five or six smooth transverse ridges. *Passiflora goniosperma* is likewise very similar and is from a more similar seasonally dry habitat in southern Mexico. This poorly known species is also a larger plant, having more deeply bilobed leaves, larger fruits, and unusually sculptured seeds that have a single toothed ridge down the length of the face of the testa. Both the more glabrous race of the Pacific tropical deciduous forests and the densely pubescent typical race from central Oaxaca share this form of seed (MacDougal, unpubl.). In contrast, the seed of *P. pusilla* has a furrow in the comparable position with two rows of teeth on either side. Both Mexican species possess only a single series of coronal filaments that are conspicuously and nearly uniformly reddish purple below their yellowish tips.

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NOTES ON *RHODOGNAPHALOPSIS* AND *BOMBACOPSIS* (BOMBACACEAE) IN THE GUAYANAS

The genus *Rhodognaphalopsis* was established by A. Robyns in his revision of *Bombax* in the broad sense (1963). In his generic key, he separated *Rhodognaphalopsis* and *Rhodognaphalon* from *Bombacopsis*, *Eriotheca*, and *Pachira* using only pollen characters: "Pollina colpata vel colporata; sexinium reticulatum ad interdum fragmentimuratum" for characterizing the last three genera and "Pollina porata vel cop(or)ata [*sic*]; sexinium structura uniformi, tegellatum ad punctatitegillatum tegilloque processibus spinulatis vel baculatis praedito" for the first two. By comparing Robyns's generic descriptions, one can also find that *Rhodognaphalopsis* is often lepidote on several organs while *Bombacopsis* is not; apparently it was overlooked that at least *Bombacopsis quinata* (Jacq.) Dugand (= *Pochota quinata* (Jacq.) W. D. Stevens) has prominently lepidote flowers.

The palynological differences between *Rhodognaphalopsis* and *Bombacopsis* are not impressive (e.g., see fig. 25 in Robyns, 1967), but perhaps more importantly, *Bombacopsis* is palynologically diverse (see Nilsson & Robyns, 1986), enough so as to accommodate *Rhodognaphalopsis* easily. Since this questionable palynological difference is not correlated with any gross morphological characters, it appears more appropriate to merge the two genera. It should be noted, however, that while *Rhodognaphalopsis* is relatively homogeneous, *Bombacopsis* is not. It could well be that some species of *Bombacopsis*, as circumscribed by Robyns, will eventually be found to be better placed in *Pachira*. *Rhodognaphalopsis* most resembles the type element of *Bombacopsis* and there is little danger of *Rhodognaphalopsis* falling into the synonymy of *Pachira*. It can also be noted that Hutchinson (1967) judged the palynological difference to be of little importance and considered *Rhodognaphalopsis*, as well as the African genus *Rhodognaphalon*, to be indistinguishable from *Bombacopsis*.

Pittier erected the genus *Bombacopsis* for two Central American species that he considered intermediate between *Pachira* and *Bombax*. These, *Bombacopsis sessilis* (Benth.) Pittier and *B. fendleri* (Seem.) Pittier (= *Bombacopsis quinata* (Jacq.) Dugand), have the seeds embedded in wool, characteristic of the genus *Bombax*, as contrasted with *Pachira*, in which the seeds are embedded in the fleshy dissepiments of the capsule. They further share with *Bombax* the manner in which staminal fascicles divide at once into single filaments. Pittier distinguished *Bombacopsis* from *Bombax* by the fewer stamens and more slender flowers of the former. Later, Robyns (1963) also recognized the genus *Bombacopsis*. He distinguished it from *Bombax* by its persistent or even accrescent calyx, while from *Pachira* it was separated by having abundant, wooly, elongated investiture of the seed; by possession of smaller flowers; by differences in the pollen and cotyledons; and usually by smaller and more numerous seeds. Many of the species were transferred from *Bombax*, while some others had previously been recognized in *Pachira*.

Recently, it has been reiterated that *Pochota* Ramirez Goyena has nomenclatural priority over *Bombacopsis* (Stevens, 1987). Since then, *Bombacopsis* has been proposed for conservation (Nicolson & Robyns, 1987).

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Given that we cannot accept *Rhodognaphalopsis* and *Bombacopsis* as distinct genera and that several of these species will be treated in the upcoming *Flora of the Venezuelan Guayana*, we are left with the dilemma of how to treat them. One could make the new combinations of *Bombacopsis* in anticipation of conservation, but it must be taken into consideration that the two previous proposals to conserve *Bombacopsis* against *Pochota* have been rejected and that there is no assurance that the current proposal will be successful, a process which in any case will require years to complete. If, on the other hand, the more strictly correct approach of making the combinations in *Pochota* is followed, the distinct possibility of the names being overturned will remain. Although the latter choice will require the larger number of transfers, to account for *Bombacopsis* as well as for *Rhodognaphalopsis*, we have reluctantly concluded that it is preferable. Accordingly, the following new combinations are proposed:

Pochota amazonica (Robyns) Steyerm. & W. D. Stevens, comb. nov. *Bombacopsis amazonica* Robyns, Bull. Jard. Bot. État 33: 186. 1963.

Pochota coriacea (Martius & Zucc.) Steyerm. & W. D. Stevens, comb. nov. *Bombax coriaceum* Martius & Zucc. in Martius, Nov. Gen. Sp. Pl. 1: 93. 1826. *Rhodognaphalopsis coriacea* (Martius & Zucc.) Robyns, Bull. Jard. Bot. État 33: 289. 1963.

Pochota coriacea subsp. **orinocensis** (Robyns) Steyerm. & W. D. Stevens, comb. nov. *Rhodognaphalopsis coriacea* subsp. *orinocensis* Robyns, Mem. New York Bot. Gard. 17: 197. 1967.

Pochota cowanii (Robyns) Steyerm. & W. D. Stevens, comb. nov. *Bombacopsis cowanii* Robyns, Mem. New York Bot. Gard. 17: 190. 1967.

Pochota flaviflora (Pulle) Steyerm. & W. D. Stevens, comb. nov. *Bombax flaviflorum* Pulle, Recueil Trav. Bot. Néerl. 9: 150. 1912. *Rhodognaphalopsis flaviflora* (Pulle) Robyns, Bull. Jard. Bot. État 33: 285. 1963.

Pochota gracilis (Robyns) Steyerm. & W. D. Stevens, comb. nov. *Rhodognaphalopsis gracilis* Robyns, Mem. New York Bot. Gard. 17: 199. 1967.

Pochota humilis (Spruce ex Decne.) Steyerm. & W. D. Stevens, comb. nov. *Pachira humilis* Spruce ex Decne., Fl. Serres Jard. Eur. 23: 52. 1880. *Rhodognaphalopsis humilis* (Spruce ex Decne.) Robyns, Bull. Jard. Bot. État 33: 294. 1963.

Pochota maguirei (Robyns) Steyerm. & W. D. Stevens, comb. nov. *Rhodognaphalopsis maguirei* Robyns, Mem. New York Bot. Gard. 17: 200. 1967.

Pochota minor (Sims) Steyerm. & W. D. Stevens, comb. nov. *Carolinea minor* Sims, Bot. Mag. 34: pl. 1412. 1811. *Pachira minor* (Sims) Hemsley, Biol. Cent.-Amer., Bot. 1: 124. 1879. *Bombax minus* (Sims) Ducke, Arch. Jard. Bot. Rio de Janeiro 6: 65. 1933. *Rhodognaphalopsis minor* (Sims) Robyns, Bull. Jard. Bot. État 33: 278. 1963.

Bombax jenmani[i] Oliver, Hooker's Icon. Pl. 18: pl. 1720. 1887. *Pachira jenmani* (Oliver) A. Terracc., Contr. Biol. Veg. 2: 167. 1898. *Bombacopsis jenmani* (Oliver) Lasser in H. Pittier et al., Catalogo de la Flora Venezolana 2: 133. 1947.
Pachira cardonae Cuatrec., Trop. Woods 101: 15. 1955.

Pochota nitida (Kunth) Steyerm. & W. D. Stevens, comb. nov. *Pachira nitida* Kunth, Nov. Gen. Sp. 5: 302. 1821. *Rhodognaphalopsis nitida* (Kunth) Robyns, Bull. Jard. Bot. État 33: 282. 1963.

Bombax poissonianum Schumann in Martius, Fl. Bras. 12(3): 225. 1886.
Pachira obtusa Spruce ex Schumann in Martius, Fl. Bras. 12(3): 232. 1886. *Bombax obtusum* (Spruce ex Schumann) Bakh., Bull. Jard. Bot. Buitenzorg, sér. 3, 6: 171. 1924.

Pochota obovata (Robyns) Steyerm. & W. D. Stevens, comb. nov. *Bombacopsis* *obovata* Robyns, Mem. New York Bot. Gard. 17: 192. 1967.

Pochota orinocensis (Robyns) Steyerm. & W. D. Stevens, comb. nov. *Bombacopsis orinocensis* Robyns, Mem. New York Bot. Gard. 17: 193. 1967.

Pochota pseudamazonica (Robyns) Steyerm. & W. D. Stevens, comb. nov. *Bombacopsis pseudamazonica* Robyns, Mem. New York Bot. Gard. 17: 193. 1967.

Pochota pseudofaroensis (Robyns) Steyerm. & W. D. Stevens, comb. nov. *Rhodognaphalopsis pseudofaroensis* Robyns, Mem. New York Bot. Gard. 17: 201. 1967.

Pochota sordida (R. Schultes) Steyerm. & W. D. Stevens, comb. nov. *Bombax sordidum* R. Schultes, Bot. Mus. Leafl. 16: 75. 1953. *Rhodognaphalopsis coriacea* var. *sordida* (R. Schultes) Robyns, Bull. Jard. Bot. État 33: 292. 1963.

Rhodognaphalopsis discolor Robyns, Mem. New York Bot. Gard. 17: 198. 1967.

Pochota trinitensis (Urban) Steyerm. & W. D. Stevens, comb. nov. *Pachira trinitensis* Urban, Notizbl. Bot. Gart. Berlin-Dahlem 8: 28. 1921. *Bombacopsis trinitensis* (Urban) Robyns, Bull. Jard. Bot. État 33: 191. 1963.

Bombacopsis mucronulata Pittier, Arb. Arbust. Venez. 2/3: 34. 1923.

Bombacopsis pachiroides Pittier, Arb. Arbust. Venez. 2/3: 35. 1923.

Pochota wurdackii (Robyns) Steyerm. & W. D. Stevens, comb. nov. *Bombacopsis wurdackii* Robyns, Mem. New York Bot. Gard. 17: 194. 1967.

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—*Julian A. Steyermark and Warren Douglas Stevens, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.*

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POLLEN MORPHOLOGY OF *PILLANSIA* L. BOLUS (IRIDACEAE)[1]

Peter Goldblatt[2] *and Bruce A. Stein*[3]

ABSTRACT

The monotypic southwestern Cape genus Pillansia *is a taxonomically isolated member of Iridaceae subfamily Ixioideae. It shares some synapomorphies with Ixioideae, although it differs in its unspecialized leaf anatomy and inflorescence structure, a panicle rather than a spike. The pollen is typical of Ixioideae in having a micropunctate exine with minute supratectal papillae. Exine of most other genera and subfamilies of Iridaceae is reticulate. Membership of* Pillansia *in Ixioideae is thus supported by pollen morphology. Micropunctate exine must be regarded as the basic condition for the subfamily and an additional feature separating Ixioideae from other Iridaceae.*

Pillansia L. Bolus is a monotypic genus of Iridaceae–Ixioideae, the largest of the four subfamilies currently recognized. It is a relatively rare, narrow endemic of the southwestern Cape, South Africa (Goldblatt, 1977) and is restricted to rocky sandstone sites in the Caledon district. It has a basic chromosome number of $x = 20$ and thus appears to be paleopolyploid. Most other genera of Ixioideae have base numbers in the $x = 11–9$ range or are neopolyploid with $n = 16–13$. Although *Pillansia* diverges in some important respects from other members of the subfamily, it is widely accepted as belonging to Ixioideae. Nevertheless, it is taxonomically isolated and appears to have no identifiable close relatives. It accords with Ixioideae in several specialized features (synapomorphies) (Goldblatt, in prep.) that characterize the subfamily. These include a long-lasting perianth; sessile flowers subtended by a pair of opposed bracts; a well-developed, though short, perianth tube; and a basal rooting corm.

The pollen morphology of *Pillansia* has

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[1] *Supported by U.S. National Science Foundation grants DEB 81-19292 and BSR 85-00148 to P.G. We thank Mr. Mike Veith, Washington University, for technical assistance.*

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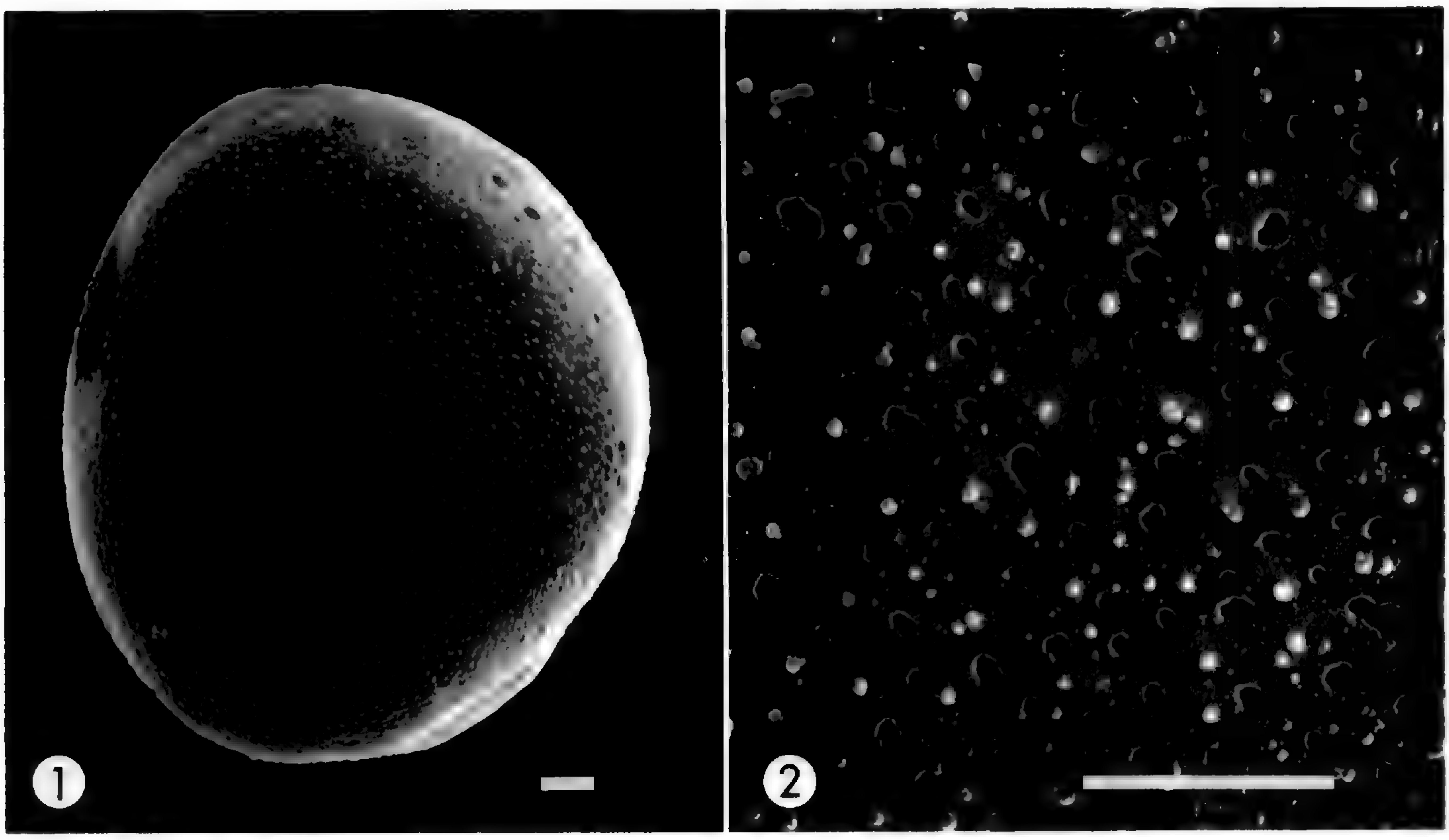

FIGURE 1, 2. *Scanning electron micrographs of* Pillansia templemanii.—*1. Whole grain in equatorial view ×1,200.—2. Detail of the exine surface ×6,000. Scale bars = 5 µm.*

until now been unknown, and it is important to establish whether it has the basic reticulate (to retipilate) exine of most Iridaceae (Schulze, 1971) or the specialized micropunctate and micropapillate exine characteristic of Ixioideae (Schulze, 1970, 1971).

METHODS

Pollen of *Pillansia templemanii* (Baker) L. Bolus was extracted from flowers from herbarium specimens (voucher: *Bolus s.n.*, MO 2080184) and subjected to standard acetolysis treatment (Erdtman, 1960). Acetolyzed pollen was mounted on aluminum stubs, gold coated, and viewed in a Hitachi S-450 scanning electron microscope.

OBSERVATIONS

Pollen of *Pillansia* is 65–75 µm long (polar axis as measured from scanning electron micrographs), ellipsoid to widely ellipsoid (Fig. 1), and monosulcate with the sulcus running the length of the grain. The exine is densely micropunctate (punctitegillate of some authors) and micropapillate (Fig. 2). The pores in the tectum are round to irregular in shape and 0.15–1 µm in diameter. There are ca. 50 pores/100 µm². The papillae are small, mostly rounded excrescences, and up to 0.4 µm in diameter and height. They are scattered fairly regularly with a density of ca. 52/100 µm² between the pores.

DISCUSSION

Pillansia differs from all other Ixioideae in its paniculate inflorescence and leaves lacking a distinct central vein or central cluster of veins, both unspecialized conditions. Other Ixioideae have a spicate inflorescence or one believed to be derived from a spike (flowers solitary on branches or flowers sessile in a corymbose panicle) and have distinct (or more or less distinct) central veins. *Pillansia* differs further from other Ixioideae in leaf anatomy (P. Rudall, pers. comm.) by having isodiametric to longitudinally elongated mesophyll cells and epidermal cells with nearly straight walls and one or no papillae. Other Ixioideae have transversely elongated mesophyll cells and epidermal cells with sinuous walls and two or more papillae.

The pollen of *Pillansia* clearly matches that of other Ixioideae, which lends further support for its retention in that subfamily. In a survey of pollen morphology in 21 of the 45 genera of Ixioideae, Schulze (1970, 1971) found that 20 have micropunctate exines. Only *Micranthus* is reported to deviate, having the retipilate exine characteristic of the other subfamilies. Schulze's observations have been confirmed by SEM studies by de Vos (1974a, b, 1982) for *Syringodea*, *Duthieastrum*, and *Tritonia*, and by Straka & Friedrich (1984) for a Malagasy species of *Gladiolus* (as *Geissorhiza*). Pollen morphology provides no additional evidence for the relationships of *Pillansia* within Ixioideae—it remains a puzzling isolated and apparently relictual genus. Its unusual combination of features suggests that it may represent a link between Ixioideae and the remaining Iridaceae and could, it fact, be very close to the ancestral type of Ixioideae.

It now seems all but certain that micropunctate exine is basic for Ixioideae, and the presence of retipilate exine in *Micranthus*, an apparently typical member of the subfamily, is surprising, particularly as the closely allied *Thereianthus* is reported to have micropunctate exine. This may represent an example of a reversal to an ancestral condition, but pollen of all three species of *Micranthus* should be critically reexamined.

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EIGHT NEW SPECIES AND ONE NEW COMBINATION OF NEOTROPICAL LAURACEAE[1]

Henk van der Werff[2]

ABSTRACT

*Work in progress on the systematics of neotropical Lauraceae had yielded several undescribed species. In this contribution, eight species (*Aiouea obscura *van der Werff,* Aiouea vexatrix *van der Werff,* Caryodaphnopsis cogolloi *van der Werff,* Licaria velutina *van der Werff,* Nectandra mirafloris *van der Werff,* Persea pajonalis *van der Werff,* Phoebe elegans *van der Werff, and* Pleurothyrium hexaglandulosum *van der Werff) are described, illustrated, and discussed. A new combination,* Ocotea erectifolia *(Allen) van der Werff is made.*

Lauraceae are a large tropical family of trees and shrubs with the number of species in the New World estimated at 700–800. The taxonomy of the neotropical Lauraceae is poorly understood, and the entire family needs much work. The facts that many Lauraceae have small, inconspicuous flowers and are not frequently collected, that the genera are poorly defined, and that many species are known only from a few poor specimens have rendered the family almost inaccessible for the nonspecialist. Recent collections have shown that quite a few very distinct species await descriptions. In this contribution, eight species, mostly belonging to the smaller and relatively better-known genera, are described and discussed. A new combination is made and its synonymy given.

Aiouea obscura van der Werff, sp. nov. TYPE: Costa Rica. Puntarenas: along highway from Palmar Norte to Chacarita, ca. 2 km N of Chacarita. Tree, 10 m. Flowers pale green. *B. Hammel, M. Grayum & G. de Nevers 15197* (holotype, MO; isotypes, BM, CR, F, MEXU, NY, PMA, U). Figure 1.

Arbor, 10 m. Ramuli graciles, teretes, glabri. Gemma terminalis glabra. Folia alterna, anguste elliptica, basi apiceque acuta, 15–18 × 3–4 cm, membranacea, subtriplinervia, brochidodroma, in sicco olivacea; nervi laterales 2–3. Venatio super parve elevata, subtus magis elevata. Domatia plerumque in axillis nervorum lateralium basalium. Petioli teretes, glabri, 1–1.5 cm longi. Inflorescentiae axillis bractearum deciduarum super partem foliiferam, 15 cm longae, graciles. Pedicelli 8–10 mm longi. Tepala 6, aequalia, glabra, ca. 2 mm longa, late elliptica. Stamina 9, 2-locellata; 6 exteriora introrsa, ca. 1 mm longa, anthera parum latiore quam filamento, apice antherae locellos excedenti, filamento pubescenti; 3 interiora extrorsa, ca. 1.2 mm longa, apice locellos excedenti. Glandulae magnae, ca. 0.4 mm diametro, parum super basem affixae. Staminodia non visa. Ovarium glabrum, ovatum, ca. 1 mm longum, sensim in stylo brevi attenuatum. Fructus ignotus.

Tree, 10 m tall. Twigs slender, terete, glabrous. Terminal bud glabrous. Leaves alternate, narrowly elliptic, the base and tip acute, 15–18 × 3–4 cm, membranaceous, subtripliveined, the basal veins reaching ± ⅔ to the apex, the other 2–3 pairs of lateral veins in the upper half of the lamina, the lateral veins all curving toward the apex and loop-connected, drying olive green. Venation and reticulation slightly raised on upper surface, slightly more so on the lower surface. Domatia often present in the axils of the large lateral veins. Petioles terete, glabrous, 1–1.5 cm

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[1] *I thank the various botanists working in Mexico, Panama, and Colombia for their often excellent collections, sent to me for identifications. Their work is essential for a better understanding of the Lauraceae. Dr. W. Burger commented on parts of the manuscript. Dr. J. Dwyer kindly checked the Latin descriptions. John Myers made the illustrations. Loans from BR, F, G, and NY are gratefully acknowledged.*

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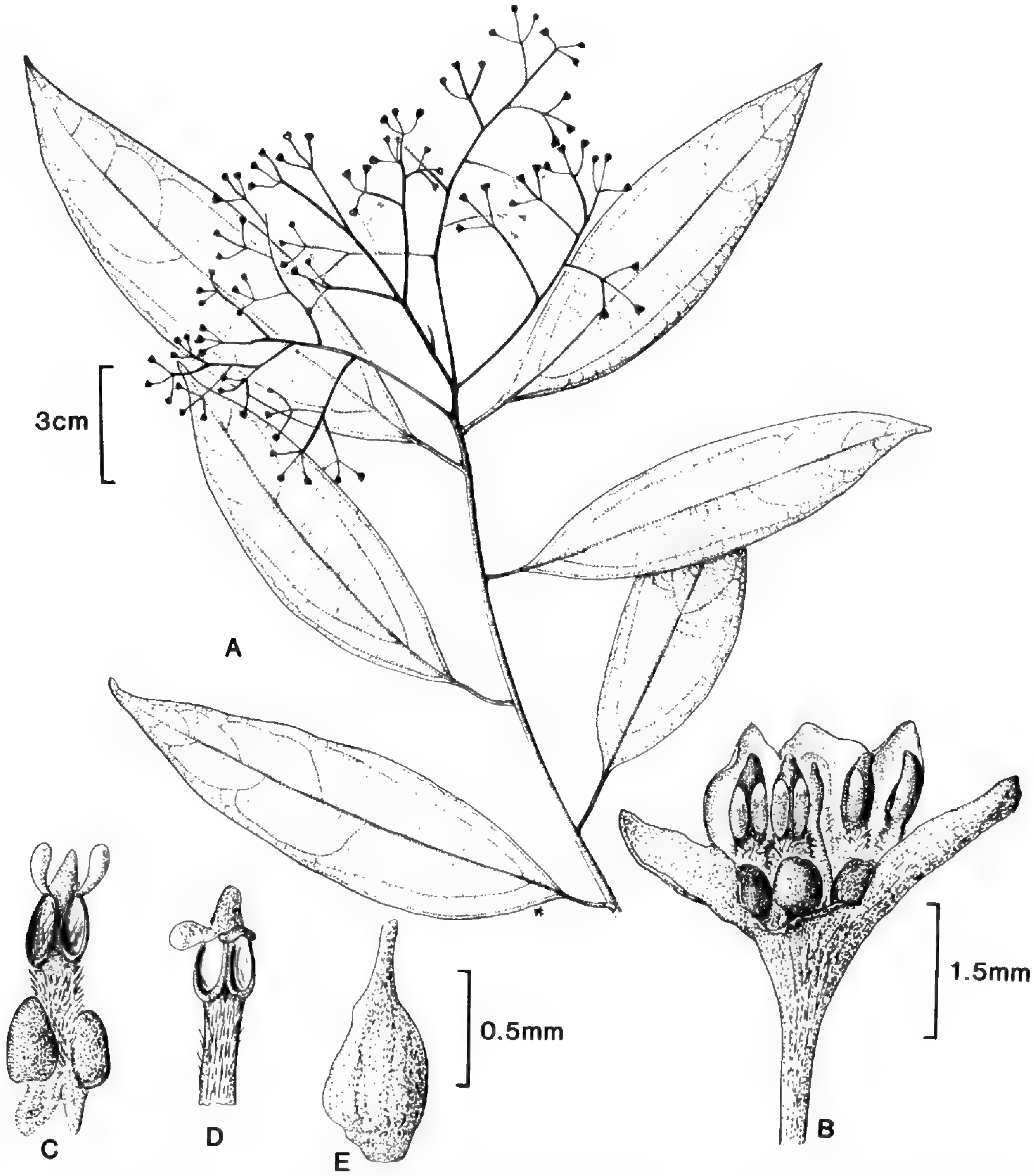

FIGURE 1. Aiouea obscura.—*A. Flowering branch.—B. Flower.—C. Inner stamen with basal glands.—D. Outer stamen.—E. Ovary.*

long. Inflorescences above the leaf-bearing part of the twigs, in the axils of deciduous bracts; terminal buds inconspicuous but always present above the lateral inflorescences. Inflorescences glabrous, to 15 cm long, slender, paniculate. Flowers pale green. Pedicels 8–10 mm long. Tepals 6, equal, glabrous, 2 mm long, broadly elliptic. Stamens 9, 2-celled; the outer 6 introrse, ca. 1 mm long, the anther slightly wider than the filament, the tip of the anther protruding beyond the anther cells, the filaments pubescent; inner 3 stamens extrorse, ca. 1.2 mm long, the glands large, ca. 0.4 mm diam., attached slightly above the base of the filaments, reaching the upper part of the filaments, leaving the anthers exposed but shielding the ovary; connective tissue also protruding beyond anther cells. Staminodia not seen. Ovary glabrous, ovate, ca. 1 mm long, gradually narrowed into the short style. Fruit unknown.

Aiouea obscura is only known from the type collection. Characteristics are laxly flowered inflorescences, relatively long pedicels, and dark-drying, subtriplivelned leaves with loop-connected lateral veins. It resembles closely several other dark-drying Lauraceae with membranaceous leaves and lax inflorescences, such as *Ocotea tenera* Mez & J. D. Smith (known from Costa Rica) and *Phoebe glabra* van der Werff (southern Mexico).

Aiouea obscura differs from both species in having two-celled anthers; from *O. tenera* it differs further in having subtripliveined leaves and from *P. glabra* in having narrower leaves with less prominently raised reticulation. None of the other Central American species are similar to *A. obscura*. These observations re-emphasize that our current generic concepts place seemingly closely related species in different genera and that these concepts urgently need re-examination.

Aiouea vexatrix van der Werff, sp. nov. TYPE: Panama. Panamá: Cerro Campana, above Capira, elev. ca. 900 m, 8°40'N, 79°50'W. Slender treelet, 3 m tall. Stem with small red ants in center. Perianth green. *McPherson 9226* (holotype, MO). Figure 2A–G.

Frutex vel arbor parva, ad 7 m. Ramuli juvenales angulati, minute fusco-puberuli, vetustiores teretes glabrique. Ramuli fistulosi frequenter formicis habitati. Petioli ad 1.5 cm longi, glabri vel minute puberuli. Folia alterna, in sicco atro-olivacea, glabra, chartacea, elliptica, basi apiceque acuta, 13–27 × 5–9 cm, super costa nervisque immersis, reticulatione parve elevata, subtus costa nervisque elevatis. Nervi laterales utroque costae latere 6–8. Inflorescentiae axillares, glabrae vel minute puberulae versus basim, ad 9 cm longae; ramuli inflorescentiarum complanati in sicco. Flores in vivo virides, ad 3 mm longi. Tepala 6, aequalia, glabra, erecta per anthesin, late ovata, 2 mm longa, 1.7 mm lata. Stamina 9, 2-locellata, glabra, inclusa, 6 exteriora introrsa, 3 interiora extrorsa filamentis quam antheris angustioribus. Staminodia nulla. Ovarium glabrum, ellipsoideum, sensim in stylo attenuatum. Infructescentiae ad 7 cm longae. Cupula ca. 8 mm diametro, tepalis in margine cupulae persistentibus, pedicello paulatim in cupula dilatato. Fructus ellipsoideus, ad 2 cm longus, fere omnino exsertus.

Shrub or small tree, 5(–7) m tall. Leafy twigs angular, minutely brownish puberulous, becoming round and glabrous on older parts; twigs consistently hollow and with pores giving access to the hollow center; often ants present in the hollow twigs (fide collectors). Terminal bud small, with very fine, copper-colored pubescence. Petioles to 1.5 cm long, minutely puberulous or glabrous, the lamina decurrent as narrow ridges. Leaves drying dark olive green, rarely gray-green, glabrous, chartaceous, elliptic, rarely slightly obovate, the base and apex both acute, 13–27 × 5–9 cm, the upper surface with immersed midrib and lateral veins, the final reticulation slightly raised; lower surface with midrib and lateral veins elevated, the final reticulation less elevated. Lateral veins 6–8 pairs. Inflorescences axillary, often seemingly terminal, glabrous or with some minute puberulence especially near the base, 6(–9) cm long, the branchlets not terete, these flattened after drying. Flower glabrous, ca. 3 mm long, on pedicels to 3 mm long; tepals 6, equal, glabrous, erect at anthesis, broadly ovate, ca. 2 mm long, 1.7 mm wide. Stamens 9, all 2-celled, the outer 6 introrse, the inner 3 extrorse. Outer stamens 1.5 mm long, the filament glabrous and ca. 0.6 mm long, the anther narrowly triangular, wider than the filament, ca. 0.9 mm long with a sterile apical section; anther cells large, ca. 0.3 mm long. Inner stamens 1.5 mm long, the anther 0.8 mm long, with sterile tip; filament slender with 2 large glands attached near the base. Glands collar-shaped, the basal part spreading horizontally, then abruptly curved inward and downward (toward the ovary), the tip of the gland flattened and resting on the upper part of the ovary. Staminodia lacking. Ovary glabrous, ellipsoid, ca. 0.8 mm long, largely sunken in the flower tube, at the tip gradually narrowed into the style, this 0.8 mm long. Infructescences to 7 cm long. Cupule ca. 8 mm diam., the tepals persistent on the rim, the pedicels gradually widened into the cupule. Fruit ellipsoid, ca. 2 cm long, almost completely exserted. Occasional stamens remaining attached to the cupule in late fruiting stage.

Paratypes (all MO). PANAMA. PANAMÁ: Cerro Campana, *Correa 295, 1026*; same locality, *Croat 12153, 14689, 17203, 25120, 35960*; same locality, *Garner 13*; same locality, *Gentry 1832, 5776*; same locality, *Hamilton 4056, 4061*; same locality, *Hammel 3776*; same locality, *Kirkbride 245*; same locality, *Luteyn 1812*; same locality, *McPherson 7461, 7921*; same locality, *Miller 975*; same locality, *Mori 1917, 2457, 7701*; same locality, *Nee 11611*; same locality, *Sytsma 1150, 2942, 2962*; Cerro Trinidad, *Kirkbride 1656*. COLÓN: Santa Rita Ridge Road, *Correa 1056*; same locality, *Dressler 3705*; same locality, *Foster 1735*; same locality, *Sytsma 4238, 4252*; Cerro Brewster, *de Nevers 5573*. COMARCA DE SAN BLAS: El Llano–Carti Road, *de Nevers 4240*.

Aiouea vexatrix has a limited distribution

TABLE 1. *Diagnostic characters for* Aiouea vexatrix, Ocotea paulii, O. atirrensis, *and* O. nicaraguensis. *The numbers in parentheses given with the flowering and fruiting periods represent the number of collections examined.*

	Aiouea vexatrix	*Ocotea paulii*	*Ocotea atirrensis*	*Ocotea nicaraguensis*
Anthers	2-celled	4-celled	4-celled	4-celled
Cupule	tepals persistent	tepals deciduous	tepals deciduous	tepals persistent
Leaf color when dry	dark olive green	green	dark olive green	green
Leaf shape	elliptic	elliptic	obovate	obovate to oblanceolate
Leaf texture	thinly chartaceous	stiffly chartaceous	thinly chartaceous	thickly chartaceous
Length of inflorescence	½ leaf length or less	± equal to leaves	± equal to leaves	± equal to leaves
Flowering period	April–July (15)	October–January (11)	January–April (22)	
Fruiting period	July–November (20)	January–May (12)	April–September (13)	

in central Panama, where the abundance of collections indicates that it is common.

The placement of this new species in the genus *Aiouea* is provisional. The Central American species of *Aiouea* are quite different morphologically from the South American species, which include the type of the genus (van der Werff, 1984, 1987). *Aiouea vexatrix* is another example of such an aberrant *Aiouea* species. It has the following characters unusual for *Aiouea*: lack of staminodia, short inflorescences with flattened axes, dark olive green leaves, and persistent tepals on the cupule. It is included in *Aiouea* solely because of its hermaphrodite flowers with nine two-celled stamens and because it does not agree with the other, much better defined genera with nine two-celled stamens (*Aniba, Beilschmiedia, Cryptocarya, Kubitzkia, Phyllostemonodaphne, Urbanodendron*). As discussed below, *A. vexatrix* is probably related to *Ocotea*. The current circumscriptions of the neotropical genera of Lauraceae attach much importance to the number of cells of the anthers. This is an artificial character that obscures true relationships. However, discarding the present imperfect generic classification implies its replacement with a better classification, which I cannot offer at this moment. Therefore, I place this new species in *Aiouea*, a genus consisting of a group of closely related species in the lowlands of Venezuela, the Guianas, Brazil, and Paraguay, plus several unrelated species in the Andes and Central America. It is likely that the Andean and Central American species have been independently derived from *Ocotea* or *Nectandra* ancestors that lost two of their four anther cells.

Aiouea vexatrix is related to a group of *Ocotea* species that grow as shrubs or treelets, have angular (or almost winged), hollow twigs frequently inhabited by ants, flattened inflorescence branchlets, and glabrous flowers with erect tepals. The following names have been applied to these species: *Ocotea nicaraguensis* Mez, *O. paulii* Allen (Fig. 2H), *O. pedalifolia* Mez, *O. pentagona* Mez, *O. atirrensis* Mez & J. D. Smith and *O. wedeliana* Allen. Their distributions are in Panama, Costa Rica and Nicaragua. A survey of specimens at the Missouri Botanical Garden suggests that four species are involved, *A. vexatrix, O. paulii* (isotype, MO!), *O. atirrensis* (isotype, US!), and *O. nicaraguensis* (type W, probably destroyed; type photo, MO!). The main differences between these species are presented in Table 1. *Ocotea wedeliana* is known to me only from three isotypes (MAD, US, GH), all rather poor specimens from which one cannot draw firm conclusions. The flowers have four-celled anthers; the leaves are chartaceous and dry dark. A fruiting collection identified by Allen as *O. wedeliana* has the cupule of *O. paulii*, but thinner leaves.

The distributions of the four recognized species follow: *Aiouea vexatrix* is only known from areas rather close to Panama City (Pa-

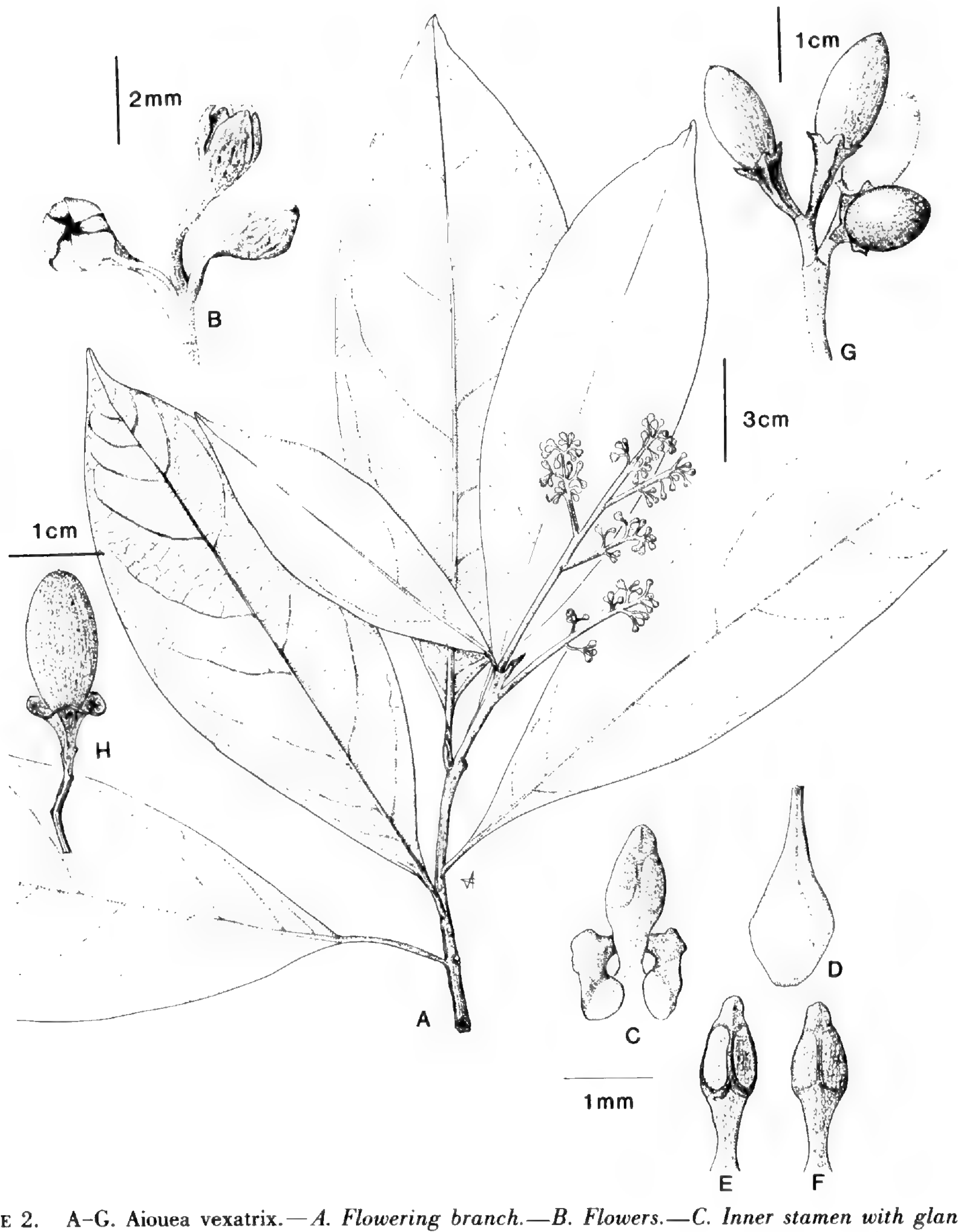

FIGURE 2. A–G. Aiouea vexatrix.—*A. Flowering branch.—B. Flowers.—C. Inner stamen with glands.—D. Ovary.—E, F. Outer stamens seen ventrally and dorsally.—G. Fruits.—H. Fruit of* Ocotea paulii.

namá, Colón, Comarca de San Blas). *Ocotea paulii* has a wider distribution in Panama (from Darién to Veraguas) and is uncommon in Costa Rica. It occurs with *A. vexatrix* on Cerro Campana, but no intermediates have been found there. Three collections, intermediate between *A. vexatrix* and *O. paulii*, are known from the western edge of the distribution of *A. vexatrix*. Both *Hammel 3557* (MO) and *Sytsma 4407* (MO) have leaf texture and color of *A. vexatrix*, flowers with four-celled anthers, and inflorescences longer than typical for *A. vexatrix*, but shorter than for *O. paulii*. *Allen 3439* (AA), identified as *O. wedeliana* Allen by Allen, has the thin leaves of *A. vexatrix* and cupule shape of *O. paulii*. These specimens, as well as the type of *O. wedeliana* Allen (US!, GH!, MAD!) are probably hybrids between *A. vexatrix* and *O. paulii*.

Ocotea atirrensis has been collected frequently in Costa Rica, but I have seen only two collections from Panama, both from Bocas del Toro. No intermediates between *O. atirrensis* and *O. paulii* are known to me. *Ocotea atirrensis* is characterized by large, obovate, chartaceous leaves that dry dark green and have acuminate tips; its tepals are not persistent on the cupule.

Ocotea nicaraguensis includes *O. pentagona* (syntypes: *Biolley 7106, Tonduz 7613, 8362,* all BR!) and a syntype of *O. pedalifolia* (*Pittier 9172,* BR!). The other syntype of *O. pedalifolia* (*Pittier 9179,* BR!) is *O. atirrensis.* Not as well represented as the other species, *O. nicaraguensis* awaits more specimens for a better understanding. Diagnostic characters are the strongly angled stems and stiffly chartaceous, green-drying leaves with acute tips; the cupule is crowned with persistent tepals. The few collections do not indicate a well-defined flowering period. Its obovate to oblanceolate leaves are distinct from the other species. *Ocotea nicaraguensis* is known from Costa Rica and Nicaragua.

Old collections of *A. vexatrix* have been distributed as *O. subsericea* Standley and as *O. atirrensis* and may be present in other herbaria under these names.

Caryodaphnopsis cogolloi van der Werff, sp. nov. TYPE: Colombia. Antioquia: Municipio de San Luis, left bank of Río Claro, 325–500 m, 5°53′N, 74°39′W. Tree, 15–18 m, flowers yellow. *A. Cogollo & R. Borjo 2019* (holotype, JAUM, n.v.; isotype, MO). Figure 3.

Arbor, 30 m. Ramuli teretes, juniores minute ferrugineo-pubescentes, vetustiores glabrescentes. Folia opposita, decussata, venatione pinnata, nervis utroque costae latere 8–12. Laminae ellipticae, 15–20 × 5–8 cm, basi acuta, apice acuminata; super glabrae, venatione immersa; subtus glaucae, costa nervisque elevatis et minute ferrugineo-pubescentibus, nervis minoribus paucis pilis ferrugineis praeditis. Petioli teretes, 1.5–2 cm longi, minute ferrugineo-pubescentes. Inflorescenciae axillares, ramulis oppositis, pyramidato-paniculatae, foliis perbreviores, minute et dense ferrugineo-pubescentes. Flores flavi. Tepala 6, inaequalia; 3 exteriora anguste triangularia, ca. 1.5 mm longa, apicibus saepe recurvatis, minute pubescentia; 3 interiora anguste ovata, apicibus acutis recurvatisque, ca. 4 mm longa, minute pubescentia; stamina 9, 4-locellata; 6 exteriora ca. 2 mm longa, glabra, filamentis ca. 0.6 mm longis, antheris ca. 1.3 mm longis, locellis introrsis; 3 interiora ca. 2 mm longa, glabra, filamentis ca. 1.2 mm longis, basibus 2 glandulis globosis auctis, antheris ca. 0.6 mm longis, locellis extrorsis. Staminodia 3, glabra, apicibus dilatata. Ovarium globosum, ca. 0.5 mm diametro. Stylum gracile, ca. 1.2 mm longum. Fructus pyriformis, in sicco ca. 4 cm longus.

Tree, to 30 m tall. Twigs terete, the younger ones with minute, ferruginous pubescence, becoming glabrous with age. Leaves opposite, decussate, pinnately veined, lateral veins 8–12 pairs. Laminae elliptic, 15–20 × 5–8 cm, the base acute, the apex acuminate, the upper surface glabrous with immersed veins, the lower surface gray-glaucous, waxy, the midrib and lateral veins elevated and with minute, ferruginous pubescence, the smaller veins with few ferruginous hairs. Petioles 1.5–2 cm long, with minute ferruginous pubescence, terete. Inflorescences axillary, to 8 cm long, much shorter than the leaves, branched from the base, pyramidal-paniculate, minutely and densely ferruginous pubescent. Flowers yellow; pedicels 2–3 mm long. Tepals 6, unequal; the outer 3 narrowly triangular, ca. 1.5 mm long, the tip often recurved, minutely brown pubescent; inner three ca. 4 mm long, narrowly ovate, the tip acute and recurved, minutely brown pubescent. Stamens 9, all 4-celled, the outer 6 ca. 2 mm long, glabrous, filaments ca. 0.6 mm long; anthers ca. 1.3 mm long, the cells introrse; the inner 3 slender, glabrous, ca. 2 mm long, filaments ca. 1.2 mm long, with anthers ca. 0.6 mm long, the cells extrorse; the filaments with 2 rather small, globose, basal glands. Staminodia 3, glabrous, ca. 1 mm long, the tip widened. Ovary globose, ca. 0.5 mm diam., the upper part with brown hairs; style slender, ca. 1.2 mm long. Fruit avocado-shaped, ca. 4 cm long when dry.

Paratype. COLOMBIA. ANTIOQUIA: Municipio de San Luis, Río Claro, 350 m (fr), *A. Cogollo et al. 2195* (JAUM, MO).

Caryodaphnopsis cogolloi is known only from a small (± 2 km^2) forest remnant in the Magdalena Valley in Colombia. This forest patch is home to, based on collections by Cogollo, two other undescribed species of *Caryodaphnopsis* (known from fruiting material)

FIGURE 3. Caryodaphnopsis cogolloi.—*A. Flowering branch.—B. Detail of lower leaf surface.—C. Flowers.—D. Flower with several tepals removed, showing outer and inner stamens, staminodia, and ovary with slender style.—E. Outer stamen.—F. Inner stamen with basal glands.—G. Ovary.—H. Fruit.*

and two undescribed species of *Licaria*. This shows how poorly collected neotropical Lauraceae are.

Caryodaphnopsis cogolloi is closely related to *C. inaequalis* (A. C. Smith) van der Werff & Richter, a species known from the Peruvian–Brazilian border area. Both species have pinnately veined leaves, a rare character in *Caryodaphnopsis* (van der Werff & Richter, 1985). The two species differ as follows: *C. cogolloi* has four-celled anthers, outer tepals 1.5 mm long having acute, recurved tips, denser tomentum on the flowers, and a glaucous undersurface of the leaves. *Caryodaphnopsis inaequalis* has two-celled anthers, outer tepals ca. 0.5 mm long with blunt tips and not recurved, rather scarce tomentum on the flowers, and leaves green below.

Recent collections of *Caryodaphnopsis* show that the neotropical species fall into two groups. One group includes the species with pinnately veined (or subtripliveined) leaves and an avocado-shaped fruit (*C. cogolloi*, *C. inaequalis*, *C. theobromifolia*); the other group includes the species with strongly three-veined leaves (the basal lateral veins reach the leaf apex) and small, round fruits (*C. fosteri* and three or four undescribed species).

The new species is named after its collector, Alvaro Cogollo, who collected several undescribed species of Lauraceae in the Magdalena Valley in Colombia.

Licaria velutina van der Werff, sp. nov. TYPE: Mexico. Veracruz: Mpio. San Andres Tuxtlas, Cerro Vigía near Estación de Biología Tropical Las Tuxtlas, 300 m, tree 18 m with yellowish flowers, *G. Ibarra M. & S. Sinaca C. 100* (holotype, MEXU; isotypes, CHAPA, HBG, MO). Figure 4.

Arbor, 8–20 metralis. Ramuli obtuse angulati, lenticellati, juveniles albido-vel bubalino-velutini, veteres fusco-pubescentes. Folia alterna, anguste elliptica vel anguste ovata, apice basique acuta, 12–30 × 2.5—6.5 cm; glabrescentia, nervis lateralibus 10–14, venatione super immersa vel perobscure elevata, subtus costa manifeste elevata, nervis et venatione elevata. Petioli 1–2 cm longi. Inflorescentiae foliis perbreviores, paniculatae, in axillis bractearum deciduarum, ad 13 cm longae, immaturae velutinae, veteres pubescentes sparsiore. Flores pedicellis 2–4 mm longis, glabri, globosi vel late elliptici, ca. 2 mm longi, 1.5 mm lati; tepala 6, exteriora parum majoria interioribus, incurvata, ca. 0.3 mm longa, ca. 0.5 mm lata; stamina 3, 2-locellata, connata, ca. 1 mm longa, inclusa; locelli extrorsi, aperientes ad apicem antherarum. Glandulae staminum praesentes. Ovarium glabrum, ellipsoideum, sensim in stylum attenuatum, ca. 1.3 mm longum. Infructescentia ad 7 cm longa, plerumque solo fructu. Cupula cylindrica, ad 2 cm longa, 2.5 cm lata, 1.5 cm profunda margine simplici; fructus (in sicco) cupula ca. 1 cm longior.

Tree, 8–20 m tall. Twigs obtusely angled, with gray lenticels, the inflorescence-bearing part covered with white or yellowish velutinous pubescence, this changing to very short, brown pubescence on fruiting twigs. Leaves alternate, narrowly elliptic or narrowly ovate, the tip gradually acute or narrowly rounded, the base acute, 12–30 × 2.5–6.5 cm, when young with appressed pubescence, but soon glabrescent, with 10–14 pairs of lateral veins, the venation immersed or faintly elevated above, the midrib prominently raised below, the lateral veins and tertiary venation raised below. Petioles 1–2 cm long. Inflorescences much shorter than leaves, paniculate, in the axils of deciduous bracts, to 13 cm long; immature inflorescences velutinous; older inflorescences with sparser pubescence; bracts of the inflorescence with white pubescence on the outside, glabrous inside, ovate, ca. 2.5 mm long, deciduous at anthesis. Flowers on glabrous pedicels, these 2–4 mm long; flowers glabrous, globose or broadly elliptic, ca. 2 mm long and 1.5 mm wide; tepals 6, incurved, the outer 3 broader than the inner 3, ca. 0.3 mm long, 0.5 mm wide; fertile stamens 3, their tips just exposed; anther cells almost apical, small, opening toward the tip and extrorse. Stamens fully connate, forming a dome ca. 1 mm high and ca. 1.3 mm wide at the base; ovary globose, ellipsoid, gradually narrowed into style, ca. 1.3 mm long. Staminal glands 6, reduced to small flaps, ca. 0.3 mm tall, visible at the base of the anthers. Infructescences to 7 cm long, usually with only one fruit. Cupule deeply cup-shaped, 2 cm long, 2.5 cm wide, the cup ca. 1.5 cm deep with gray lenticels, rather thin, ca. 1 mm thick at the margin, not double-rimmed, often with dried stamens attached to the margin. Fruit to 1 cm longer than the cupule when dry, ovoid, ca. 2.5 cm long.

Common names. Laurel baboso, Laurel pimienta.

Paratypes. MEXICO. CHIAPAS: Mpio. Tecpatán, Colonia El Diamante, cerce del punto Trine de Chiapas–Tabasco–Vera Cruz, Aug. 1984 (fr), *Serrano B. & Rojas s.n.* (CHAPA, HBG, MEXU, MO). VERACRUZ: Mpio. San Andres Tuxtlas, Estación de Biología Tropical Las Tuxtlas (fr), *Calzada 178* (F, MO); same locality (fr), *Calzada 695* (F, MO); same locality, May 1981 (fr), *Gentry & Lott 32260* (MO); same locality, June 1981 (st), *Gentry & Lott 32521* (MO); same locality, April 1984 (fr), *Ibarra M. 1462* (CHAPA, HBG, MEXU, MO); same locality, lote 67, July 1984 (fr), *Ibarra M. & Sinaca C. 1916* (CHAPA, HBG, MEXU, MO); Laguna Escondida, 3 km NW of Estación Las Tuxtlas, 200 m, June 1985 (fl), *Sinaca C. 107, 110, 111* (CHAPA, HBG, MEXU, MO); Camino a Cárdenas, 4.5 km de la Estación Las Tuxtlas, June 1985 (fl), *Sinaca C. 114* (MO); lote 71, Estación Las Tuxtlas, 350 m, Aug. 1985 (fr), *Sinaca C. 207* (CHAPA, HBG, MEXU, MO); Estación Las Tuxtlas, June 1981 (fr), *Wendt et al. 3418* (CHAPA, CAS, LL, MEXU, MO).

Licaria velutina is closely related to *L. excelsa,* known from southern Mexico and Panama. *Licaria velutina* differs by having narrow leaves 4–6 times longer than wide, densely pubescent young twigs, less pubescent inflorescences, the pubescence contrasting with the glabrous flowers, and large cupules with simple margins (our fruiting material of *L. excelsa* shows always double-rimmed cupules). All collections of *L. excelsa* are from above 1,000 m elevation, whereas *L. velutina* is only known from elevations of 200–300 m.

Measurements and illustrations of stamens, staminal glands, and ovary are based on boiled parts, which shrink and change shape while drying.

Nectandra mirafloris van der Werff, sp. nov. TYPE: Nicaragua. Jinotega: Laguna de Miraflores, small tree at edge of swamp, 12 May 1976, 1,200 m, *Neill 329* (distributed by Seymour as no. *7204*), (holotype, MO). Figure 5.

Arbor parva, 2–8(–15) m. Ramuli modice appresse strigosi, glabrescentes, vetustiores lenticellati. Folia alterna, elliptica, firme chartacea, 15–20 × 7–10 cm, apice obtuse acuta, basi acuta vel obtusa; petioli 1–1.5 cm longi; laminae super nitidae, reticulatione elevata sed costa nervisque immersis, glabra; subtus opacae, leviter adpresse pubescentes, praesertim prope basim, domitiis axillaribus, costa manifeste elevata, nervis reticulationeque elevatis; nervi 6–9 jugi. Inflorescentiae in axillis foliorum vel bractearum deciduarum, foliis perbreviores; axes centrales adpresse pubescentes, ramuli pubescentia densiore, saepe albo-pubescentes. Flores pedicellati, extus dense albo-pubescentes; tepala 6, aequalia, basi connata, intus dense papillosa, ca. 3 mm longa; stamina 9, 4-loculata, 6 exteriora ca. 0.9 mm longa filamentis brevissimis, antheris quadrangularibus, locellis introrsis; 3 interiora ca. 1.2 mm longa, filamentis ca. 0.3 mm longis, 2 glandulis magnis munitis, locellis lateralibus; staminodia 3, ca. 0.8 mm longa, claviformia. Ovarium globosum, glabrum; stylus ovario perbrevior. Fructus late ellipticus, 2 × 1.5 cm, cupula parva, discoidea; pedicellus frugifer inflatus.

Small tree, 2–8(–15) m tall. Twigs gray, with small, appressed hairs, becoming glabrous, often developing lenticels after the first year. Leaves alternate, elliptic, firmly chartaceous, 15–20 × 7–10 cm, the tip bluntly acute, the base acute to obtuse, petioles 1–1.5 cm long, laminae shiny above, glabrous with raised reticulation, but with immersed midvein and lateral veins, these in 6–9 pairs, opaque below, these with some appressed short hairs (especially near the base) and frequently tufts of axillary hairs, the midvein prominently raised, the lateral veins and final reticulation raised. Inflorescences in the axils of persistent leaves or deciduous bracts, 6–12 cm long, paniculate, the main axis with some appressed pubescence, the branchlets with much denser pubescence, sometimes appearing white pubescent. Flowers pedicellate, the pedicels ca. 2 mm long, densely white-pubescent; tepals 6, all equal, united at their bases, densely white pubescent outside, densely papillose inside, ca. 3 mm long; stamens, 9, 4-celled, the outer 6 with a very short filament, appearing sessile, quadrangular, ca. 0.9 mm long, the anther cells introrse, occupying almost the entire anther and arranged ± in an arc, papillose; the inner 3 anthers ca. 1.2 mm long, with lateral anther cells, the filament ca. 0.3 mm long, each with 2 large glands near the base; staminodia present, club-shaped, ca. 0.8 mm long. Ovary globose, glabrous; style much shorter than ovary, glabrous. Fruit broadly ellipsoid, 2 × 1.5 cm, seated on a small, platelike cupule; pedicel swollen in fruit.

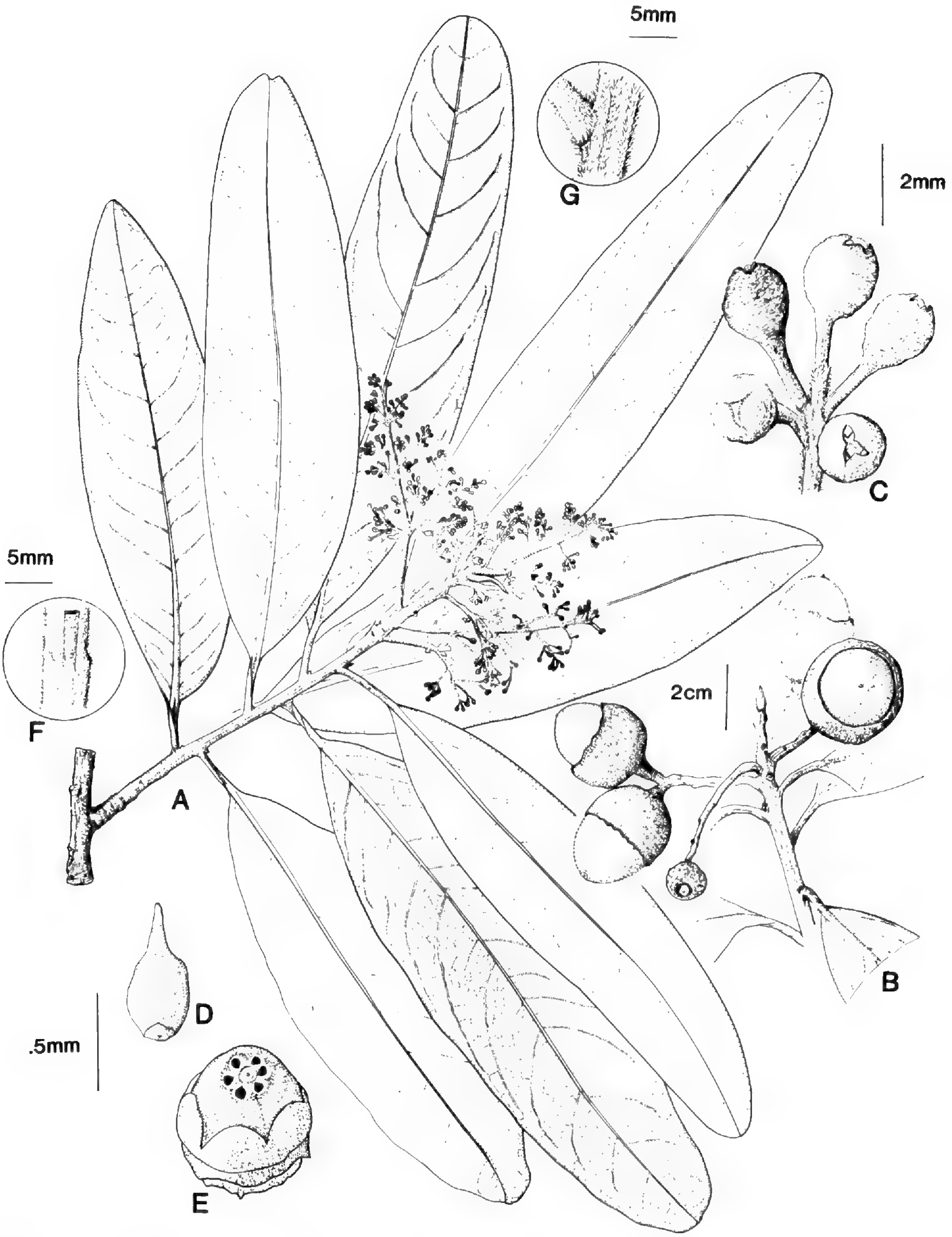

FIGURE 4. Licaria velutina.—*A. Flowering branch.—B. Fruits.—C. Flowers.—D. Ovary.—E. Flower with tepals removed, showing three two-celled stamens with fused filaments and lobe-shaped basal glands.—F. Detail of twig, showing pubescence.—G. Detail of inflorescence branch, showing pubescence.*

Paratypes. NICARAGUA. ESTELI: Laguna Miraflor, *Laguna 336* (MO); same location, *Moreno 19434, 21118, 8227* (MO); Cerro Quiabú, *Stevens 16918, 16247* (MO); same locality, *Grijalva & Araquistain 641* (MO); same locality, *Moreno 1309, 19266, 21185A* (MO); Mesas Plan Helado, 2 km from Laguna Miraflor, *Moreno 15846* (MO); El Chaparral, 1 km W of Laguna Miraflor, *Moreno 22382* (MO); Mesas Plan Helado, 21.5 km E of Esteli, *Moreno 15410* (MO). JINOTEGA: km 150 de la carretera Matagalpa–Jinotega, *Moreno 472* (MO); Laguna de Miraflores, *Neill 339* (MO) (distributed by Seymour as *Neill 7198*).

Nectandra mirafloris is only known from an area with cloud forest on the border of the

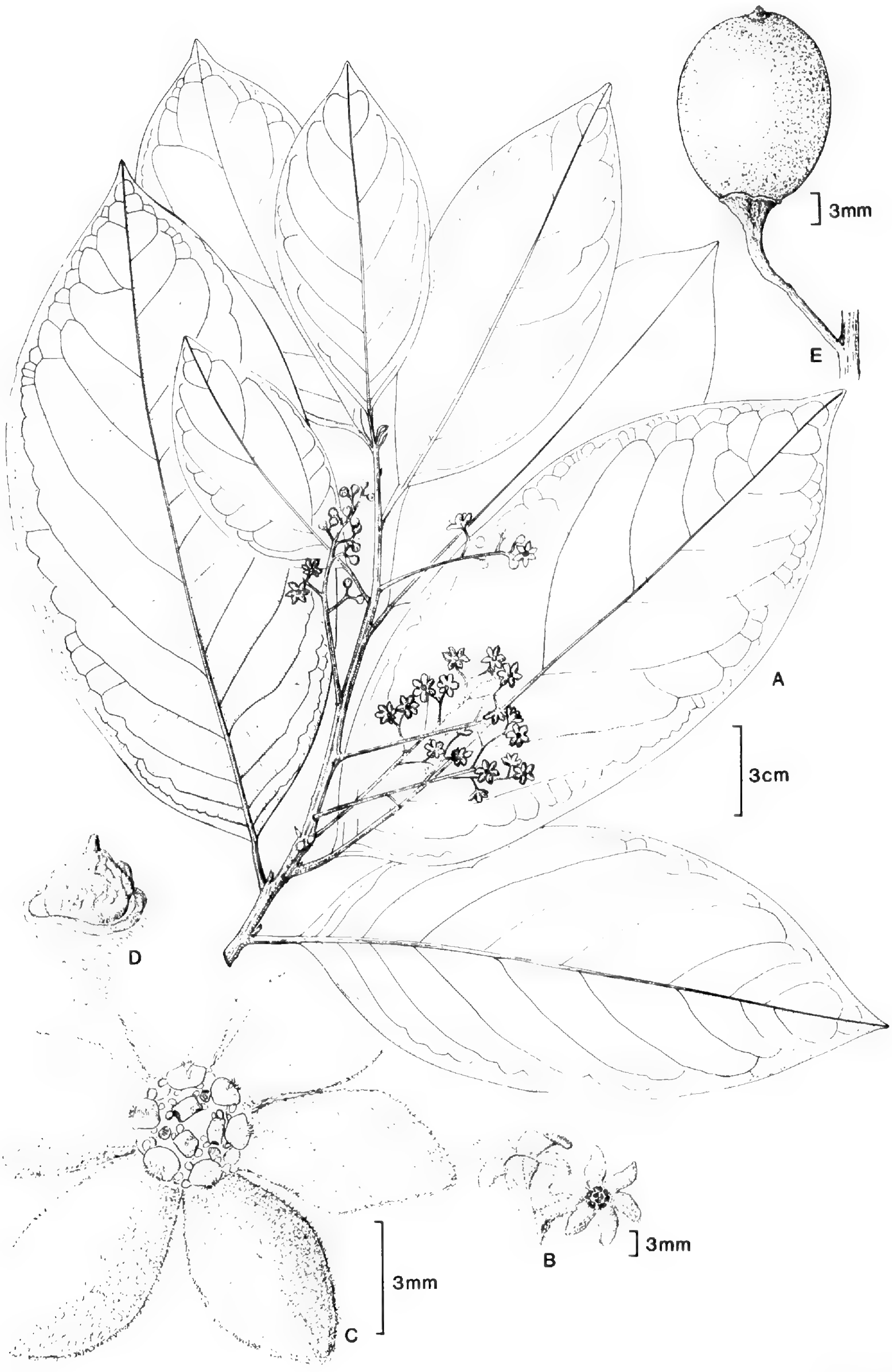

FIGURE 5. Nectandra miraﬂoris.—*A. Flowering branch.—B. Flowers.—C. Dehisced tepals with attached stamens.—D. Young fruit, showing abscission line of tepals.—E. Fruit.*

departamentos of Esteli and Jinotega. This is one of the best-developed montane areas in Nicaragua and is inhabited by several species otherwise unknown in Nicaragua, such as *Osmunda regalis* (W. D. Stevens, pers. comm.). Specimens with buds or flowers have been collected from late December to May; the fruiting collection (*Stevens 16347*) was made in November.

Nectandra and *Ocotea* are the two largest genera of neotropical Lauraceae. The differences between the two genera are not always easy to see and some authors have proposed to merge them under *Ocotea* (Kostermans, 1957; Howard, 1981; Liogier, 1982; the last-mentioned two transferred several West Indian *Nectandra* species to *Ocotea*). The character most frequently mentioned in the literature as separating the two genera is the position of the anther cells; they are arranged in an arc in *Nectandra* and in two rows in *Ocotea*. This character separates most species quite readily but is intermediate in some. Two additional characters help separate *Nectandra* from *Ocotea*. In *Nectandra* the inner faces of the tepals and the anthers have papillose pubescence; in *Ocotea* these surfaces are either glabrous or strigose. Also, in *Nectandra* the tepals are usually basally connivent, and in older flowers an abscission line forms underneath the tepals, which fall off as a unit together with all anthers. In *Ocotea* the tepals are free and fall off individually, often leaving stamens attached to the floral tube. Thus, on the young cupules of *Nectandra* species, one never finds stamens, but in *Ocotea* very frequently a few stamens can be found on young cupules.

In *Nectandra mirafloris* the position of the anther cells is intermediate between *Nectandra* and *Ocotea*, but the papillose indumentum on the tepals and anthers and the dehiscence of the tepals as a unit lead me to place this species in *Nectandra*. I regard a montane species from Panama and Costa Rica, *Nectandra cufodontisii* (O. Schmidt) Allen (basionym: *Ocotea cufodontisii* O. Schmidt; heterotypic synonym: *Ocotea seibertii* Allen according to W. Burger in litt.), as its closest relative. This species is very similar in leaf shape, venation type, and fruit shape but differs by lacking white pubescence on flowers and buds; its flowers are slightly larger, as are the leaves; and the outer stamens have anthers on filaments ca. 0.3 mm long, contrasted with nearly sessile anthers in *N. mirafloris*. Several collections of *N. mirafloris* were annotated as *Persea*, one as *Nectandra sanguinea* and one (the type) as *Anacardium occidentale*.

The epithet *mirafloris* refers to the type locality and is a reminder to collectors to look out for flowering Lauraceae.

Persea pajonalis van der Werff, sp. nov. TYPE: Peru. Boundary of provinces Oxapampa and Pasco: San Gotardo; 3 m shrub in pajonal, 2,500–3,000 m, 29 Dec. 1983, *Foster, Chanco & Alban 7647* (holotype, MO). Figure 6A–E.

Frutex vel arbor parva. Ramuli crassi, 5–8 mm in diametro, angulares, hornotini sparsim adpresse cinereopubescentes, vetustiores glabri; cicatricibus conspicuis aggregatis. Folia alterna, coriacea, obovata, apice rotundata vel subacuta, basi obtusa vel subcordata, 10–17 × 4–8 cm; super glabra costa nervisque (10–12 jugis) immersis; subtus sparsim adpresse pubescentia, praecipue secus costam nervosque; costa, nervis venationeque elevata. Petioli crassi, 5–8 mm longi. Inflorescentiae axillares, 5–18 cm longae, paniculatae; flores pedicellique aeneo-puberuli, pubescentia evanescente versus basim inflorescentiae. Tepala 6, inaequalia, 3 exteriora ovata, 3 × 3 mm, 3 interiora ellipsoidea, 4.5 × 2.5 mm, aeneo-puberula. Stamina 9, 4-locellata, 6 exteriora introrsa, 3 mm longa; 3 interiora extrorsa, 3.5 mm longa, basi filamentorum 2 glandulis sessilibus praedita. Staminodia 3, 1.5 mm longa, pubescentia. Ovarium glabrum subobovatum, 2 mm longum. Fructus immaturus viridis, magnopere tepalis persistentibus obtectus.

Shrub or small tree, 2–6 m tall. Twigs thick, 5–8 mm diam. during first year, angled, hollow, when young with gray appressed pubescence, glabrescent, 2-year-old twigs glabrous. Terminal buds with appressed gray pubescence, usually hidden by the leaves. Twigs with conspicuous clusters of scars from bracts of old terminal buds. Leaves alternate, evenly distributed along twigs, coriaceous, obovate, the tip rounded or slightly acute, the base obtuse or subcordate, 10–17 × 4–8 cm; laminae glabrous above, sparsely ap-

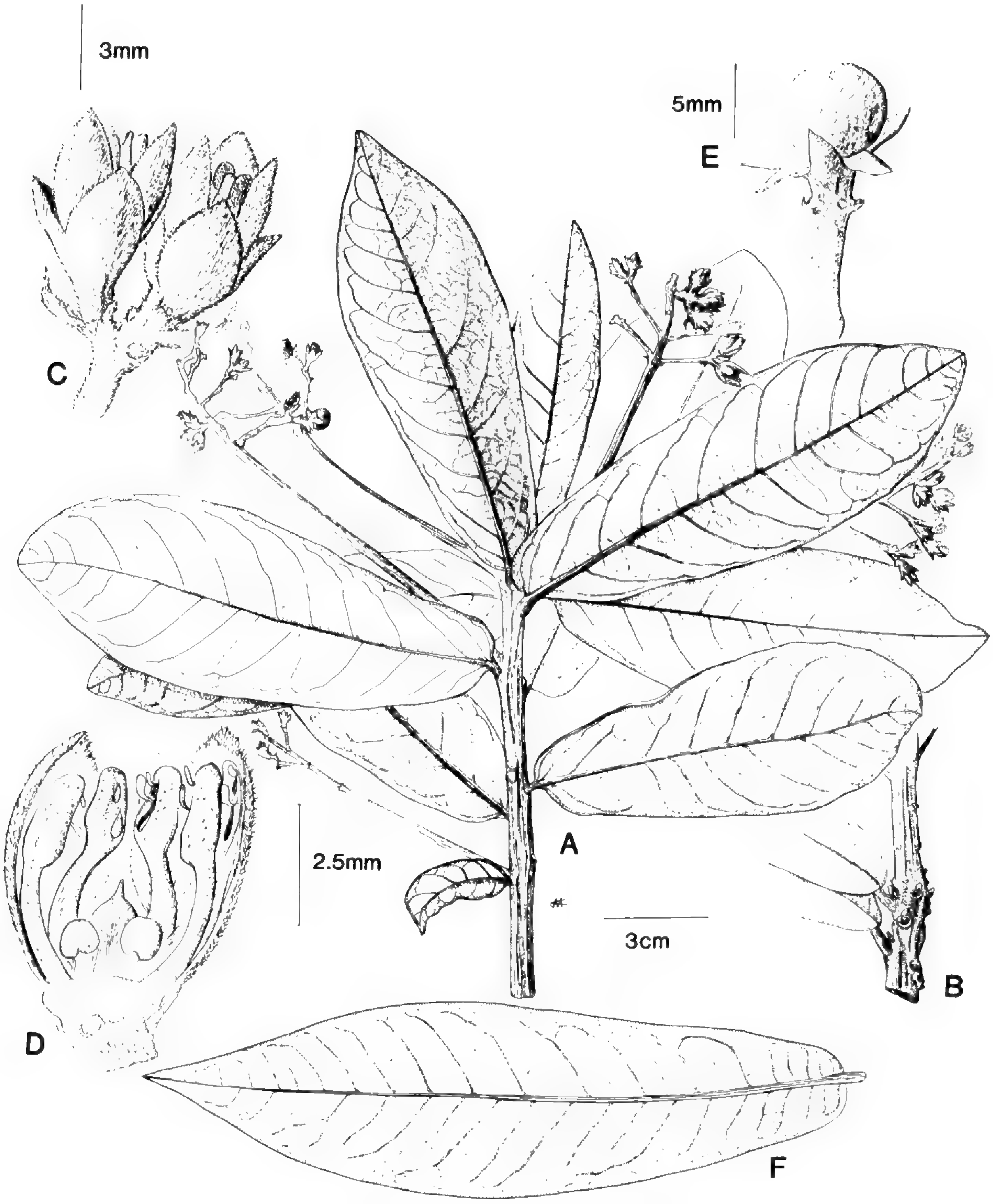

FIGURE 6. A–E. Persea pajonalis.—*A. Flowering branch.—B. Detail of twig with scars from bracts.—C. Flowers.—D. Flower with tepals removed, showing stamens, two basal glands, and staminode.—E. Fruit.—F. Leaf of* Persea sessilis.

pressed pubescent below, especially along major veins; midrib and lateral veins (10–12 pairs) immersed above, prominently raised on lower surface, tertiary venation also raised on lower surface. Petioles thick, 5–8 mm long. Inflorescences in axils of persistent leaves, 5–18 cm long, shorter than or about as long as the subtending leaves; paniculately branched, the peduncle to 12 cm long; flowers and pedicels with dense, bronze-colored puberulence, this becoming much sparser toward the base of the inflorescence. Tepals 6, unequal, the outer 3 ovate, ca. 3 × 3 mm, the inner 3 ellipsoid, ca. 4.5 × 2.5 mm, bronze-puberulent outside. Stamens 9, all 4-celled, the outer 6 introrse, ca. 3 mm long, the filaments ca. 1.5 mm long, narrower than the anther; the anther cells arranged in 2 rows; inner 3 stamens extrorse, ca. 3.5 mm long, with 2 globose glands attached near the base of the filaments. Staminodia 3, ca. 1.5 mm long, pubescent, with a broad triangular head. Ovary glabrous, round or slightly obovate, ca. 2 mm long; style distinct, ca. 1.5 mm long. Immature fruits green, largely hidden by persistent tepals.

Paratypes. PERU. BOUNDARY OF OXAPAMPA AND PASCO: San Gotardo, in dwarf forest, 2,650–2,800 m, *Gentry et al. 39998* (MO); same locality, *van der Werff et al. 8578* (MO).

Persea pajonalis is only known from a few collections from the San Gotardo area west of Oxapampa at rather high elevations. It is restricted to a vegetation type called *pajonal*, a name used for open, nonforest vegetation. Some of the pajonales seem to have an edaphic origin (only found on nutrient-poor sandstone), but in the San Gotardo area the pajonal represents a subparamo scrub rich in Ericaceae and Myrsinaceae; other taxa frequently found in high-elevation vegetation (Araliaceae, *Jamesonia*, *Weinmannia*) were present as well. However, groups indicative of nutrient-poor soil, such as Eriocaulaceae, terrestrial *Utricularia*, and *Pinguicula*, were found in the area too.

Persea pajonalis belongs to subg. *Eriodaphne* sect. *Eriodaphne*, using Kopp's (1966) classification. Among the South American species of this subgenus, *Persea pajonalis* can be immediately recognized by its nearly sessile leaves with rounded or subcordate base. *Persea sessilis* Standley & Steyerm., a Guatemalan species only known from the fruiting type collection, has similar leaves (Fig. 6F) The holotype (F!) consists of good vegetative material and remnants of infructescences. The following differences are evident between *P. pajonalis* and *P. sessilis*: in *P. pajonalis* the leaves have scarce scattered hairs on the lower surface, 10–12 pairs of lateral veins, and rounded or slightly acute tips, and the twigs are hollow; in *P. sessilis* the leaves have glabrous lower surfaces, acute to acuminate tips, and 15 or more pairs of lateral veins, and the twigs are solid. I expect that when flowers of *P. sessilis* become available, additional differences will be found and that the striking leaf shape is more a habitat adaptation (both are shrubs occurring on high-elevation mountain ridges) than an indication of close relationship.

Phoebe elegans van der Werff, sp. nov. TYPE: Mexico. Oaxaca: Mpio. San Miguel Chimalapa, Cima del Cerro Salomón, 16°46′15″N, 94°11′45″W, 1,770 m, 3 m tree, flowers green with red margin, pedicels reddish. Abundant. 11 Apr. 1986 (fl, fr) *M. Ishiki 1501* (holotype, MO; isotypes, CHAPA, HBG, LL, MEXU, n.v.). Figure 7.

Arbor parva, ad 6 m. Ramuli tenues, teretes, glabri; gemma terminalis glabra vel aliquot pilis adpressis aucta. Petioli glabri, 1–2 cm longi, leviter canaliculati. Folia alterna, glabra, ovata, 5–9 × 2–3 cm, basi obtusa vel rotundata, apice valde acuminata; acumine ad 2 cm longo; laminae trinerves, ceteris nervis lateralibus (3–4 jugis) debilibus; super venatione immersa subtus venatione leviter elevata; minute sub lente punctatae. Inflorescentiae axillares, glabrae, 2.5–4 cm longae, pauciflorae. Flores glabrae. Tepala 6, aequalia, per anthesin erecta, ca. 1.5 mm longa, ca. 2 mm lata, apice rotundata. Stamina 9, quadrilocellata, 6 exteriora introrsa, ca. 1.2 mm longa; 3 interiora extrorsa, ca. 1.5 mm longa, omnia basi filamentorum pilis translucentibus aucta; glandula staminum interiorum parva; staminodia 3 ca. 1 mm longa, apice triangulari. Ovarium globosum, glabrum, stylo ca. 0.8 mm longo. Fructus ellipsoideus, ca. 1 cm longus, 0.7 cm latus; cupula parva, non profunda, sensim in pedicello attenuata tepalis persistentibus.

Small tree, 3–6 m tall, the main stem thin, ca. 1 cm diam., branches smooth, delicate, horizontal. Twigs slender, terete, glabrous, the terminal bud with few appressed hairs or glabrous. Petioles glabrous, 1–2 cm long, the margins of the laminae decurrent as narrow ridges and the petioles thus slightly canaliculate. Leaves alternate, glabrous, ovate, mostly 5–9 × 2–3 cm, the base obtuse or rounded, the apex strongly acuminate, the acumen to 2 cm long, often falcate; laminae tripliveined, the basal laterals leaving the midvein at or very near the base of the laminae; other laterals (3–4 pairs) weakly developed; upper leaf surface with immersed venation, the lower surface with slightly raised venation; numerous small oil cells present on lower surface; margins of laminae smooth and slightly thickened. Inflorescences in the axils of normal leaves, glabrous, 2.5–4 cm long, shorter than the leaves, once or twice cymosely branched,

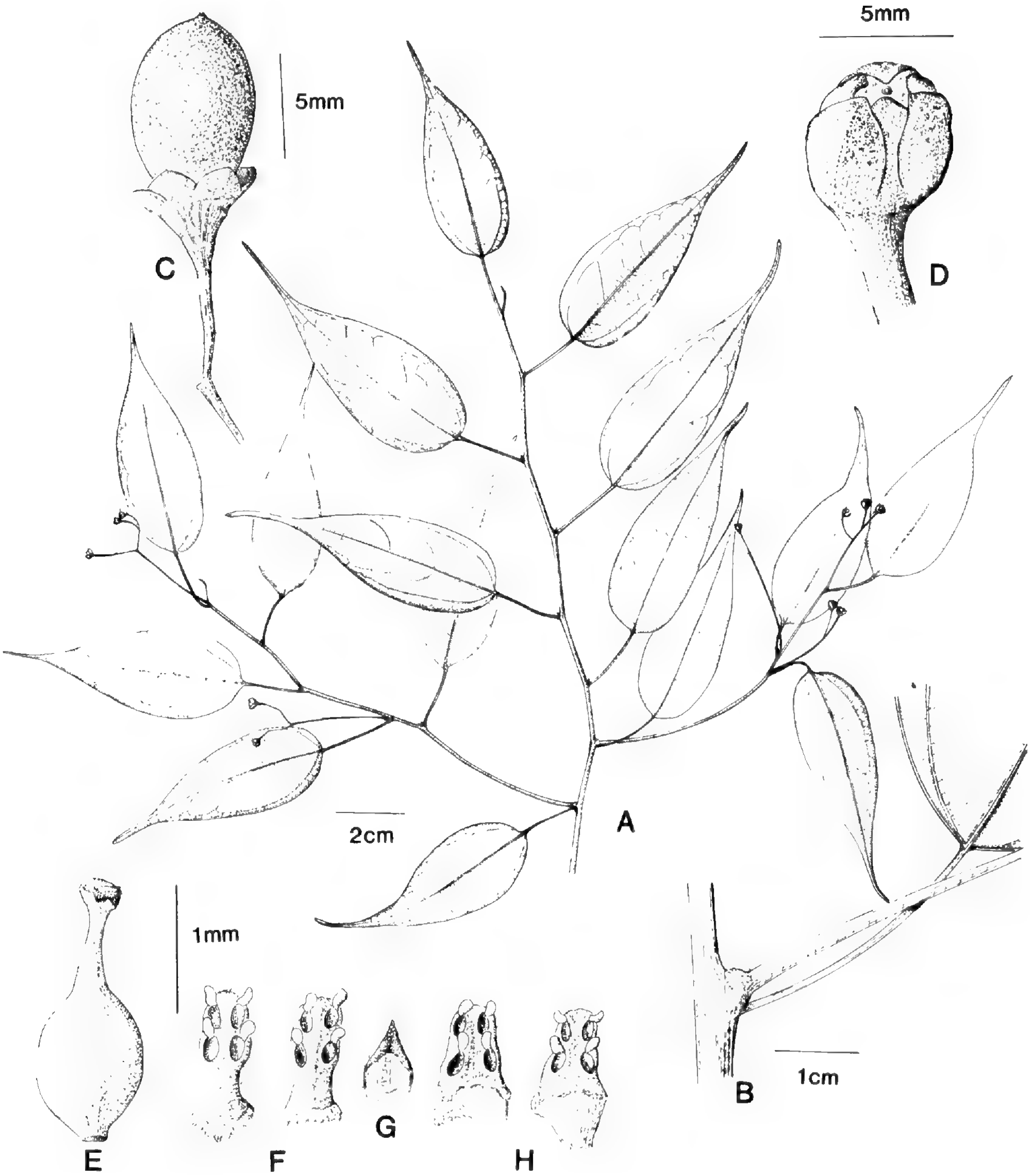

FIGURE 7. Phoebe elegans.—*A. Flowering branch.—B. Detail of twig showing petiole and base of inflorescence.—C. Fruit.—D. Flower.—E. Ovary.—F. Outer stamens.—G. Staminode.—H. Inner stamens with small basal glands.*

but on each inflorescence usually 2 or 3 flowers; bracts present in young inflorescences, linear, ca. 1.5 mm long, deciduous with age; pedicels slender, to 1 cm long. Flowers glabrous, ca. 2 mm long, 3.5 mm wide. Tepals 6, equal, erect at anthesis, rounded at tip, ca. 1.5 mm long and 2 mm wide. Fertile stamens 9, all 4-celled, glabrous, the outer 6 ca. 1.2 mm long, the filament slightly wider than the anther, the locelli arranged in 2 rows, introrse; the inner 3 stamens with extrorse cells, the filaments wider than the anthers, ca. 1.5 mm long; staminal glands small and visible as two small bulges at the base of the inner anthers. Staminodia 3, ca. 1 mm long, with a triangular head. Ovary globose, glabrous, ca. 1 mm diam. Style distinct, ca. 0.8 mm long with a large stigma. Base of the floral tube and base of the stamens covered with stiff, translucent hairs. Fruit an ellipsoid berry, ca. 1 cm long, 0.7 cm wide; cupule small plate, gradually narrowed into the pedicel and crowned with persistent tepals.

Paratypes. MEXICO. OAXACA: Mpio. San Miguel Chimalapa, Cima del Cerro Salomón, (buds) *Ishiki 1454,* (fr) *1529* (MO, CHAPA), (fl) *Ishiki 1616* (CHAPA, MEXU, MO).

Phoebe elegans is a very delicate and attractive species, so far only known from one mountain in Oaxaca, Mexico, near the border with Chiapas; it is said to be abundant in elfin forest and transition into cloud forest. The relatively long, spreading petioles, and the ovate, long-acuminate, triveined leaves separate it at once from the other neotropical *Phoebe* species, although it possesses all diagnostic characters for the group: tepals erect at anthesis, tepals persistent in fruit, flowers with long pedicels, staminodia present, and tripliveined leaves.

Phoebe, as accepted here, is a large (at least 180 binomials) genus occurring in the Asian and American tropics. Agreement on the generic boundaries of *Phoebe* has not yet been reached, and it is not clear how and if *Phoebe* can be separated from *Cinnamomum* and *Ocotea* (Kostermans, 1961; van der Werff, 1987). Until a careful study of these three groups has been made, I will continue the traditional usage of *Phoebe* for a heterogenous group of species in the Neotropics. I realize that the discordant species have to be transferred to other genera, and earlier (van der Werff, 1987) I discussed the characters I consider diagnostic for neotropical *Phoebe.* Altogether, the neotropical *Phoebe* species form a large group to which more than 70 species have been attributed.

Pleurothyrium hexaglandulosum van der Werff, sp. nov. TYPE: Panama. Colón: Río Guanche, ca. 5 km upstream from Portobelo, 50 m, tree, 5 m, inflorescence pendent, flowers green, becoming yellow. *Hammel & Trainer 14781* (holotype, MO; isotype, BR, others to be distributed). Figure 8.

Arbor parva, 5 m. Folia alterna, chartacea; petioli dense tomentelli; laminae anguste obovatae, 30–45 × 10–15 cm, versus basim sensim attenuatae, basi abrupte rotundatae vel subcordatae, apice acuminatae; super venatione immersa, subtus elevata; nervi secundarii sursum curvati et in nervo submarginili uniti. Inflorescentiae axillares, puberulae, paniculatae, 40–65 cm longae. Pedicelli cinereo-pubescentes, 1.5–2 cm longi. Flores virides, 8–9 mm diametro. Tepala 6, aequalia, extus cinereo-pubescentia, intus glabra ubicumque in alabastro antheras glandulasque staminum contingentia, demum pubescentia. Stamina 4-locellata, 6 exteriora locellis lateralibus, 3 interiora locellis extrorso-lateralibus. Filamenta staminum interiorum 2 glandulis magnis, stamina exteriora cingentibus aucta. Ovarium late globosum, pubescens. Fructus ignotus.

Small tree, 5 m tall. Twigs terete, densely brown tomentellous, 5 cm below the tip 4–5 m diam. Leaves alternate, chartaceous; the petioles ca. 5 mm long, densely tomentellous; laminae narrowly obovate, 30–45 × 10–15 cm, gradually narrowed toward the base, there abruptly rounded to subcordate, the tip acuminate; glabrous above, with appressed hairs on main veins below, especially near the base, otherwise glabrous; venation immersed above, midvein prominently raised below, secondary veins (14–18 pairs) raised and the final reticulation slightly less raised; secondary veins arching upward near the margin and prominently loop-connected in the upper ⅔ of the lamina. Inflorescences axillary, 40–65 cm long, brown puberulous, paniculate, laxly branched, the basal lateral branches 20–25 cm long, the upper ones gradually shorter. Pedicels 1.5–2 cm long, densely gray-pubescent. Flowers ca. 8–9 mm diam., greenish becoming yellow (fide collector). Tepals 6, equal, 4 mm long, glabrous inside except where in bud the glands and stamens not pressed against tepals, thus showing a narrow line of hairs central in the lower part of the tepal (the 6 glands not completely fused in this species), this line expanded in a diamond-shaped outline marking the space between anther and glands and with lines to the margin and tip of the tepal. Glands of the inner 3 stamens prominent, surrounding the outer stamens, but not becoming fused. Stamens 9, raised above the glands, the filament with some hairs on the back, 0.8–1 mm long; anthers 4-celled, the outer 6 anthers curved

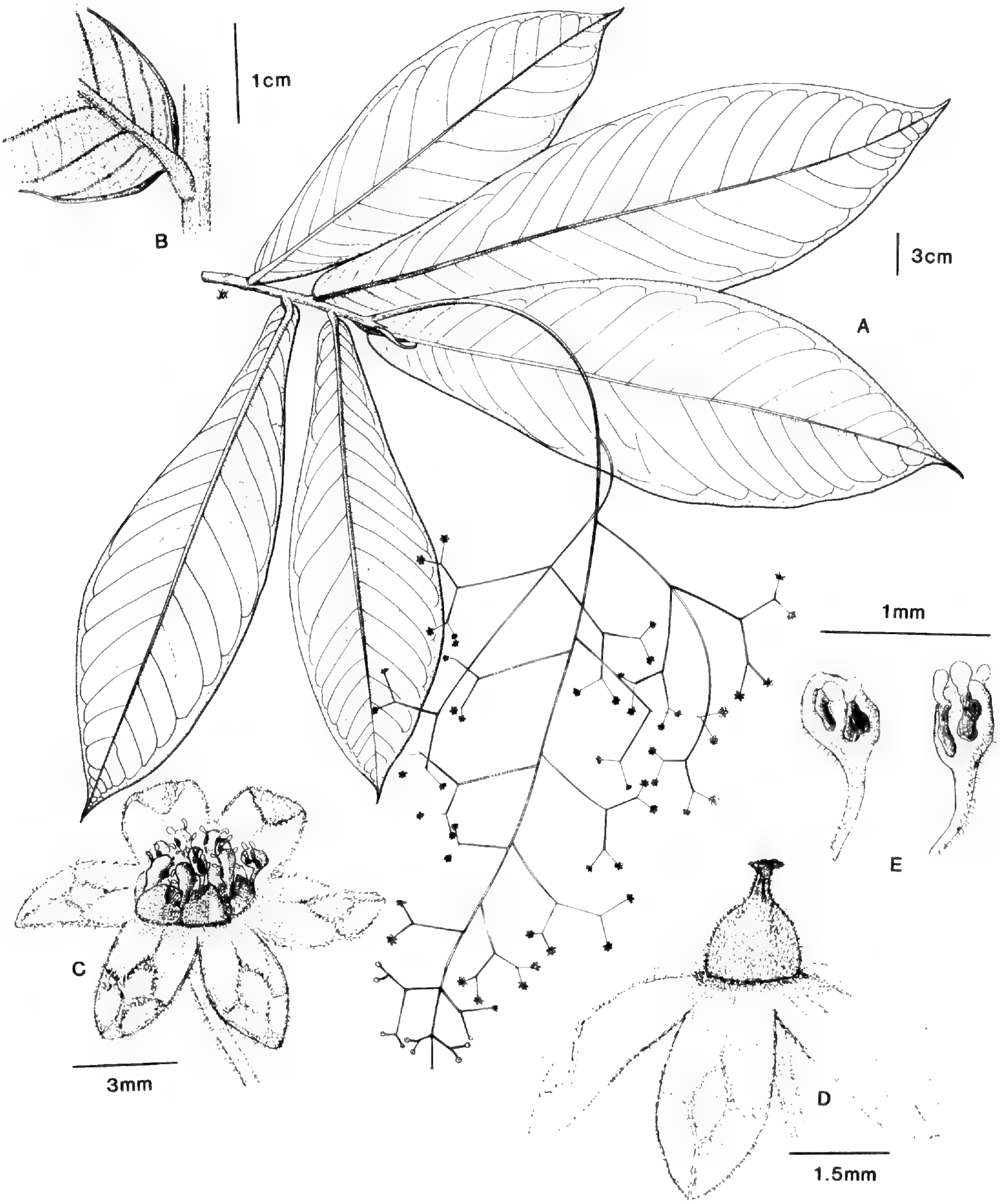

FIGURE 8. Pleurothyrium hexaglandulosum.—*A. Flowering branch.—B. Detail of leaf base and petiole.—C. Flower, showing pubescence pattern on tepals, large staminal glands, and stamens.—D. Old flower, glands and stamens fallen off.—E. Outer (left) and inner (right) stamen.*

inward, the anther cells lateral; inner anthers shorter, the anther cells lateral. No staminodia seen. Ovary broadly ovate, 1 mm long, 1.5 mm wide, with short, gray pubescence. Style short, 0.2–0.3 mm long, gray pubescent. Stigma platelike. Glands and stamens deciduous in older flowers and the tepals becoming reflexed, thus fully exposing the ovary. Fruit unknown.

Pleurothyrium hexaglandulosum is only known from two collections. It is closely related to *P. maximum* O. Schmidt from Amazonian Peru. Shared characters are large inflorescences, oblanceolate-obovate leaves with thick, short petioles, and loop-connected secondary veins, forming a submarginal vein. It differs in having gray or brown pubescence (rufous in *P. maximum*), much smaller flowers with dense gray pubescence (rufous in *P. maximum*), and more widely branched inflorescence (lateral branches ca. 2 cm long in *P. maximum*, to 20 cm long in *P. hexaglandulosum*). Schmidt (1933) noted a relationship between *P. maximum* and *P. williamsii* O. Schmidt. I have not seen material of the latter species; it differs from *P. hexaglandulosum*, according to its description, in the shorter inflorescences (to 12 cm long), shorter pedicels (4–6 mm long), and brown-tomentose flowers.

Pleurothyrium hexaglandulosum is the first record of *Pleurothyrium* in Panama. Its specific epithet refers to the six glands of the inner three stamens. In nearly all *Pleurothyrium* species these are fused and cannot be recognized individually, and for a long time it was assumed that in *Pleurothyrium* all nine stamens had two glands. In *Pleurothyrium hexaglandulosum* (and to a lesser degree in *P. maximum*), the glands remain separated and show clearly that in *Pleurothyrium* only the inner stamens have glands, as Rohwer & Kubitzki (1985) stated.

Croat & Grayum 59792 (F, MO), collected in Costa Rica, Puntarenas, along road between Rincón de Osa and Rancho Quemado, is provisionally placed here. It differs from the type collection in being less pubescent.

Ocotea erectifolia (Allen) van der Werff, comb. nov. BASIONYM: *Phoebe erectifolia* Allen, Mem. New York Bot. Garden 23: 860. 1972. TYPE: Venezuela. Bolívar: Meseta del Jaua, *Steyermark 97926* (holotype, NY!).

Ocotea budowskiana Bernardi, Candollea 30: 256. 1975. TYPE: Venezuela. Bolívar: Meseta de Jaua, *Steyermark 109330* (holotype, G!; isotype, F!).

Ocotea erectifolia is very distinct with coriaceous, few-veined, ascending leaves. It was first published as a *Phoebe* species. When Bernardi later recognized it as an undescribed *Ocotea* species, he overlooked the earlier description of *Phoebe erectifolia*. However, there is no doubt that the two species are the same, and hence the new combination in *Ocotea* is made.

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A REVISION OF *PANICUM* SUBGENUS *PHANOPYRUM* SECTION *STOLONIFERA* (POACEAE: PANICEAE)[1]

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Tatiana Sendulsky[3]

ABSTRACT

A revision of Panicum *subgenus* Phanopyrum *section* Stolonifera *is presented.* Panicum soderstromii *is described as new, and* P. andreanum, P. biglandulare, P. crateriferum, P. irregulare, P. chapadense, P. rude, P. piauiense, P. stoloniferum, P. latissimum, P. pulchellum, *and the controversial* P. venezuelae *are included in this section, which can be characterized by the inflorescences with unilateral racemose branches, the upper anthecium short stipitate at its base and glabrous and smooth, and the presence of non-Kranz leaf anatomy. The presence of one or two (rarely three) pairs of crateriform, ocellate glands is a singular feature of this section; these glands may be constantly present, present or absent in some specimens, or completely absent in others. Keys to all 13 species and SEM micrographs of the upper anthecium and glands on the lower lemma are provided. Each species is illustrated.*

Section *Stolonifera* is one of the most attractive and interesting sections of the genus *Panicum*. The name was given as an informal group by Hitchcock & Chase (1910), who included in it *P. stoloniferum* Poiret, *P. frondescens* G. Meyer, *P. pulchellum* Raddi, and *P. biglandulare* Scribner & Smith. These species were mainly distinguished in the view of Hitchcock & Chase as summarized in the following diagnosis:

> Decumbent or creeping perennials, rooting at the lower nodes, with branching culms; ligule short, membranous; leaf blades lanceolate or ovate-lanceolate; panicles of racemose, secund, spikelike, ascending branches, ± divergent from the axis, with spikelets in pairs along one side of the branches; upper glume and lower lemma exceeding the anthecium in length.

In 1940, Pilger gave the rank of section to species of the Stolonifera group. Hsu (1965), in his worldwide treatment of *Panicum*, characterized this section basically as having a papery ligule, panicles with spikelike racemes, upper glume and lower lemma longer than the upper anthecium, the latter smooth, lodicules very thin and weakly three-nerved. Hsu placed this section in his subgenus *Sarmentosum*, along with, among others, sections *Sarmentosa* Pilger, *Parviglumia* (A. Hitchc. & Chase) Pilger, and *Parvifolia* (A. Hitchc. & Chase) Pilger.

In the present work, *Stolonifera* is treated, according to the infrageneric classification of

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This paper is based on material examined from the following herbaria: B, BAA, CEPEC, COL, CTES, F, GH, HRB, LIL, MO, MSC, P, R, RB, SI, SP, UB, US, and VEN.

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Zuloaga (1987) within subg. *Phanopyrum* (Raf.) Pilger, being most closely related to sect. *Phanopyrum* and *Laxa*. Section *Phanopyrum* Raf. was raised to generic rank by Nash (1903), taking into consideration as diagnostic characters spikelet compression, habitat, length of the upper anthecium, and presence of a stipe in the base of the upper anthecium. This idea was accepted in recent years by various authors (Brown, 1977; Gould & Shaw, 1983; Lazarides & Webster, 1984). However, we believe that none of these characters are strong enough to maintain *Phanopyrum* apart from *Panicum*. As Hitchcock & Chase (1910) stated: "this species [*P. gymnocarpon*] departs somewhat from the usual characters of the genus *Panicum*, but the divergence does not seem sufficient to justify segregating the single species as the type of a separate genus."

Subgenus *Phanopyrum* includes non-Kranz species, these being anatomically distinguished by having two bundle sheaths around the vascular bundles, the inner mestome sheath with thick-walled cells surrounded by a parenchymatous sheath with thick-walled and completely empty cells (with these parenchymatous sheath cells bigger than the mesophyll cells). The number of mesophyll cells between the vascular bundles ranges from 5 to 12, with a distance of (150)230–270 (–380) μm. Exomorphologically, the spikelet is characterized by having a lower glume 1–3 (occasionally –5)-nerved and upper glume and lower lemma 5(occasionally –7)-nerved. The species are usually found in shady and humid places, with some exceptions in species of sect. *Lorea*, *Parvifolia*, and *Stolonifera*, some of which grow in open and more or less drier habitats.

Within this subgenus, sect. *Stolonifera* is defined by the following diagnostic features:

Inflorescence type. All species are characterized by having the spikelets congested on short, unequal pedicels along racemose, unilateral branches (occasionally with short tertiary branchlets in *P. latissimum* Mikan ex Trin., *P. rude* Nees, and *P. venezuelae* Hackel), with the branches usually alternate, remote, and diverging from the axis. This character is also present in sect. *Phanopyrum* and sect. *Laxa* (A. Hitchc. & Chase) Pilger. In the former, the spikelets are usually borne on tertiary branchlets appressed unilaterally along secondary branches. Within sect. *Laxa* there is a variation from short-pedicelled spikelets in unilateral racemose branches (as for example in *P. pilosum* Sw. and *P. leptachne* Doell) to spikelets disposed along either side of short tertiary branchlets (e.g., *P. boliviense* Hackel, *P. bresolinii* L. B. Smith & Wassh.). Sections *Parvifolia*, *Monticola* Stapf, and *Verrucosa* (A. Hitchc. & Chase) C. C. Hsu, included in subg. *Phanopyrum*, are characterized by open and lax panicles with long-pedicelled spikelets; in sect. *Lorea* Zuloaga some species have open and lax panicles, whereas others have spikelike inflorescences. In sect. *Megista* Pilger, all the branches of the panicle are whorled, with the spikelets short-pedicelled along the branches. In sect. *Parviglumia*, there is a gradation from species with spikelets arranged in open and diffuse panicles to others with short-pedicelled spikelets along racemose, not unilateral branches.

Surface and ornamentation of the upper anthecium. The epidermis of the upper anthecium is completely glabrous, indurate, smooth, and shiny, with scattered stomata toward the upper margins of the palea (Fig. 2c, d). A similar pattern is present within the subgenus in sect. *Phanopyrum* and sect. *Lorea* (in the latter it is possible to find occasional prickle hairs, stomata, and bicellular microhairs toward the apex of lemma and palea). On the other hand, sect. *Laxa* differs by having conspicuous prickle hairs toward the apex as well as simple papillae regularly distributed in longitudinal rows. Membranous anthecia are present in some species of this section.

Stipe presence, type of spikelet, and relative length of the upper anthecium. In all of the species of the section, the spikelets are biconvex with the upper anthecium shortly stipitate at the base; additionally, the anthecium is reduced in relation to the length of the upper glume and lower lemma (usually ½–¾ the length of the upper glume and lower lemma).

Sections of subg. *Phanopyrum* can be separated by the following key:

KEY TO THE SECTIONS OF SUBG. *PHANOPYRUM*

1a. Upper glume and lower lemma 7–9-nerved; panicles with all the branches whorled .... sect. *Megista*
1b. Upper glume and lower lemma 3–5(occasionally –7)-nerved; with the branches alternate to opposite, not whorled.
2a. Leaf branches stiff, pungent .... sect. *Lorea*
2b. Leaf blades not pungent, not stiff.
3a. Upper anthecium covered with long, cylindric hairs (occasionally glabrous, when glabrous lower palea absent, lower glume ⅕ the length of the spikelet) .... sect. *Parviglumia*
3b. Upper anthecium without long, cylindric hairs all over its surface (if glabrous lower palea present, and lower glume more than ⅕ the length of the spikelet).
4a. Panicles with racemose, unilateral branches, the spikelets disposed in pairs on short pedicels along one side of the branches, sometimes with the spikelets short-pedicelled in short tertiary branchlets on both sides of the branches; upper anthecium smooth, glabrous or with short prickle hairs at the summit.
5a. Upper anthecium glabrous, smooth and shiny, indurate, shortly stipitate, and shorter than the upper glume and lower lemma.
6a. Grasses aquatic, culms succulent; lower glume ⅘ the length of the spikelet; upper anthecium ⅓ the length of the spikelet. Southeastern United States .... sect. *Phanopyrum*
6b. Grasses inhabiting forests or edges of forests or in open habitats, culms not succulent; lower glume ⅓–¾ the length of the spikelet; upper anthecium ½–¾ the length of the spikelet. Mesoamerica to South America .... sect. *Stolonifera*
5b. Upper anthecium papillose, with simple papillae regularly distributed in longitudinal rows and prickle hairs toward the apex of lemma and palea, indurate to membranous, almost reaching the same length of the upper glume and lower lemma, not stipitate .... sect. *Laxa*
4b. Panicles lax and diffuse, the spikelets long- to short-pedicelled, not in unilateral, racemose branches; upper anthecium pilose, with bottlelike bicellular microhairs all over the surface, rugose to smooth.
7a. Upper anthecium smooth and shining .... sect. *Parvifolia*
7b. Upper anthecium rugose, with transverse or longitudinal and transverse wrinkles.
8a. Upper anthecium with transverse wrinkles. Lower glume ⅕ the length of the spikelet; upper glume and lower lemma verrucose. Eastern United States .... sect. *Verrucosa*
8b. Upper anthecium with longitudinal and transverse wrinkles. Lower glume ⅓–½ the length of the spikelet; upper glume and lower lemma not verrucose. Mesoamerica to Argentina .... sect. *Monticola*

A singular and isolated, although not constant, feature of species of sect. *Stolonifera* is the presence of one or two (rarely three) pairs of crateriform and ocellate glands on either side of the midnerve on the outer surface of the upper lemma. These glands are always present in *P. pulchellum*, *P. biglandulare* (Fig. 1a, b), *P. soderstromii* Zuloaga & Sendulsky (Fig. 1c–f), and *P. crateriferum* Sohns, while in *P. rude*, *P. piauiense* Swallen, *P. chapadense* Swallen, and *P. venezuelae* they are sporadic; they are completely absent in *P. stoloniferum*, *P. andreanum* Mez, *P. brachystachyum* Trin., *P. latissimum*, and *P. irregulare* Swallen. Occasionally, one pair of glands is present on the upper glume of spikelets of *P. venezuelae*; in this species the glands differ from those of the other species by being slightly depressed rather than crateriform (Fig. 2a, b). *Panicum venezuelae* has cleistogamous flowers in most of its spikelets, this character showing up elsewhere in *Panicum* only in subg. *Dichanthelium*. *Panicum irregulare* is the only species within the genus with the lower flower hermaphrodite.

The pubescence of the spikelet may vary from pilose to hispid (as in *P. chapadense*, *P. andreanum*), papillose-pilose (in *P. brachystachyum*), or entirely glabrous (in *P. irregulare* and *P. stoloniferum*).

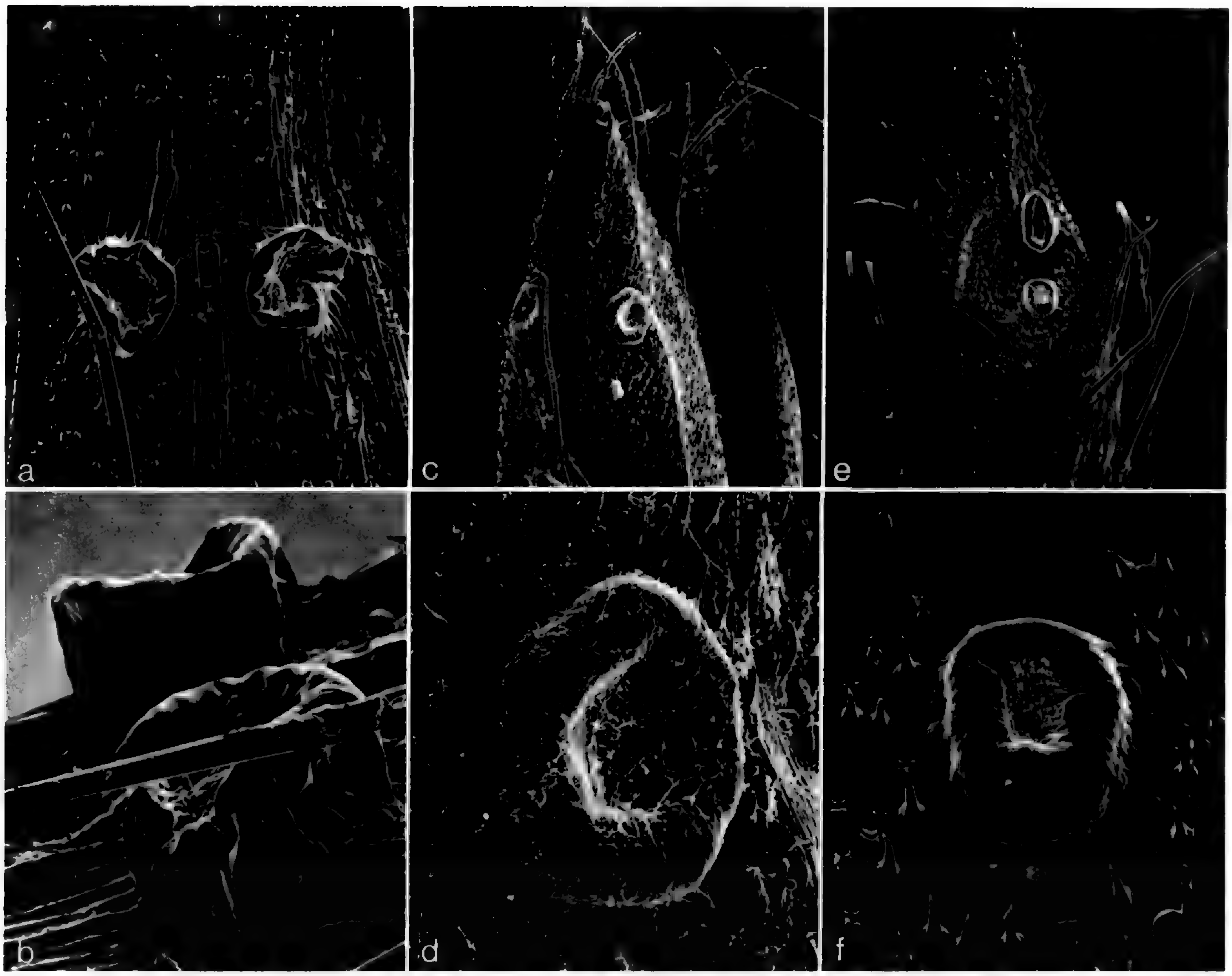

FIGURE 1. *Scanning electron micrographs of spikelets of* Panicum *species. a, b.* P. biglandulare.—*a. Lower lemma.*—*b. Detail of glands on lower lemma. c–f.* P. soderstromii.—*c. Spikelet, ventral view.*—*d. Detail of gland on lower lemma.*—*e. Spikelet with two pairs of glands, lateral view.*—*f. Detail of gland on lower lemma. a, b based on* Matuda 316 *(US); c–f based on* Pereira 2138 *(US). Magnifications: a, ×75; b, ×175; c, ×35; d, ×200; e, ×35; f, ×200.*

Swallen (1966) included eight species in the group Latissima of *Panicum,* but he did not delimit it or indicate its links with other species of *Panicum.* The species accepted as valid from the Latissima group (*P. rude, P. latissimum,* and *P. piauiense,* together with *P. chapadense* and *P. soderstromii*) are treated in the present work in sect. *Stolonifera,* since we regard the habit and size of the plants as insufficiently strong characters to keep them in a different section. It should be pointed out that further anatomical studies would be useful to establish the relationship between species of the Latissima group and the rest of species of sect. *Stolonifera.*

Species of sect. *Stolonifera* occur from Mexico to Argentina. Some are widely distributed while others are found only in restricted areas. To the former group belong *P. stoloniferum* and *P. pulchellum,* the first ranging from Mexico, the Lesser Antilles, and South America to Argentina; *P. pulchellum* ranges from Mexico to Brazil and Bolivia. Two species are confined to Mesoamerica; *P. biglandulare* in Mexico and Guatemala and *P. crateriferum* in Mexico. *Panicum irregulare* grows from Costa Rica to Colombia and *P. andreanum* in Colombia and Venezuela, while *P. venezuelae* is found from Mexico to Brazil. The other species are all endemic to Brazil: *P. brachystachyum* from Minas Gerais, *P. rude* from Espírito Santo to Rio Grande do Sul, *P. latissimum* from Espírito Santo and Rio de Janeiro, *P. chapadense* from Goiás,

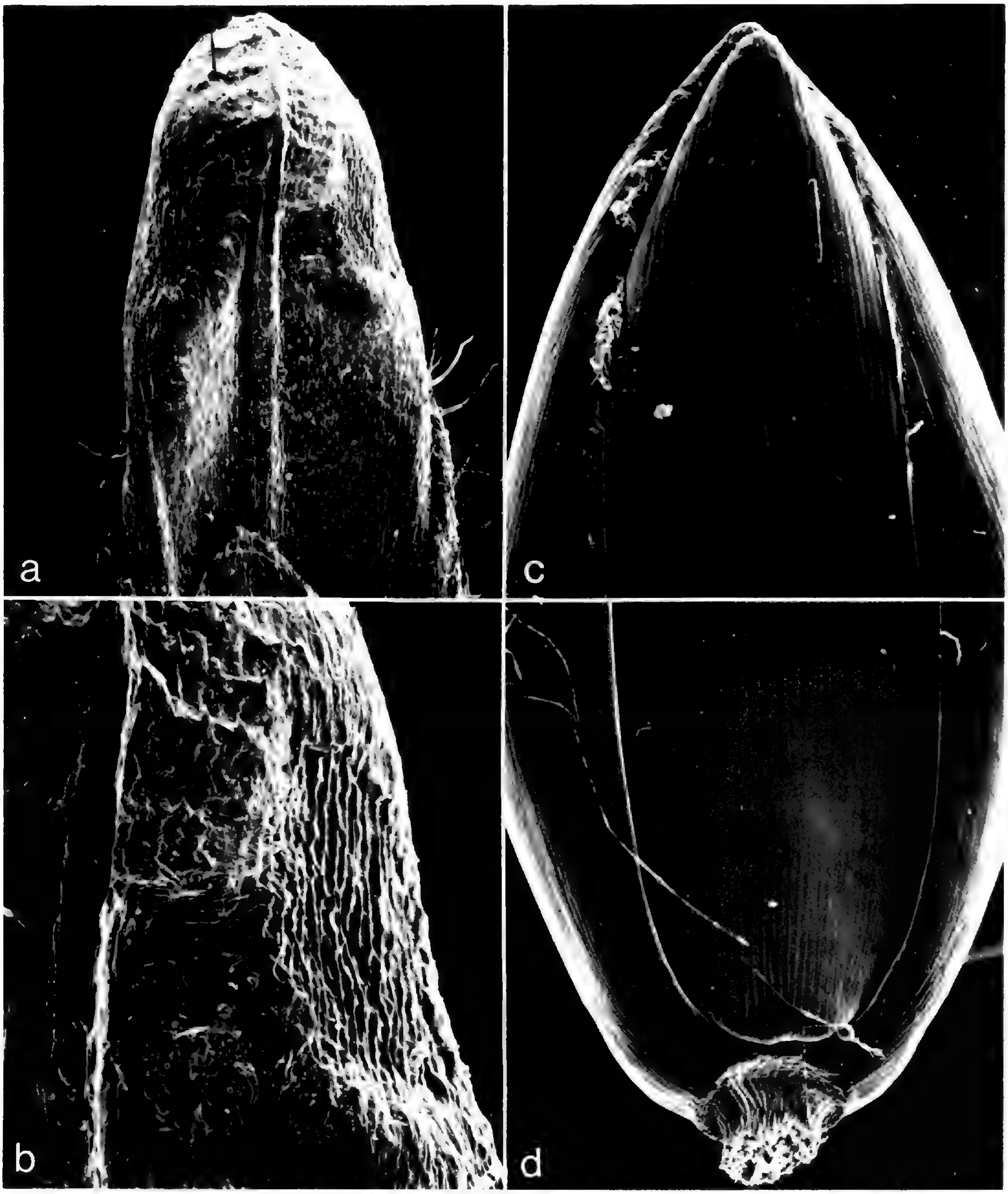

FIGURE 2. *Scanning electron micrographs of* Panicum *species. a, b.* P. venezuelae.—*a. Spikelet, ventral side.*—*b. Detail of gland on lower lemma. c, d.* P. pulchellum.—*c. Apex of the upper anthecium, ventral side.*—*d. Base of the upper anthecium showing stipe. a, b based on* Pinto 307 *(US); c, d based on* Hitchcock 20536 *(US). Magnifications: a, ×35; b, ×100; c, ×100; d, ×100.*

P. piauiense from Piauí and Bahia, and *P. soderstromii* from Bahia.

Classical taxonomic methods have been applied utilizing a Wild M5 dissecting microscope. Observations at higher magnification were made using the scanning electron microscope. Anthecia were removed from dried herbarium specimens, secured on stubs, carbon coated in a vacuum evaporator, coated with a gold-palladium alloy, and examined in a Cambridge S4-10 or Cambridge Stereoscan 250 Mk2 scanning electron microscope operating at 10–20 kV.

TAXONOMIC TREATMENT

Panicum section **Stolonifera** A. Hitchc. & Chase ex Pilger, in Engler, Nat. Pflanzenfam. ed. 2, 14e: 16. 1940. TYPE: *P. stoloniferum* Poiret.

Group Stolonifera A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 120. 1910 (nom. inval.); Contr. U.S. Natl. Herb. 17: 461, 500. 1915.

Perennial, plants small to robust, stoloniferous or decumbent, rooting and branching at the lower nodes to erect, leaning in the vegetation or not leaning; *culms* hollow, rarely solid, simple or branching. *Ligule* membranous-ciliate to membranous. *Leaf blades* ovate-lanceolate to long-lanceolate, flat, densely pilose to glabrous, shortly pseudopetiolate. *Panicles* pyramidal, sometimes oblong, composed of few to numerous, unilateral, racemose branches arranged along either side of the axis and bearing secund, paired, short-pedicellate spikelets. *Spikelets* ellipsoid to lanceolate, pilose to glabrous. *Lower glume* 3(rarely –5)-nerved, ¼–¾ the length of the spikelet, pilose toward the apex or glabrous. *Upper glume* and *lower lemma* subequal (or upper glume shorter than the lemma), acute to acuminate, 5(occasionally –7)-nerved; lower lemma with or without 1 or 2 (occasionally 3) pairs of crateriform, ocellate glands on the middle portion. *Lower palea* hyaline, glabrous; male flower present or absent (hermaphrodite flower present in *P. irregulare*). *Upper anthecium* ellipsoid to lanceolate, glabrous, smooth and shiny, indurate, shortly stipitate at the base; upper lemma with the margins inrolled over the palea. Lodicules 3-nerved. *Caryopsis* with punctiform or ovate hilum, the embryo less than half the length of the caryopsis.

An American section, including 13 species distributed from Mexico to Argentina, commonly found in forests or at the margins of forests, occasionally on "campos rupestres" (*P. brachystachyum*) and on "cerrados" (*P. chapadense, P. soderstromii, P. piauiense*). Collections come from 0–2,800 m elevation.

KEY TO THE SPECIES OF SECTION *STOLONIFERA*

1a. Lower flower hermaphrodite; caryopsis free from the lemma and palea, similar to the caryopsis in the upper anthecium .... 6. *P. irregulare*
1b. Lower flower male or neuter, not hermaphrodite.
2a. Spikelets 4.9–5.2 mm long .... 3. *P. brachystachyum*
2b. Spikelets 1.8–3.8(–4) mm long.
3a. Leaf blades amplexicaul, 7–12 cm wide .... 7. *P. latissimum*
3b. Leaf blades not amplexicaul, 0.3–5 cm wide.
4a. Spikelets mostly with cleistogamous flowers; anthers of these flowers 0.2–0.3 mm long; lower lemma gibbous with the upper margins inrolled; upper glume with or without glands .... 13. *P. venezuelae*
4b. Spikelets with chasmogamous flowers only; anthers 1–2 mm long; lower lemma not gibbous, the upper margins not inrolled; upper glume always without glands.
5a. Spikelets glabrous; lower lemma without glands .... 12. *P. stoloniferum*
5b. Spikelets pilose; lower lemma with or without glands.
6a. Lower glume ½–¾ the length of the spikelet; culms robust and erect; leaf blades lanceolate, 10–45 cm long; Brazil, from Bahia to Rio Grande do Sul.
7a. Lower glume with long, papillose-pilose hairs toward the apex; pedicels and branches with long hairs exceeding the length of the spikelet .... 11. *P. soderstromii*
7b. Lower glume shortly pilose to nearly glabrous, without long, papillose-pilose hairs toward the apex; pedicels and branches short-pilose to scabrous.
8a. Plants with long, creeping rootstocks, each erect culm with the lowest internodes orange and cormlike .... 4. *P. chapadense*
8b. Plants short-rhizomatous, without the lowest internodes orange and cormlike.
9a. Plants with thickened, fusiform roots; culms branched; panicles 7–22 cm long; Brazil, Bahia, Piauí .... 8. *P. piauiense*

9b. Plants with thin roots; culms simple or rarely branched; panicles 20–60 cm long; Brazil, Espírito Santo to Rio Grande do Sul .... 10. *P. rude*

6b. Lower glume ⅓–½ the length of the spikelet; culms extensively creeping and rooting at the lower nodes; leaf blades ovate-lanceolate to lanceolate, 2.5–10 cm long; Mesoamerica to Colombia and Venezuela (*P. pulchellum* in Brazil, species with leaves 2.5–5.5 cm long, spikelets 1.8–2.3 mm long).

  10a. Lower lemma without glands; spikelets length : width ratio 5–6 : 1. Leaf blades lanceolate .... 1. *P. andreanum*

  10b. Lower lemma with glands; spikelets length : width ratio 3–4 : 1. Leaf blades ovate-lanceolate to lanceolate.

    11a. Spikelets (3–)3.2–3.7(–4) mm long; nodes glabrous .... 2. *P. biglandulare*

    11b. Spikelets 1.8–3.1 mm long; nodes densely pubescent.

      12a. Spikelets 1.8–2.3 mm long; lower glume separated from the upper glume by a conspicuous internode; leaf blades length : width ratio 2.5 : 1 .... 9. *P. pulchellum*

      12b. Spikelets 2.5–3.1 mm long; internode inconspicuous between the lower and upper glume; leaf blades length : width ratio 6 : 1 .... 5. *P. crateriferum*

1. **Panicum andreanum** Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 5. 1921. TYPE: Venezuela. Trujillo: Escuque, *Moritz 1538* (lectotype, B, fragments at US (80458, 1108611)). Figure 3.

Slender, creeping perennials with the *culms* decumbent and rooting at the lower nodes, then becoming erect and climbing up to 2.5 m into the shrubs, freely and densely branching at the lower and upper nodes; internodes cylindric, hollow, glabrous to sparsely pilose, 1.5–8 cm long; nodes brown, glabrous to sparsely pilose. *Leaf sheaths* 2–7 cm long, commonly longer than the internodes at basal nodes or shorter at the upper ones, glabrous, striate and auriculate, the auricles small, densely pilose, one of the margins densely ciliate, the other glabrous. *Ligule* membranous-ciliate, 0.3–0.5 mm long; external ligule conspicuous, formed by a row of dense whitish hairs. *Leaf blades* lanceolate, 3–9 cm long, 0.3–0.6(–1.1) cm wide, flat, tapering into a finely attenuate apex, slightly narrowed to subcordate basally, hirsute, with long, thick papillose hairs to glabrous on both surfaces, the margins scabrous and cartilaginous, ciliate or glabrous basally; *pseudopetiole* glabrous, ca. 2 mm long. *Panicles* terminal, oblong, 6–16 cm long, 1–3 cm wide, with racemose primary branches alternate and divergent from the axis, the spikelets borne in pairs on short, unequal scabrous or pilose pedicels (the lower subsessile), these arranged along lower sides of branches; axis longitudinally ridged, smooth, scabrous, the axis of the branches triquetrous, scabrous, the axils of the branches pilose with dark hairs. *Spikelets* lanceolate, somewhat compressed laterally, 2.5–2.8 mm long, 0.4–0.6 mm wide, acuminate, greenish to stramineous, pilose, with the upper glume and lower lemma subequal (or the upper glume a little shorter than the lemma). *Lower glume* ovate, acute, 1.1–1.4 mm long, ⅓(–½) the length of the spikelet, 3-nerved, the midnerve scabrous toward the apex, shortly pilose on the inner surface, sparsely pilose on the outer surface, bearing a few long hairs at the base. *Upper glume* 2.2–2.4 mm long, 5(–7)-nerved, the midnerve scabrous toward the apex, with long hairs in the hyaline margins. *Lower lemma* glumiform, 2.4–2.6 mm long, 5-nerved, hispid toward the margins. *Lower palea* lanceolate, 1.8–2.1 mm long, 0.3–0.4 mm wide, hyaline, short-pubescent at the apex, otherwise glabrous, the margins scabrous; male flower present. *Upper anthecium* lanceolate, 1.7–1.8 mm long, 0.4 mm wide, stramineous. *Caryopsis* ovoid, 1.2 mm long, 0.3 mm wide; hilum oblong. In flower November to May.

Distribution. Venezuela and Colombia. In wet forests on sandy soils at 400–1,800 m elevation.

Additional specimens examined. COLOMBIA. CUNDINAMARCA: near Quetame, Río Negro valley, between Quetame and Piperal, *Killip 34220* (COL, US); entre Quetame y Sasumuco, *Triana 263* (US); Quetame, *Triana*

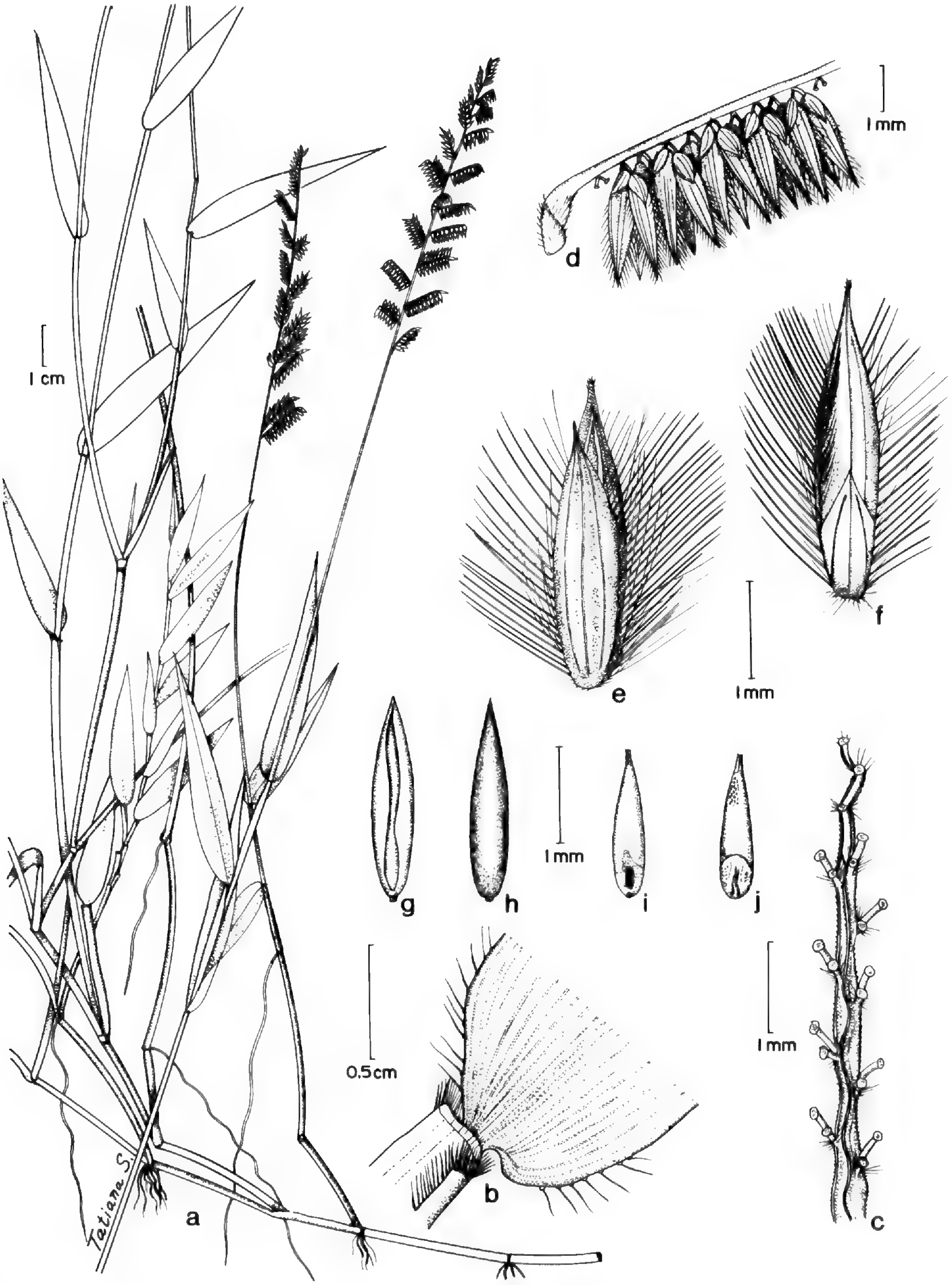

FIGURE 3. Panicum andreanum.—*a. Habit.—b. Ligule.—c. Branch of a panicle showing pedicels.—d. Racemose branch.—e. Spikelet, dorsal view.—f. Spikelet, ventral view.—g. Upper anthecium, ventral view.—h. Upper anthecium, dorsal view.—i. Caryopsis, hilum side.—j. Caryopsis, embryo side. Based on* Muller s.n. *(US-1762338)*.

13 (COL). META: Cordillera de La Macarena, mesa del Río Sansa, *Idrobo & Schultes 1291* (US); Las Lagartijas, plateau between Río Papamene and Río Duda, Colombia–Uribe trail, 11 km SW of Uribe, *Fosberg 19508* (US); carretera a Villavicencio, entre Puente Quetame y Buena Vista, *García Barriga et al. 18936* (COL); 14 km NW of Villavicencio along the road to Bogotá, *Davidse & Llanos 5516* (COL); Villavicencio, *André 871* (paratype, B). NORTE DE SANTANDER: región del Sarare, hoya del Río Marguá entre Junín y Córdoba, *Cuatrecasas 13373* (COL,

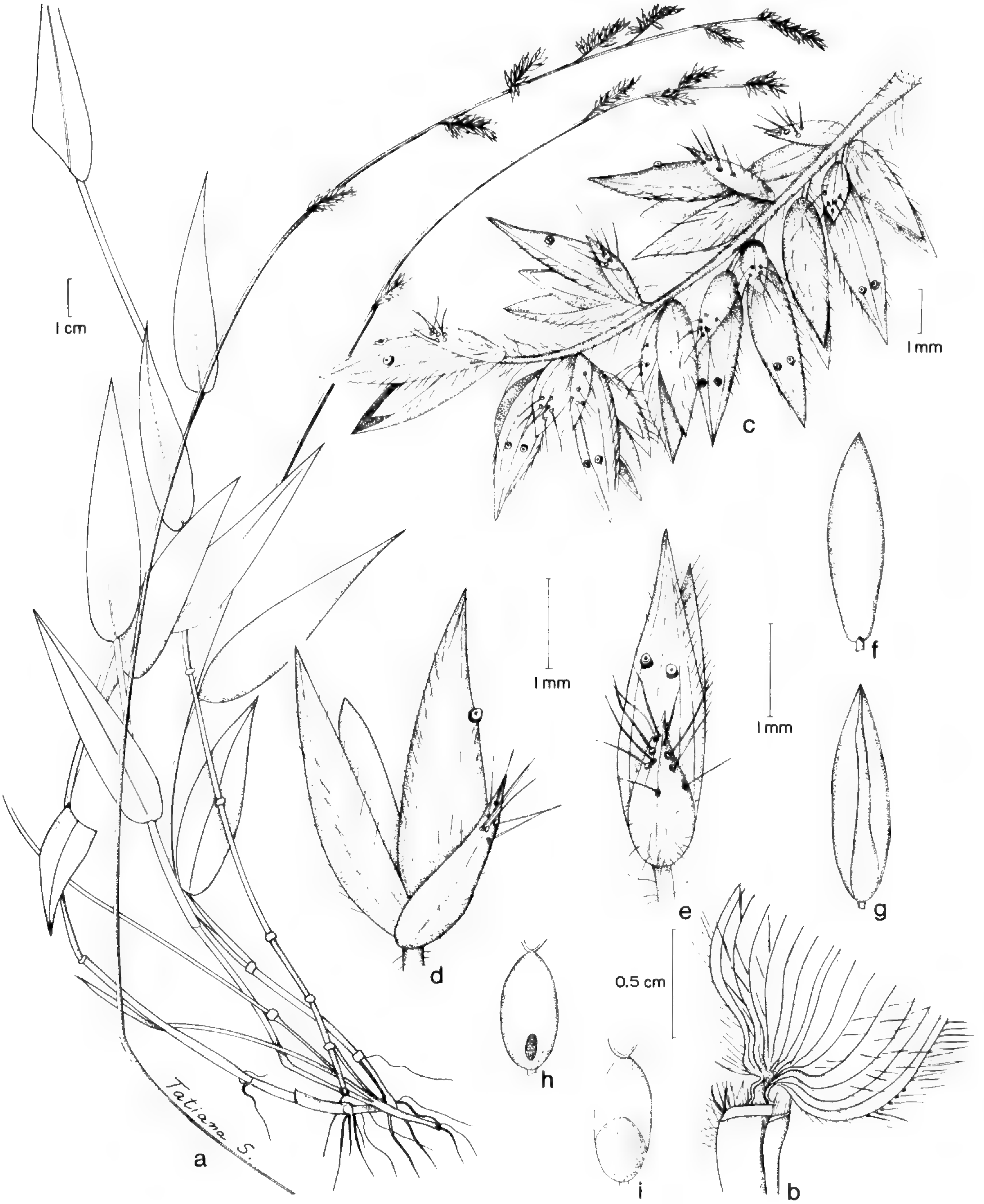

FIGURE 4. Panicum biglandulare.—*a. Habit.—b. Ligule.—c. Racemose branch.—d. Spikelet, lateral view.—e. Spikelet, ventral view.—f. Upper anthecium, dorsal view.—g. Upper anthecium, ventral view.—h. Caryopsis, hilum side.—i. Caryopsis, embryo side. a, b based on* Matuda 316 *(US); c–i based on* Matuda 2006 *(US).*

US). Without department and locality, *Karsten s.n.* (paratype, US). VENEZUELA. MÉRIDA: between Mucuchachi and Canagua, *Steyermark 56345* (US). TÁCHIRA: Cordero, *Muller s.n.*, 14 Nov. 1939 (US-1762338); Cerro Las Minas, 18 km SE of Santa Ana, *Steyermark et al. 120043* (US); Cerro La Camirí, just south of the town of Río Negro, *Davidse & González 21555* (US); 2 km E of El Variante, *Davidse & González 21523* (US).

When describing this species, Mez cited three syntypes for it, of which the specimen

Moritz 1538 is selected here as lectotype of *P. andreanum*, taking into consideration its protologue.

2. **Panicum biglandulare** Scribner & Smith, U.S.D.A. Bull. (1895–1901) 4: 13, pl. 4. 1897. TYPE: Mexico. Chiapas: near Pinabete, 8 Feb. 1896, at an altitude of 6,500 to 8,000 feet, *Nelson 3781* (holotype, US; isotype, GH). Figure 4.

Perennials 40–80(–100) cm tall. *Culms* decumbent and rooting at the lower nodes or ascending, branching, with many nodes; internodes cylindric, hollow, sparsely pilose to glabrous, with thin, whitish hairs; nodes greenish to purplish, constricted, glabrous. *Leaf sheaths* 2–4 cm long, usually shorter than the internodes, striate, densely ciliate at the margins, otherwise glabrous. *Ligule* membranous, shortly ciliate or glabrous at the apex, 0.3–0.5 mm long, external ligule a conspicuous ring of white hairs or absent; collar shortly pilose. *Leaf blades* ovate-lanceolate to lanceolate, 3–10.5 cm long, 1.1–1.9 cm wide, acuminate, with strigose to papillose hairs on both surfaces to glabrous, asymmetrical and subcordate basally, the margins ciliate to scabrous, the lateral nerves anastomosing; *pseudopetiole* short, glabrous to short-pilose. *Panicles* exserted, oblong, 8–18 cm long, 1–4 cm wide, with 5–10 short, sparse, alternate, and racemose branches, these slightly divergent from the axis, the spikelets borne in pairs (the lower one occasionally abortive) on the branches, the axis of the branches triquetrous (rather flat), hirsute, more so toward the base; the axils of the branches densely pilose; pedicels short, hispid. *Spikelets* lanceolate, acuminate, hispid, (3–)3.2–3.7(–4) mm long, 1–1.1 mm wide, greenish to purplish. *Lower glume* ovate, acute, 1.3–1.8 mm long, ⅓ the length of the spikelet, hirsute on the outer surface, sparsely and shortly pilose basally, with long, papillose-pilose hairs toward the apex, 3-nerved, the midnerve finely scabrous at the upper part. *Upper glume* shorter than the lower lemma, sometimes leaving the summit of the anthecium exposed, acute, 5(–7)-nerved, glabrous on the inner surface, with stiff, papillose hairs on the outer surface, these becoming more abundant toward the hyaline margins. *Lower lemma* acute, 5(–7)-nerved, scabrous, with long, papillose hairs toward the hyaline margins; 2 conspicuous crateriform glands present between the midnerve and the 2 immediate lateral nerves. *Lower palea* lanceolate, acute, 3–3.2 mm long, 0.8 mm wide, membranous, scabrous at the margins, otherwise glabrous; male flower present, anthers ca. 1.3 mm long. *Upper anthecium* lanceolate, acute, 2–2.5 mm long, 0.7–0.8 mm wide, stramineous. *Caryopsis* ellipsoid, 1.4 mm long, 0.6 mm wide, brown; hilum oblong. In flower November to August.

Distribution. Occurring in Mexico and Guatemala in forests between 1,300 and 2,800 m elevation.

Additional specimens examined. GUATEMALA. ALTA VERAPÁZ: Cobán, *von Tuerckheim II 1342* (GH, NY, US), *II 1956* (NY, US); hills between Cobán and Tres Cruces, *Standley 90263* (F, US). SAN MARCOS; near Aldea Fraternidad, between San Rafael Pié de la Cuesta and Palo Gordo, west-facing slope of the Sierra Madre mountains, *Williams et al. 26050* (F, NY, US); barrancas 6 mi. S and W of town of Tajumulco, northwestern slopes of Volcán Tajumulco, *Steyermark 36678* (F, US). MEXICO. CHIAPAS: 2 mi. NE of Pueblo Nuevo Solist, *Lathrop 5820* (US); Laguna Montebello, Montebello National Park, *Breedlove & Dressler 29530* (F, NY); SE of Cerro Baúl on the border with the state of Oaxaca, 16 km NW of Rizo de Oro along a logging road to Colonia Gigaroa, *Breedlove & Smith 21699* (NY); 5 km SE of Jitotol along road to Bochil, *Breedlove 23323* (NY); Montebello, *Carlson 2330* (US), *2332* (MO); Montecristo, *Matuda 2006* (F, GH, NY, US); Mt. Pasitar, *Matuda 316* (RB, US); in the paraje of Kulak'tik, *Ton 1713* (F); 25 mi. E of La Trinitaria, Lago of Monte Bello, *Breedlove 9680* (US); Clínica Yerba Buena, 2 km NW of Pueblo Nuevo Solistahuacán, *Raven & Breedlove 19846* (US); Sierra Madre, *Tateoka 1009* (US).

3. **Panicum brachystachyum** Trin., Gram. Pan. 138. 1826. TYPE: Brazil. Minas Gerais: Serra do Cipó, Jan. 1825, *Langsdorff s.n.* (holotype, LE, not seen, fragment at US; isotype, P). Figure 5.

Perennials ca. 18–35 cm tall. *Culms* erect, branching at the base; internodes cylindric, hollow, sparsely pilose; nodes stramineous,

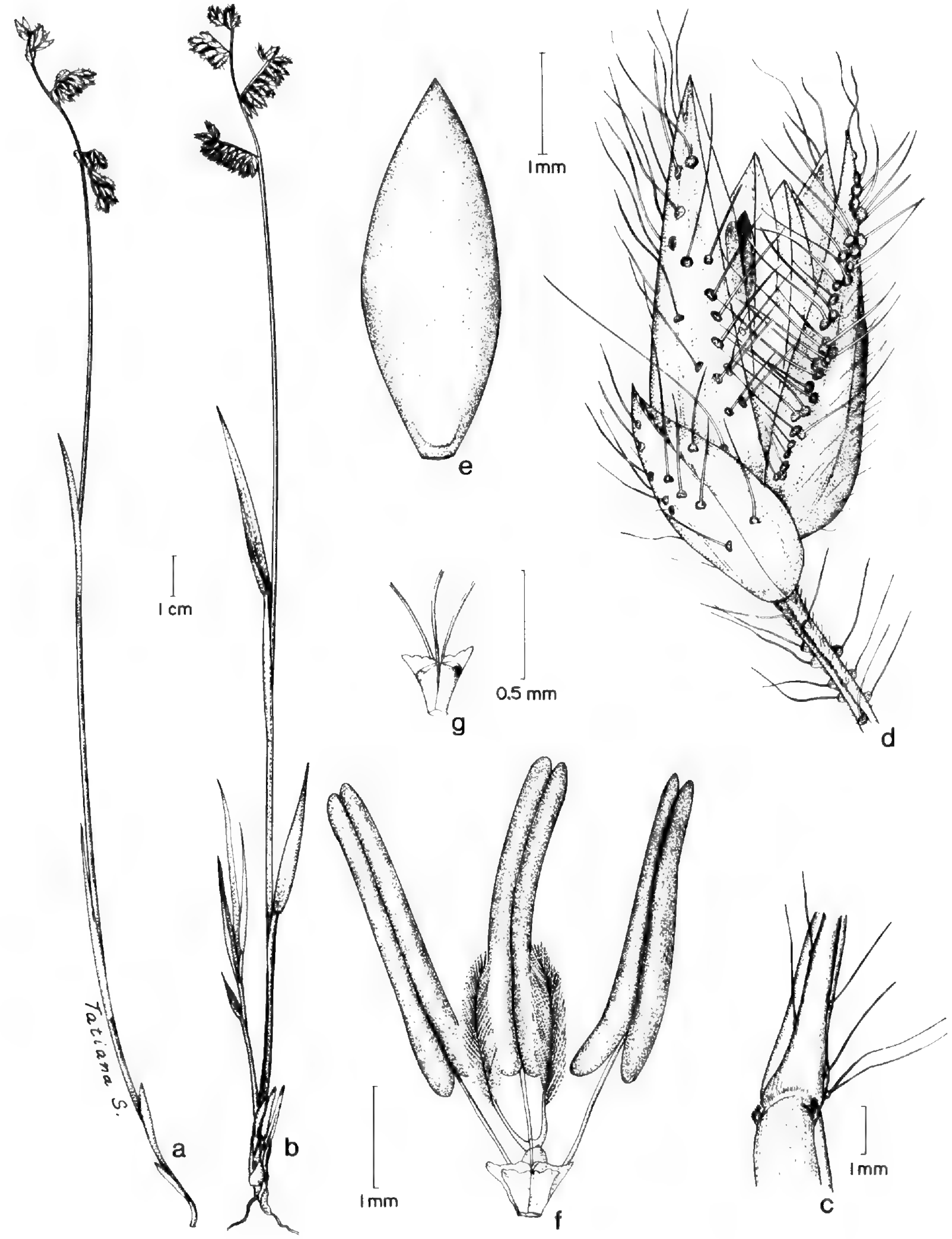

FIGURE 5. Panicum brachystachyum.—*a, b. Habit.—c. Ligule.—d. Spikelet, lateral view.—e. Upper anthecium, dorsal view.—f. Flower.—g. Lodicules. a, c–g based on* Langsdorff s.n. *(US); b based on plate of Trinius (1829).*

glabrous to short-pilose. *Leaf sheaths* stramineous, striate, sparsely pilose, with small auricles, densely pilose, the margins short-ciliate. *Ligule* membranous-ciliate, arcuate, 0.3–0.4 mm long. *Leaf blades* lanceolate, 3–4.5 cm long, 0.2–0.3 cm wide, acuminate, flat or subinvolute, glabrous, subcordate to narrowed basally, the margins scabrous and with sparse, papillose hairs; the midnerve inconspicuous. *Panicles* exserted, formed of 2–4 alternate, densely flowered, distant and spreading racemose branches 1–4 cm long;

peduncle hispid; axis flattened, scabrous and long-hispid, the axils of the branches densely papillose; axis of the branches hispid to scabrous, the pedicels arranged in pairs on one side of the branch, the pedicels triquetrous, hispid and with long papillose-pilose hairs. *Spikelets* broadly ellipsoid, 4.9–5.2 mm long, ca. 3.5 mm wide, grayish, gaping; glumes and lower lemma with long papillose-pilose hairs, the upper glume and lower lemma subequal, acute to acuminate, exceeding the upper anthecium in length. *Lower glume* ovate, acuminate, 2.8–3 mm long, ⅓–½ the length of the spikelet, covered with thick, papillose hairs, 1–3(–5)-nerved, the midnerve scabrous. *Upper glume* broadly ovate, 5-nerved, with thick papillose hairs near the margins, the rest of the surface with fine whitish hairs. *Lower lemma* glumiform, 3–5-nerved, with sparse, irregularly scattered, papillose hairs, these more dense toward the apex, the margins hyaline. *Lower palea* lanceolate, 3.9–4.5 mm long, 1.2 mm wide, membranous, the margins shortly ciliate; male flower present, the anthers dark purple, 3.2 mm long. *Upper anthecium* lanceolate, 4–4.4 mm long, 1.2 mm wide, membranous, acute to acuminate, whitish to stramineous; lemma slightly carinate, 3–5-nerved; anthers ca. 3.3 mm long, lodicules ca. 0.5 mm long, cuneate, with raised distal margins; ovary ovoid; anthers dark purple. *Caryopsis* not seen.

This species has been collected only once, in 1825, by *Langsdorff* "in saxosis montis alti da Lapa," now the Serra do Cipó, Minas Gerais, Brazil. The collection presumably consisted of a single individual, which was divided in three parts. One part is the holotype in LE, from which the plate in Trinius (1829) was probably drawn. The second part is the P isotype. The third part is a fragment of the type (taken from the LE specimen) in US and consists of a single branch without base. The plant from the Trinius plate and the US specimen are illustrated in the present paper to give a more complete view of this rare and probably extinct grass. Many collecting trips have been made to the Serra of Cipó by T. Sendulsky and by other botanists, but this species has never been collected again.

4. **Panicum chapadense** Swallen, Contrib. Science 22: 8, fig. 4. 1958. TYPE: Brazil. Goiás: collected on sandstone outcrop, 7 km south of Veadeiros, region of the Chapada dos Veadeiros, 24 Apr. 1956, *Dawson 14602* (holotype, R; isotype, US). Figure 6.

P. pirineosense Swallen, Phytologia 14: 78. 1966. TYPE: Brazil. Goiás: collected between rocks, at Pirineus, 18 Oct. 1956, *Macedo 4805* (holotype, US; isotypes, BAA, SP, US).

Rather robust perennials with long, creeping, horizontal rootstocks, the *culms* erect, 50–140 cm tall, with a cormlike base, 2 or 3 basal internodes orange-colored, 1–4 cm diam., glabrous, shining, lightly covered with aphyllous, velutinous old scales; new innovations appearing between those thickened internodes and covered by small, hard, yellow, pilose scales; upper internodes cylindric, solid, shortly pilose or glabrous, striate; nodes dark, constricted and shortly pilose, the first node swollen, yellow, glabrous, shining. *Leaf sheaths* stramineous, 5–11 cm long, longer (basal) or shorter than the internodes, densely villous to papillose-pilose all over the surface or pilose toward the apex only; the upper margins ciliate, the lower ones membranous; auricles small, rounded, sometimes densely pilose. *Ligule* membranous, ciliate, ca. 0.5 mm long, with or without long hairs behind the membrane at the base of the blade; external ligule present or absent. *Leaf blades* lanceolate, 12–23 cm long, 1.3–2.5 cm wide, with ciliate to scabrous margins, subcordate basally and velutinous to glabrous on both surfaces, the midnerve not prominent; *pseudopetiole* small. *Panicles* terminal, lax, oblong to pyramidal, with many flowers, 13–26 cm long, 2–6 cm wide, the primary branches racemose, dense and alternate, appressed or slightly divergent from the axis (the lower branches shortly branching at the very base), the spikelets secund and arranged in pairs on

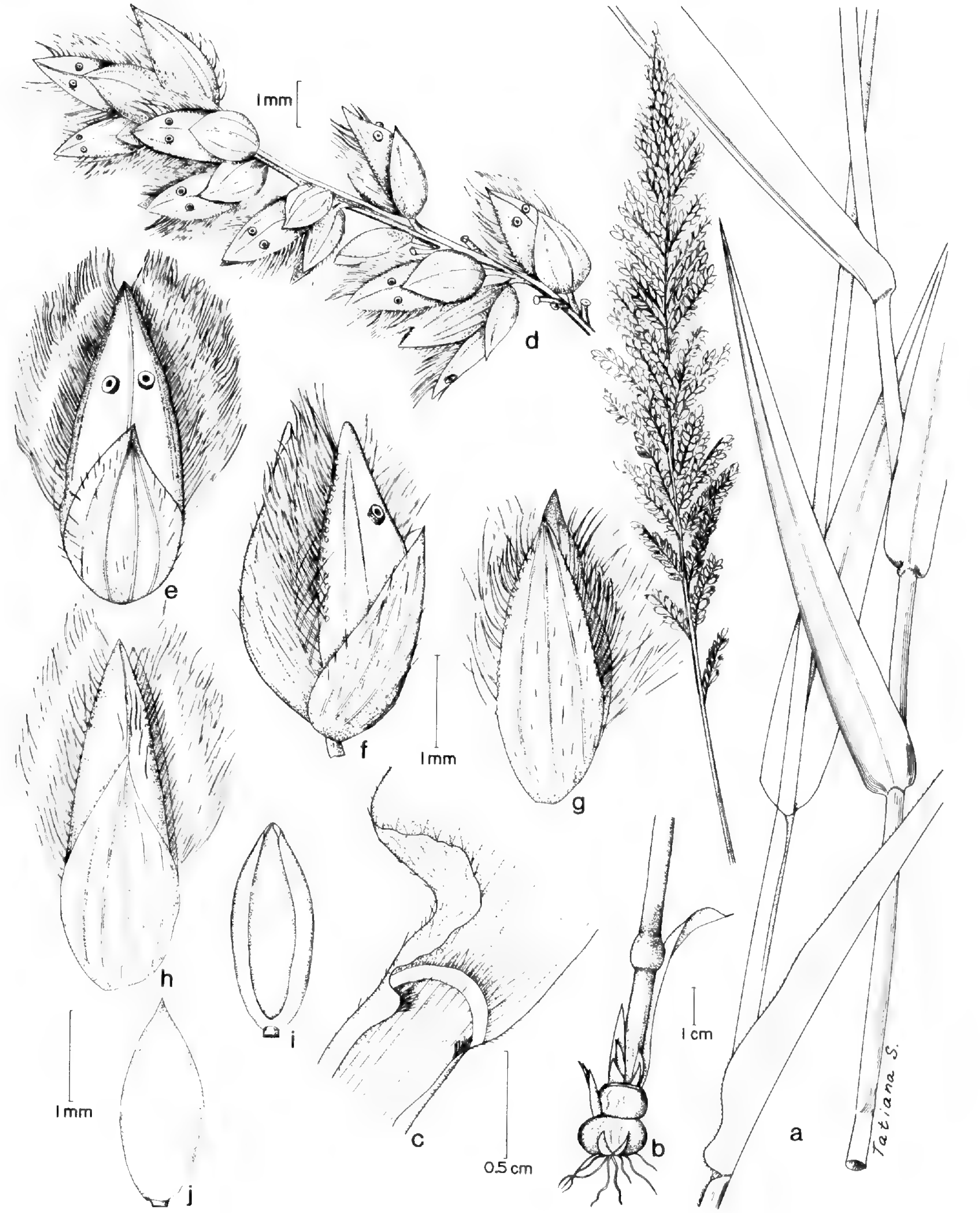

FIGURE 6. Panicum chapadense.—*a. Leafy stems.—b. Culm showing cormlike base.—c. Ligule.—d. Portion of a racemose branch.—e. Spikelet, ventral view, lower lemma with glands.—f. Spikelet, lateral view.—g. Spikelet, dorsal view.—h. Spikelet, ventral view, lower lemma without glands.—i. Upper anthecium, ventral view.—j. Upper anthecium, dorsal view. Based on* Burman & Filgueiras 450 *(SP)*.

short, unequal pedicels, on the lower side of the branches; axis longitudinally ridged, nearly glabrous or finely hispid, the axis of the branches triquetrous, hispid to scabrous, the axils of the branches densely pilose, brownish, sometimes with 1 or 2 long hairs; pedicels hispid and slightly pubescent. *Spikelets* narrowly ellipsoid, 2.5–3(–3.3) mm long, 0.6–

0.8 mm wide, stramineous, with purplish traces, the upper glume and lower lemma subequal and exceeding the upper anthecium in length. *Lower glume* ovate, acute, 1.6–1.9 mm long, ½–¾ as long as the spikelet, 3(–5)-nerved, shortly pubescent on both surfaces (more so on the upper surface). *Upper glume* acute, 2.2–2.8 mm long, 5-nerved, the midnerve scabrous, densely hispid on the outer surface, with long, papillose, whitish and fringed hairs toward the margins, the inner surface pilose toward the apex. *Lower lemma* glumiform, 2.2–2.8 mm long, 5-nerved, with a pubescence similar to that of the upper glume, with or without 2–4 crateriform glands on the middle portion. *Lower palea* lanceolate, 1.8–2.2 mm long, 0.5–0.7 mm wide, stramineous, shortly pubescent, the margins ciliate; male flower present. *Upper anthecium* narrowly ovoid, 1.5–1.9 mm long, 0.5–0.7 mm wide, acute, stramineous. *Caryopsis* not seen. In flower March to October.

Distribution. Endemic to Goiás, Brazil. Occurring in "campos rupestres" and "cerrados" between stones in rocky habitats at 1,000–1,600 m elevation.

Additional specimens examined. BRAZIL. GOIÁS: 5–15 km S of Veadeiros, road to São João d'Aliança, *Prance & Silva 58824* (MO, NY, US); 22 km N of Alto do Paraíso, *Irwin et al. 32492* (F, NY); 20 km by road N of Alto Paraíso, *Anderson 6760* (NY, UB, US); ca. 15 km S of Goiás Velho, *Anderson 9976* (UB); ca. 15 km N of Corumbá do Goiás, *Anderson 10305* (UB); serra do Pirineus, *Burman & Filgueiras 410, 450* (SP); 12 km NW of Veadeiros, road to Cavalcante, *Irwin et al. 9419* (US); ca. 15 km S of Veadeiros, *Irwin et al. 12782* (MO, NY); Corumbá, Montes Pirineus, *Onishi et al. 98* (R). Without locality, *Macedo 4380* (US).

A remarkable feature of this species is the presence of cormlike structures at the base of each culm, a character occasionally present in other species of *Panicum*, for example, *P. bulbosum* Kunth and *P. paucifolium* Swallen.

When describing *P. chapadense*, Swallen included it in sect. *Laxa*. This species has no affinity with sect. *Laxa*, being distinct by the type of spikelet, presence of glands on the lower lemma, and smooth and glabrous upper anthecium.

5. **Panicum crateriferum** Sohns, J. Wash. Acad. Sci. 46: 378, figs. 10–22. 1956. TYPE: Mexico. Guerrero: on steep grassy slopes and narrow ravine with open pine woods and scattered oaks on granitic soil at km 339–340 between Acahuizotla and Agua de Obispo, on highway to Acapulco, ca. 3,000 ft., 1 Oct. 1949, *Moore Jr. 5148* (holotype, US; isotype, GH). Figure 7.

Perennials, the *culms* decumbent, creeping and rooting at the lower nodes, becoming erect, 20–60 cm tall, branching; internodes hollow, 2.5–6 cm long, glabrous to sparsely pilose with whitish long hairs; nodes dark, densely pilose with whitish hairs. *Leaf sheaths* 0.8–2.5 cm long, shorter than the internodes, glabrous to hispid, more densely so toward the upper portion, the margins long-ciliate toward the apex, otherwise glabrous; collar a nitid, wide rim of dense, whitish, antrorse hairs. *Ligule* membranous-ciliate, ca. 0.4 mm long. *Leaf blades* ovate-lanceolate to lanceolate, flat, 4–6 cm long, 0.6–1.3 cm wide, asymmetrical basally, with the adaxial surface sparsely papillose-strigose, the abaxial surface glabrous to sparsely papillose-strigose, the margins ciliate basally, otherwise glabrous; midnerve inconspicuous, the lateral nerves anastomosing; *pseudopetiole* small, pilose. *Panicles* lax, 5–10 cm long, 1.5–6 cm wide, with 4–6 racemose and alternate branches, distant and divergent from the rachis, the uppermost branch consisting of a long pedicel and a single spikelet only; the spikelets borne in pairs, one subsessile (occasionally abortive), the other shortly pedicellate, arranged along the lower side of the branches; axis longitudinally ridged, glabrous, the axis of the branches triquetrous (one side flattened), scabrous, with or without scarce, long, papillose hairs, the axils of the branches densely pilose with stiff and papillose hairs; pedicels short, scabrous. *Spikelets* narrowly ovoid to lanceolate, 2.5–3.1 mm long, 0.8–1.1 mm wide, sparsely to densely papillose-pilose or hirsute, the glumes and lower lemma subequal or the upper glume a little shorter than the lemma,

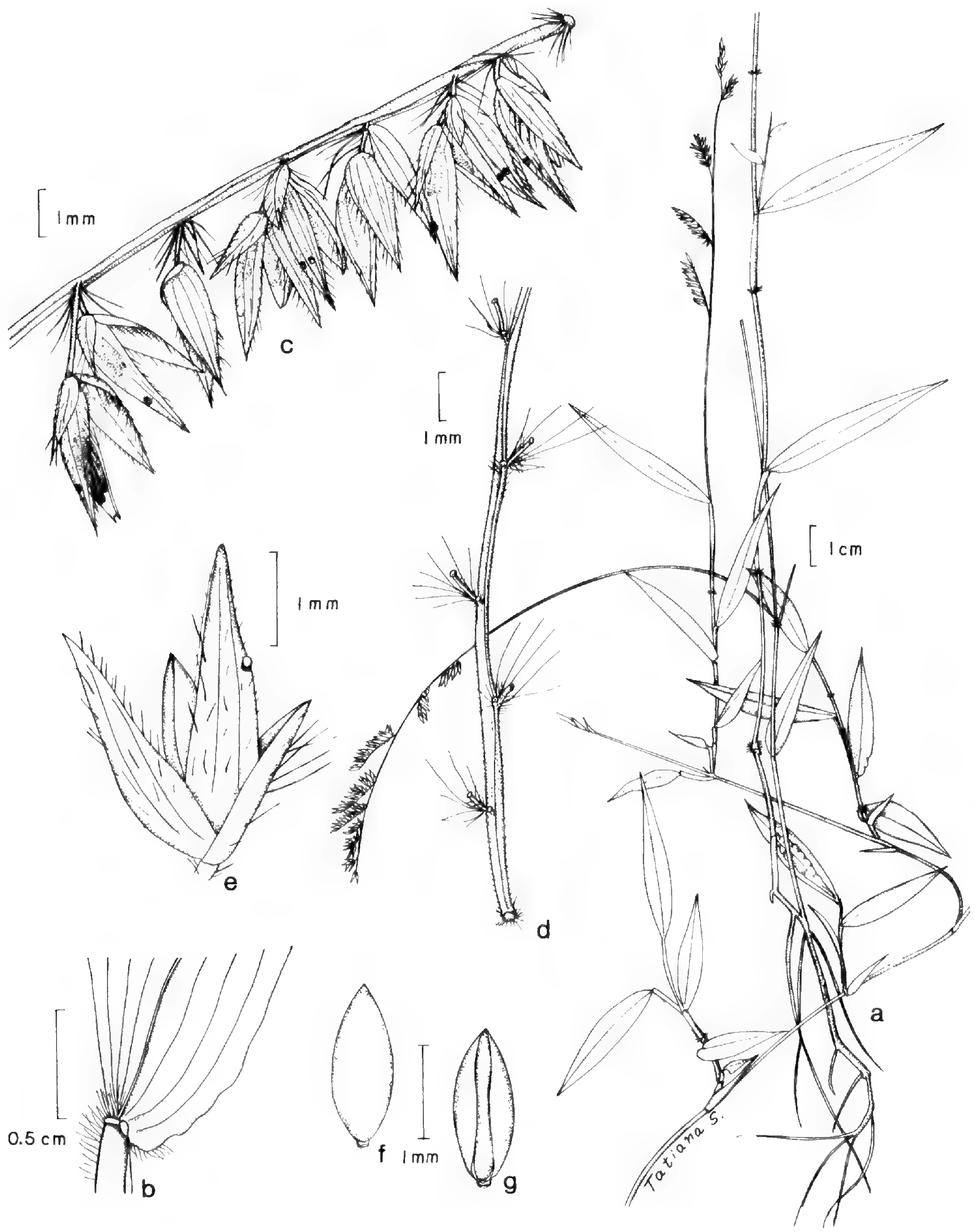

FIGURE 7. Panicum crateriferum.—*a. Habit.—b. Ligule.—c. Portion of a racemose branch.—d. Portion of a branch showing pedicels.—e. Spikelet, lateral view.—f. Upper anthecium, dorsal view.—g. Upper anthecium, ventral view. Based on* Hinton et al. 10801 *(US)*.

acute, the margins hyaline. *Lower glume* ovate-lanceolate, 1.3–2 mm long, ⅓–½ the length of the spikelet, acuminate, with long papillose-pilose hairs toward the apex and margins, the rest of the surface shortly pilose, 3(–5)-nerved, the midnerve scabrous. *Upper glume* 2.1–2.8 mm long, 5(–7)-nerved, papillose-hirsute toward the apex. *Lower lemma* 2.4–3 mm long, glumiform, 5(–7)-nerved, sparsely pilose, long-pilose or glabrous toward the margins, with 2 crateriform glands toward the upper part. *Lower palea* lanceolate, 2.2–

2.6 mm long, 0.5–0.6 mm wide, hyaline, ciliate at the margins, scabrous at the apex; male flower present. *Upper anthecium* ellipsoid, 1.5–2 mm long, 0.5–0.6 mm wide, stramineous. *Caryopsis* not seen. In flower October to November.

Distribution. Endemic to Guerrero and Oaxaca, Mexico; up to 1,000 m elevation.

Additional specimens examined. MEXICO. GUERRERO: Carrizo–Santo Domingo, *Hinton et al. 14725* (paratype, US); Plan del Carrizo, *Hinton et al. 14646* (paratype, US); Montes de Oca, *Hinton et al. 10801* (paratype, US). OAXACA: region of Chinantla, Santa María de Lovaoi, San Juan de Petlapa, *Vera Santos 3437* (US); La Soledad, *Ernst 2593* (US).

A few three-flowered spikelets were found on the collection *Hinton et al. 10801*; here the spikelets had two lower flowers, one neuter and the other with stamens, and one hermaphrodite flower in the upper anthecium. These spikelets have two lemmas, both with crateriform glands, one neuter (the lower without a palea) and the other, in an intermediate position, with its corresponding palea and male flower.

This characteristic three-flowered spikelet has been found previously and consistently in *P. quadriglume* (Doell) A. Hitchc.

6. **Panicum irregulare** Swallen, J. Wash. Acad. Sci. 30: 216. 1940. TYPE: Costa Rica. San José: vicinity of El General, 760 m, Feb. 1939, *Skutch 4115* (holotype, US; isotypes, GH, MO, NY). Figure 8.

Probably perennials. *Culms* decumbent, rooting and branching at the lower nodes, becoming erect, 60–80 cm tall; internodes cylindric, 4.3–11 cm long, glabrous, hollow; nodes glabrous. *Leaf sheaths* 3.2–4.8 cm long, shorter than the internodes, auriculate, the auricles pilose, the margins glabrous, membranous. *Ligule* membranous-ciliate, 0.3–0.5 mm long, with long hairs toward the base of the blade; adaxial surface of the collar shortly and densely pilose. *Leaf blades* ovate-lanceolate, 7–13 cm long, 1.5–3.3 cm wide, narrowed and somewhat asymmetrical basally, finely scabrid and with strigose hairs to nearly glabrous on the adaxial surface, the abaxial surface finely scabrid to nearly glabrous, the midnerve conspicuous, the lateral nerves anastomosing; *pseudopetiole* pilose, stramineous, ca. 1 mm long. *Panicles* terminal, oblong, exserted, 14–28 cm long, 3–7 cm wide, with 15–30 racemose branches ± divergent from the axis, alternate, and distant, usually drooping, the spikelets borne in pairs, one subsessile (occasionally abortive), the other shortly pedicellate arranged along one side of the branch; axis cylindric, finely scabrid, the axis of the branches somewhat flattened, scabrous, sparsely hirsute, the axils of the branches pilose; pedicels triquetrous, scabrous, pilose toward the base. *Spikelets* long-ellipsoid, biconvex, 1.8–2.3 mm long, 0.7–1 mm wide, greenish, scabrous to short pilose, the upper glume and lower lemma subequal (or the upper glume occasionally shorter), both with long hairs toward the margins to glabrous. *Lower glume* ovate, acute, 0.7–1.1 mm long, ¼–½ the length of the spikelet, 3-nerved, the midnerve scabrous. *Upper glume* 5-nerved, acute, pilose to finely scabrid toward the apex. *Lower lemma* glumiform, 5-nerved, acute, scabrous toward the apex. *Lower palea* elliptic, 1.4–1.5 mm long, 0.5 mm wide, hyaline, membranous, scabrous on the wings. *Lower flower* hermaphrodite; anthers ca. 1 mm long; stigmas 2, plumose. *Caryopsis* of the lower anthecium a little smaller than that present in the upper anthecium, 0.8–0.9 mm long, 0.4–0.5 mm wide, free from its lemma and palea. *Upper anthecium* ovoid, 1.3–1.5 mm long, 0.5–0.6 mm wide, stramineous, brown at maturity. *Caryopsis* ovoid, 0.8–1.2 mm long, 0.4–0.6 mm wide, the hilum punctiform to oblong. In flower November to April.

Distribution. Costa Rica to Colombia and Venezuela at 650–2,000 m elevation.

Additional specimens examined. COSTA RICA. ALAJUELA: Río Grande, cerca de San Ramón, *Brenes 19683* (NY). SAN JOSÉ: Basin of El General, *Skutch 4816* (GH, NY). COLOMBIA. Without locality: *Smith 2571* (GH). VENEZUELA. ARAGUA: slopes of mountainside near stream, between Choroní and Maracay, *Soderstrom 978* (US);

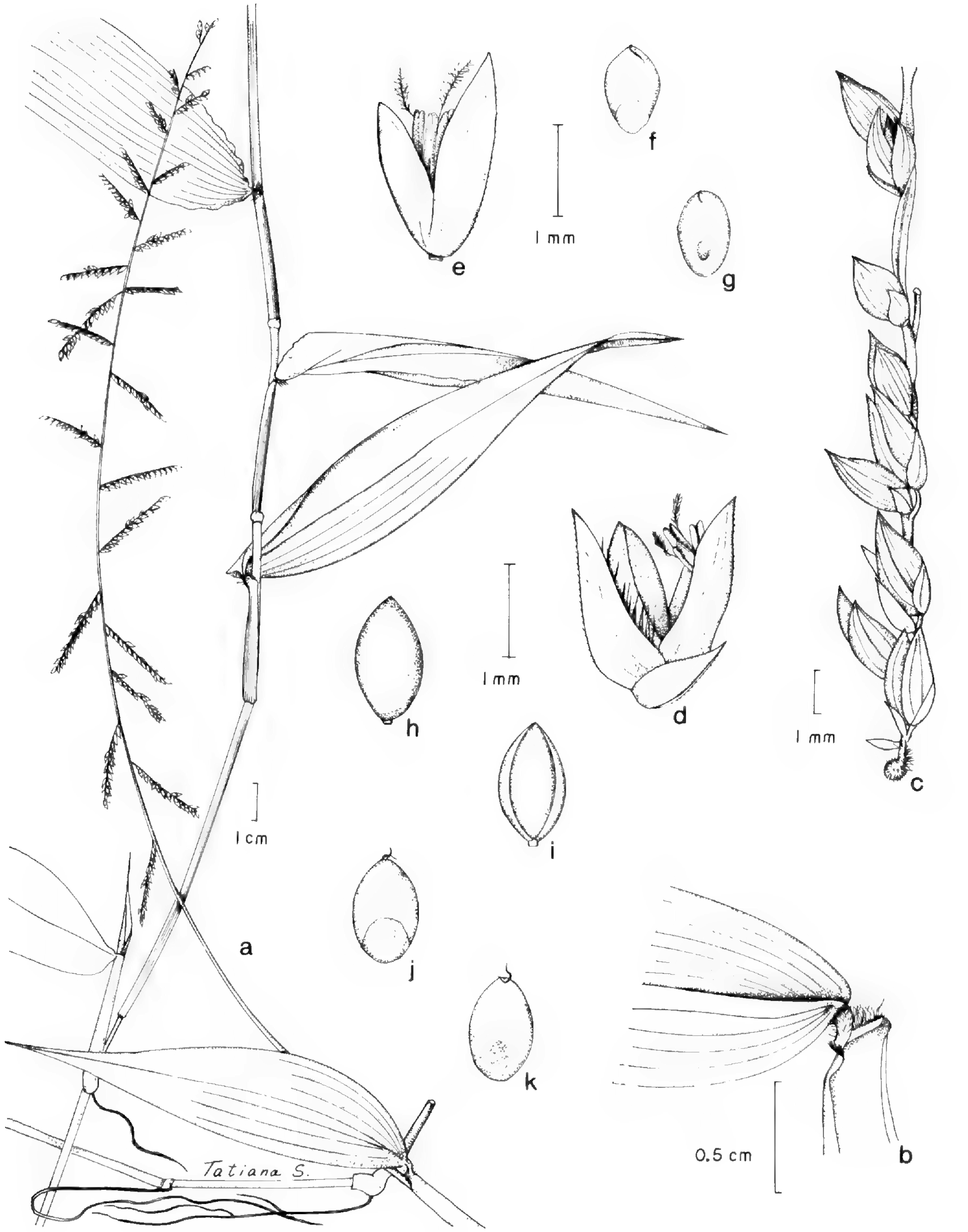

FIGURE 8. Panicum irregulare.—*a. Leafy branch.—b. Ligule.—c. Racemose branch.—d. Spikelet, lateral view.—e. Lower anthecium showing hermaphrodite flower.—f. Caryopsis of the lower anthecium, embryo side.—g. Caryopsis of the lower anthecium, hilum side.—h. Upper anthecium, dorsal view.—i. Upper anthecium, ventral side.—j. Caryopsis of the upper anthecium, embryo side.—k. Caryopsis of the upper anthecium, hilum side. Based on* Soderstrom 978 *(US)*.

Parque Nacional Henry Pittier, NW of Maracay, Rancho Grande, *Davidse 3017* (US).

Although having the diagnostic characters of sect. *Stolonifera*, *P. irregulare* differs by the presence of an hermaphrodite flower in the lower floret, a character unknown elsewhere in the genus. This lower flower develops a normal caryopsis similar to the one present in the upper floret, only a little smaller. Unlike the upper anthecium, in the lower floret the lemma and palea are membranous, and the caryopsis is completely free from these bracts. Pohl (1980) suggested that this species may be a hybrid between genus *Panicum* and *Pseudechinolaena*, but we could find no evidence to support this. As previously stated, the species matches the characters that differentiate sect. *Stolonifera* from the other sections in subg. *Phanopyrum*.

7. **Panicum latissimum** Mikan ex Trin., in Sprengel, Neue Entdeck. Pflanzenk. 2: 87. 1821. TYPE: "*Panicum latissimum* Mikan detexit in Brasil et comm. an Mikan, sub cujus nom specium descripsi in Spr. gl. n. Entdx" (holotype, LE, not seen, fragment at US (974701)). Figure 9.

P. macrophyllum Raddi, Agrost. Bras. 46. 1823. TYPE: Brazil. Without locality: *Raddi s.n.* (holotype, PI, not seen, fragment at US (80732)).

Robust perennials up to 2.5 m tall. *Culms* decumbent and rooting at the lower nodes to erect, branching at the upper nodes; internodes cylindric, hollow, glabrous, up to 1.5 cm diam.; nodes brown, constricted, glabrous. *Leaf sheaths* 12–14 cm long, striate, stramineous, densely pilose, with long, whitish, caducous hairs or glabrous. *Ligule* membranous-ciliate, small, 0.2–0.3 cm long, external ligule absent. *Leaf blades* 30–35 cm long, 6–12 cm wide, flat, acuminate, glabrous, cordate and amplexicaul basally, the margins conspicuously ciliate to glabrous, the midnerve prominent or not prominent, the lateral nerves anastomosing; *pseudopetiole* brownish, glabrous, 0.6–1.3 cm long. *Panicles* pyramidal, lax and diffuse, many-flowered, 30–45 cm long, 10–18 cm wide, with alternate, distant, hirsute to scabrous branches diverging from the axis, sometimes with secondary and tertiary branchlets; spikelets short- to long-pedicelled, along the lower side of the branches; axis longitudinally ridged, minutely scabrous, the branches hirsute to scabrous, triquetrous; axils of the branches short- to long-pilose; pedicels pilose. *Spikelets* ellipsoid, acute, 2.7–3.1 mm long, 0.9–1.1 mm wide, stramineous to brownish or purplish, the glumes and lower lemma shortly pilose and scabrous, the upper glume and lower lemma subequal, acuminate, both with long hairs toward the margins. *Lower glume* narrowly ovate, acute, 2.5–2.7 mm long, ½–¾ the length of the spikelet, acuminate, shortly pilose to scabrous on the outer surface, densely pilose toward the apex of the inner surface, 5-nerved, the midnerve scabrous. *Upper glume* 2.5–2.9 mm long, 5(–7)-nerved, the midnerve scabrous. *Lower lemma* 2.7 mm long, glumiform, 5-nerved. *Lower palea* elliptic, 1.8–2.3 mm long, 0.6–0.8 mm wide, stramineous, shortly pilose, the margins ciliate; male flower present, the anthers ca. 1.7 mm long. *Upper anthecium* ellipsoid, acute, 2–2.2 mm long, 0.8 mm wide, stramineous. *Caryopsis* not seen. In flower October to April.

Distribution. Brazil. In mountains, humid and rocky habitats at 500–1,000 m elevation.

Additional specimens examined. BRAZIL. ESPÍRITO SANTO: Municipio de Alfredo Chaves, Vila São Bento de Urânio, mata higrófila, *Zuloaga et al. 2410* (RB, SI, US). RIO DE JANEIRO: between Alto Boa Vista and Silvestre, *Chase 8377* (F, MO, NY, US); vicinity of Paineiras, Corcovado, *L. Smith 1205* (F, GH, US); Corcovado, *Riedel 329* (US); without collector, *Oct. 1836* (R); estrada do Sumaré, *Pabst et al. 127* (MO); Petrópolis, *Goes & Dionisio 451* (RB), *Peixoto s.n.* (R); Serra dos Orgãos, perto do Veu das Noivas, *Carauta 712* (F); Serra dos Orgãos, *Vidal II-5580* (R), *Pereira 187* (RB); Parque Nacional da Tijuca, Bom Retiro, *Soderstrom et al. 1855* (US); Bico do Papagaio, *Landrum 2201* (RB), *Ule 4158* (R, US); Tijuca, *Chase 12159* (US), Oct. 1883, *Schwacke & Saldanha s.n.* (R); Pico da Tijuca, *Chase 8486* (US); Estrada da Guanabara, Mata do Sumaré, *Sucre 1748* (RB); Guanabara, Alto da Boa Vista, *Sucre 2091* (R); Sumaré, *Sucre 4071* (RB); Alto da Pedra da Gavea, *Sucre 4297* (RB); Teresópolis, *Vidal 18, 374* (R); estrada Teresópolis–Friburgo, Canoas, *Braga 1532* (RB); Rio de Janeiro, *Riedel 464* (R). Without locality: *Burchell 1110, 1381, 2158* (US); *Gardner 210* (GH, US); *Glaziou 504, 6973* (US), *17928* (P, US); *Riedel s.n.* (P); *Gaudichaud s.n.* (P).

Panicum latissimum is clearly distinguished from other species of sect. *Stolonifera* and from the rest of the genus by having leaves up to 12 cm wide.

8. Panicum piauiense Swallen, Sellowia 18: 110. 1966. Based on *P. blepharophorum* Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 4. 1921. Not *Panicum blepharophorum* J. S. Presl. TYPE: Brazil. Piauí: without locality, July–Sep. 1839, *Gardner 2016* (holotype, BM, not seen, fragment at US; isotypes, GH, NY, P, US). Figure 10.

Ichnanthus gardneri Mez, Feddes Repert Spec. Nov. Regni Veg. Beih. 15: 132. 1918. TYPE: Brazil. Goiás: without locality, 1841, *Gardner 3512* (holotype, B, not seen; isotypes, BR, P, fragments at US).

Cespitose, moderately robust, short-rhizomatous perennials, 40–80 cm tall, with conspicuous, fusiform, long root tubers up to 3–5 mm thick, the cataphylls lanate. *Culms* erect, branching, many-noded, the internodes cylindric, densely to sparsely pilose or glabrous, hollow; nodes brown, constricted, shortly pilose. *Leaf sheaths* 4–6 cm long, longer than the internodes, stramineous, glabrous or scarcely pilose, one of the margins densely ciliate, with short, whitish hairs, the other glabrous. *Ligule* membranous-ciliate, 0.5 mm long, sometimes with long hairs toward the back at the base of the blade; external ligule a row of antrorse whitish hairs, the collar stramineous, pilose. *Leaf blades* lanceolate, 9–13 cm long, 1–1.5 cm wide, acuminate, flat, cordate to subcordate basally, scabrous to densely villous on both surfaces, the adaxial surface shortly pilose at the base, the margins white and cartilaginous, long-ciliate or glabrous basally, otherwise minutely scabrous; *pseudopetiole* small, shortly pilose. *Panicles* lax, oblong, 7–22 cm long, 2–4.5 cm wide, with the branches alternate and diverging from the axis, rarely with short, appressed secondary branchlets; axis longitudinally ridged, sparsely hispid, scabrous, the branches triquetrous, scabrous and sparsely hispid, bearing spikelets in pairs: one subsessile, the other shortly pedicellate, the lower one distant; axils of the branches long-pilose to villous; pedicels pilose or scabrous. *Spikelets* narrowly ellipsoid, 2.4–2.8 mm long, 0.8 mm wide, stramineous to purplish, sparsely pilose or with long hairs at the margins of the glumes and lower lemma. *Lower glume* ovate, acuminate, 1.8–2.5 mm long, ½–¾ the length of the spikelet, scabrous to sparsely pilose on the outer surface, densely pubescent toward the apex on the inner surface, 3-nerved, the midnerve scabrous. *Upper glume* acute to acuminate, 2.3–2.7 mm long, pilose to scabrous, with long, stiff and whitish hairs toward the margins on the outer surface, the inner surface shortly pilose, 5-nerved, the midnerve scabrous. *Lower lemma* glumiform, acute, 2.3–2.6 mm long, 5-nerved, with pubescence similar to that of the upper glume, with or without 2–4 prominent, ocellate and crateriform glands on the middle portion. *Lower palea* elliptic, 1.7–2 mm long, 0.6 mm wide, stramineous, shortly pilose, the margins ciliate; male flower absent. *Upper anthecium* narrowly ovoid, 1.7–2 mm long, 0.6 mm wide, stramineous. *Caryopsis* ellipsoid, 1.3 mm long; hilum oblong. In flower January to April.

Distribution. Brazil, in cerrados of Bahia and Piauí at 800 m elevation.

Additional specimens examined. BRAZIL. BAHIA: Chapadão do Panair, Serra do Mimo, *Black 55-17982* (IAN); Espigão Mestre, ca. 100 km WSW of Barreiras, *Anderson et al. 36751* (F, MO, R, US); Serra de Teririco, Gruta do Pequeño, *Zehntner 67* (R); Serra do Teririco, *Zehntner 3746* (RB, US); Serra do Sincorá, 15–20 km from Andaraí, along the road to Itaeté, *Harley et al. 18652* (MO, P).

This species can be mistaken for poorly developed plants of *P. rude,* but the latter normally reaches greater size (2 or 3 m high). *Panicum piauiense* differs further from *P. rude* by having food-storing thickened roots and by having culms that branch from the base up to the upper part of the plant. The

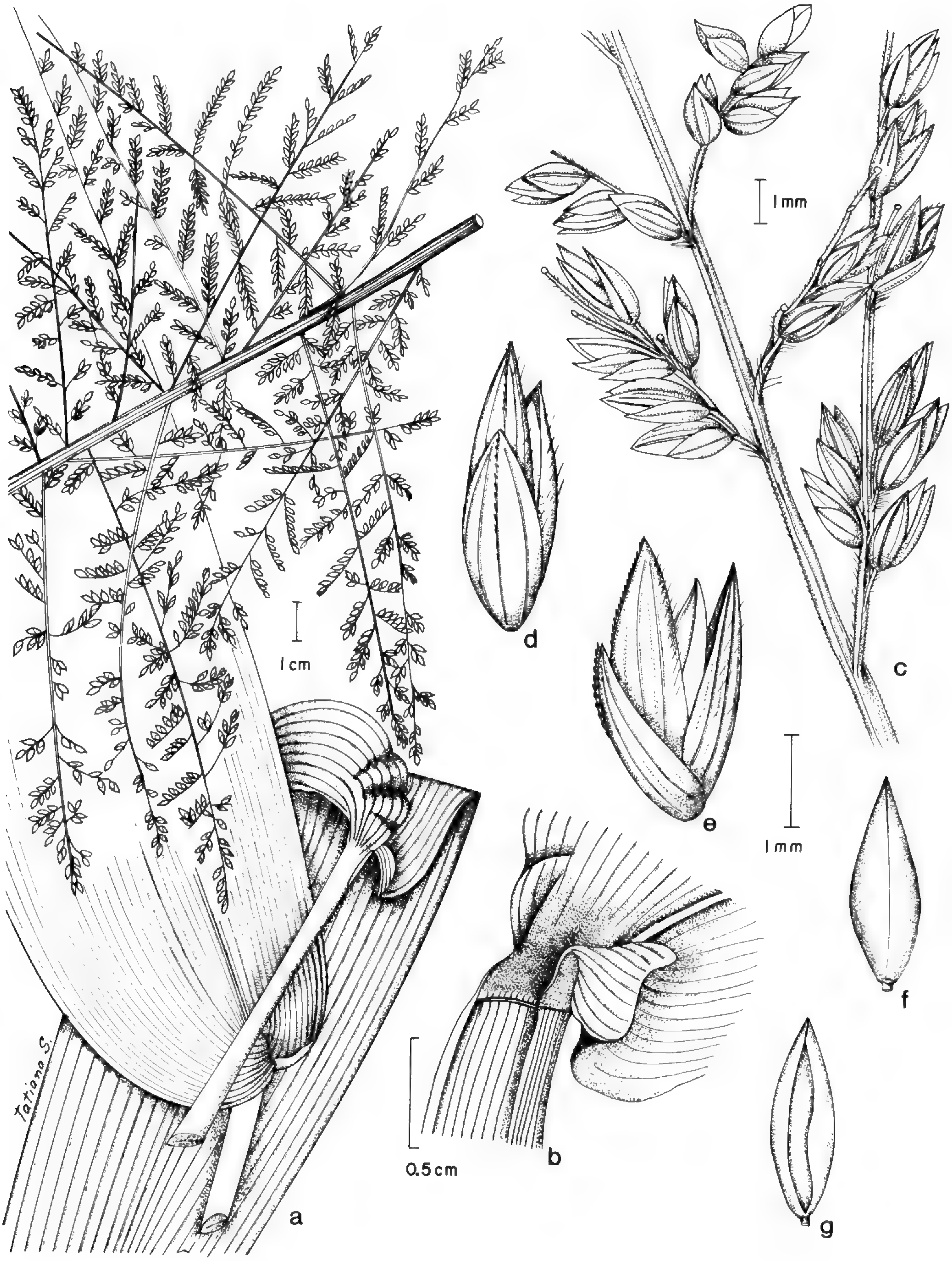

FIGURE 9. Panicum latissimum.—*a. Blades and portion of the panicle.—b. Ligule.—c. Portion of the panicle showing racemose branches.—d. Spikelet, ventral view.—e. Spikelet, lateral view.—f. Upper anthecium, dorsal view.—g. Upper anthecium, ventral view. Based on* Chase 8486 *(US)*.

two species also have different distributions, *P. piauiense* occurring only in Bahia and Piauí, *P. rude* from Espírito Santo to Rio Grande do Sul. The fusiform root tubers of *P. piauiense* are unique within *Panicum*. Soderstrom (1981) reported tubers in the nonpanicoid grasses *Puelia ciliata* Franch., *Lophatherum gracile* Brongn., *Molinia cae-*

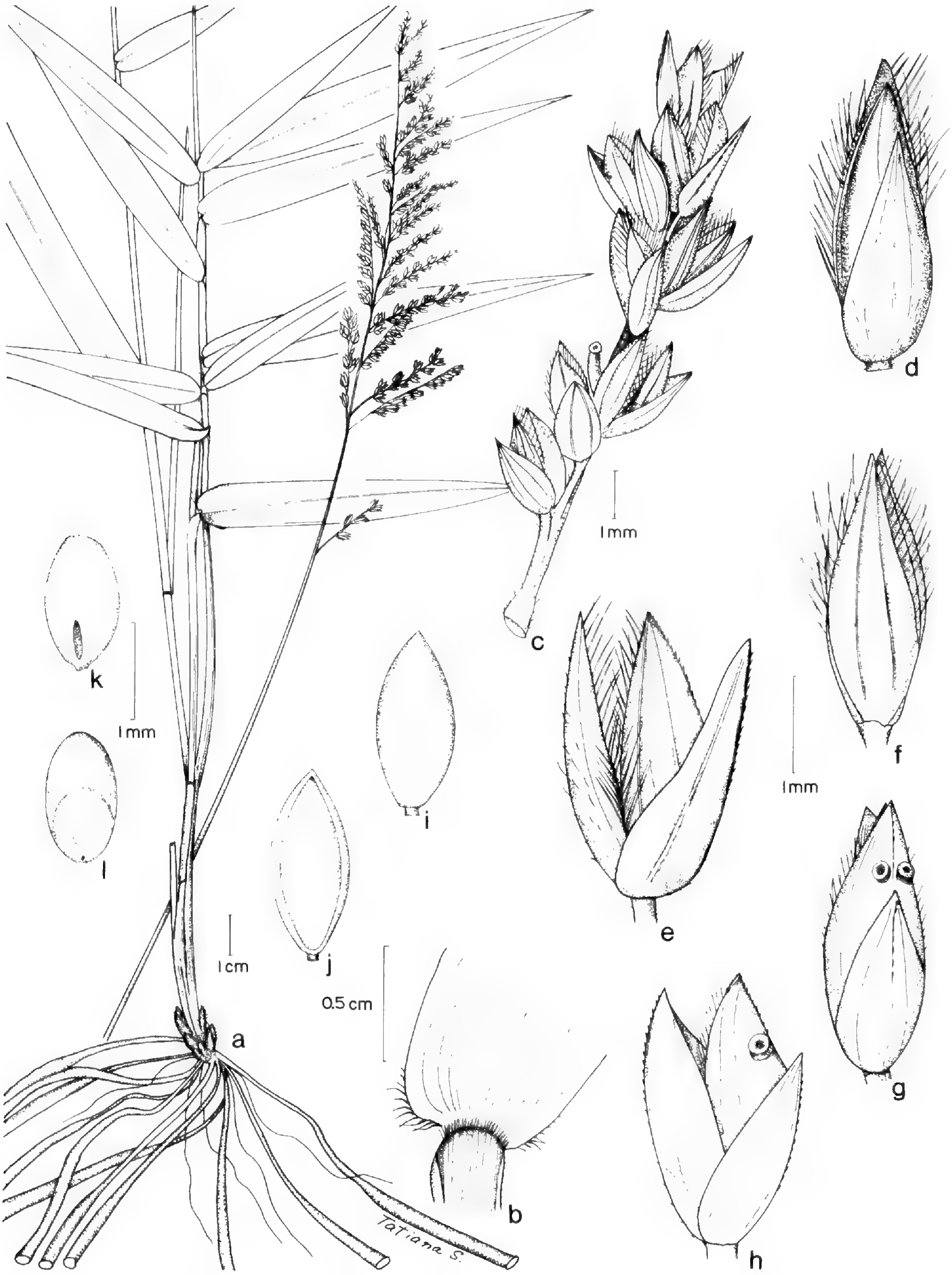

FIGURE 10. Panicum piauiense.—*a. Habit.—b. Ligule.—c. Detail of a racemose branch.—d. Spikelet, ventral view.—e. Spikelet, lateral view.—f. Spikelet, dorsal view.—g. Spikelet, ventral view, lower lemma with glands.—h. Spikelet, lateral view, lower lemma with glands.—i. Upper anthecium, dorsal view.—j. Upper anthecium, ventral view.—k. Caryopsis, hilum side.—l. Caryopsis, embryo side. a–f, i–l based on* Anderson 36751 *(US); g, h based on* Zehntner 3746 *(US)*.

rulea (L.) Moench, and *Sucrea sampaiana* (A. Hitchc.) Soderstrom.

9. **Panicum pulchellum** Raddi, Agrost. Bras. 42. 1823. *Eriochloa pulchella* (Raddi) Kunth, Rev. Gram. 1: 30. 1830. TYPE: Brazil. Rio de Janeiro: in sylvaticis prope Catumby, non procul ad urbe Rio de Janeiro, *Raddi s.n.* (holotype, PI, not seen, fragments at BAA, US). Figure 11.

P. leptostachyum J. S. Presl, Rel. Haenk. 1: 311. 1830. *Hymenachne leptostachya* (J. S. Presl) Fourn., Mex. Pl. 2: 36. 1886.
P. bipustulatum Schldl., Linnaea 26: 135. 1853.

Probably perennial. *Culms* decumbent, extensively creeping and rooting, geniculate at the lower nodes, then becoming erect, freely branching, 10–65 cm tall; internodes long, compressed, pilose to glabrous; nodes obscure, densely villous with whitish hairs. *Leaf sheaths* 0.7–2.5 cm long, shorter than the internodes, striate, membranous, densely pilose, with long, whitish hairs to glabrous, the margins ciliate. *Ligule* membranous-ciliate, ca. 0.4 mm long, the collar densely pilose. *Leaf blades* ovate-lanceolate, acuminate, 2.5–5.5 cm long, 1–2 cm wide, asymmetrical and cordate basally, strigose to glabrous on both surfaces, the basal margins long-ciliate with thick, caducous hairs, otherwise scabrous to ciliate, the abaxial surface often purplish; midnerve prominent, the lateral nerves anastomosing; *pseudopetiole* densely pilose, with long, thick hairs. *Panicles* terminal, 4–18 cm long, 1.5–4 cm wide, short- to long-exserted, the peduncle hispid, formed by 5–20 secund, alternate or occasionally opposite and racemose branches, these distant, ascending or reflexed, divergent from the axis; axis longitudinally ridged, hispid, the branches triquetrous, flattened on one side, densely hispid toward the base, hispid to scabrous on the rest of the surface, with spikelets borne in pairs, one subsessile, the other short-pedicellate (the subsessile spikelet frequently abortive), the axils of the branches pilose. *Spikelets* narrowly ellipsoid, 1.8–2.3 mm long, 0.6–0.7 mm wide, greenish, the glumes and lower lemma hirsute, the hairs papillose, rigid, short; upper glume and lower lemma subequal (or the upper glume shorter), acuminate. *Lower glume* ovate, acute, 0.8–1.1 mm long, ⅓–½ the length of the spikelet, short-pilose on the middle portion, hirsute toward the margins, separated from the upper glume by an internode, 3-nerved, the midnerve scabrous. *Upper glume* 1.8–2 mm long, 5-nerved, hirsute. *Lower lemma* 1.7–2.1 mm long, 5-nerved, short-pilose on the middle portion and long-pilose toward the margins, bearing 2 crateriform ocellate glands between the midnerve and the 2 immediate lateral nerves, or the glands occasionally absent. *Lower palea* 1.4–1.6 mm long, 0.4–0.6 mm wide, lanceolate, hyaline, short-ciliate at the margins, glabrous in the rest of the surface; male flower usually absent. *Upper anthecium* ellipsoid, acute, 1.2–1.5 mm long, 0.7–0.9 mm wide. *Caryopsis* ellipsoid, 1–1.2 mm long, 0.5–0.6 mm wide; hilum oblong. In flower all year.

Distribution. This species occurs from Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, and Panama to Colombia, Venezuela, Ecuador, Peru, Boliva, and Brazil. It grows in humid and shaded places from sea level to 2,000 m elevation.

Chromosome number. $n = 10$ (Davidse & Pohl, 1974); $2n = 20$ (Gould & Soderstrom, 1970; Pohl & Davidse, 1971).

Selected specimens examined. BELIZE. EL CAYO: Chalillo crossing, *Lundell 6513* (F, US); Norris Woods, *Dwyer et al. 173* (MO). STANN CREEK: Big Creek, *Schipp 180* (F, GH, MO, NY, US), *884* (GH, MO, NY). TOLEDO: cerca de Jacinto Hills, *Gentle 5095* (F, US); Swasey Branch, Monkey River, *Gentle 3962* (F, GH, MO, NY, US); Edwards Road, near Columbia, *Gentle 6447* (F). Without district: Gracie Rock, Sibun River, *Gentle 1539* (MO); Pine Ridge, near Manatee Lagoon; *Peck 279* (GH). BOLIVIA. LA PAZ: Prov. Larecaja, ruta entre Caranavi y Guanay, puente sobre el Río Coroico, *Croat 51685* (MO); Guanay, *Rusby 217* (NY, US). BRAZIL. MATO GROSSO: Santa Anna da Chapada, *Malme 3396* (US). MINAS GERAIS: Viçosa, *Chase 9445* (GH, MO, NY, US); Pico do Itabira, *Mattos s.n.* (R-38680). RIO DE JANEIRO: Angra dos Reis, *Castellanos 801* (F); Teresópolis, Serra dos Orgãos, *Sampaio 2426A* (US); matas do Andarahy e Trapicheira, *Kuhlmann s.n.*, Apr. 1917 (R); Parque Nacional Itatiatia, camino al Lago Azul, *Zuloaga et al. 2367* (RB, SI, US). COLOMBIA. ANTIOQUIA: 26 km al S de Zaragoza, *Denslow 2651* (MO); vicinity of Planta Providencia, 26 km S y 23 km W air of Zaragoza, in valley of Río Anorí, *Denslow 2728* (COL), *Denslow 2651* (COL); Granja de las Mercedes en Venecia, *Barkley & Gutierrez 637* (COL, US); Tirana Creek, at the confluence with Río Anorí, *Soejarto et al. 3178* (COL, MO). CHOCÓ: San José del Palmar, cerro al S de la población, *Forero et al. 3436* (COL, MO). CUNDINAMARCA: Sasaima, vereda San Bernardo, La María, *Barrios 12573* (COL); Estación Central de Investigación La Esperanza, *Obregón 19* (COL); en las cercanías del Boquerón de Santa Inés, *Pinto y Bernal 1603* (COL): Susumuco, *Triana 789* (COL). MAGDALENA: Santa Marta, *H. H. Smith 2127* (GH, MO, NY, US); San Sebastián, north of Pueblo Bello, *Angel 733* (US). META: Los Llanos, 12 km SE of Villavicencio, *Haught 2531* (COL, F, MO, NY, US); margen derecha del Río Guayabero, caudal de la

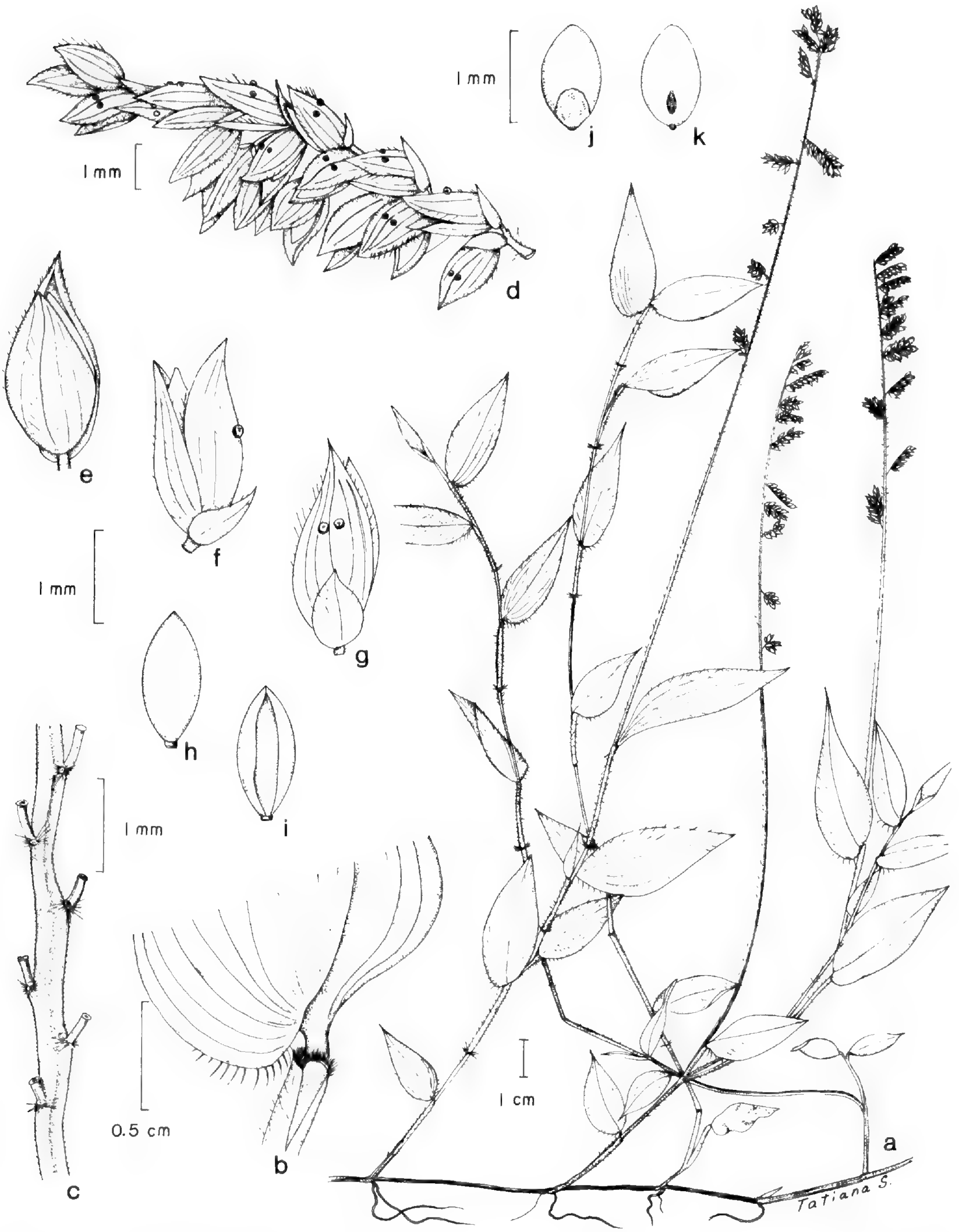

FIGURE 11. Panicum pulchellum.—*a. Habit.—b. Ligule.—c. Portion of a racemose branch showing pedicels.—d. Racemose branch.—e. Spikelet, dorsal view.—f. Spikelet, lateral view.—g. Spikelet, ventral view.—h. Upper anthecium, dorsal view.—i. Upper anthecium, ventral view.—j. Caryopsis, embryo side.—k. Caryopsis, hilum side. Based on* Chase 12421 *(US)*.

Macarena, *Pinto y Bischler 344* (P, COL); Villavicencio, *Cuatrecasas y García Barriga 4496* (COL, F, US), *Triana 14* (COL); Cordillera la Macarena, mesa del Río Sansa, *Idrobo & Schultes 1282* (COL); Reserva Nacional de La Macarena, junction of Río Sansa and Río Guejar, *Thomas et al. 1426* (COL); valley of Río Tigre, *Fosberg 19043* (US). NARIÑO: Ricaurte, *von Sneidern A-539* (GH). SANTANDER: Cordillera Este, Mesa de Los Santos, *Killip & Smith 15346* (MO, NY, US). NORTE DE SANTANDER: Región del Sarare, Hoya del Río Margua, bosques en la quebrada del Río Negro, *Cuatrecasas 12910* (COL, US). VALLE DEL CAUCA: Costa del Pacífico, Río Cajambre, *Cua-*

trecasas 17090 (F). Costa Rica. ALAJUELA: San Ramón, *Brenes 21388* (NY); 8 km al NE de Villa Quesada, *Molina et al. 17181* (F). CARTAGO: 5 km al N de El Muñeco, *Pohl & Davidse 11696* (F); 5 km al NE de Paraíso, *Pohl 12793* (MO, NY); cercanías de Pejivalle, *Skutch 4616* (F, GH, MO, US). HEREDIA: banks of Río María Aguilar, *Godfrey 66533* (US); valle del Río Sarapiquí, E de La Virgen, *Pohl 12827* (MO, NY). PUNTARENAS: 1 km al N de la Carretera Interamericana, *Pohl & Davidse 11605* (F). SAN JOSÉ: environs de Buenos Aires, *Tonduz 4881* (US); vicinity of La Verbena, *Standley 32232* (US); vicinity of El General, *Skutch 2214* (GH, NY, US), *3874* (GH, MO, NY, US); El General, *Skutch 3890* (GH, MO, NY, US); San Antonio de Desamparados, *Pohl & Lucas 12992* (MO). Ecuador. AZUAY: entre el Río Gamolotay y el Río Ñorcay, *Steyermark 52886* (F). CHIMBORAZO: Sibambe, *Acosta Solís 5338* (F, US), *5339* (US). GUAYAS: Teresita, 3 km W of Bucay, *Hitchcock 20536* (NY, US). IMBABURA: entre El Pajón y Cachaco, *Acosta Solís 12709* (US). EL ORO: between La Cholita and Portobello, *Hitchcock 21212* (NY, US). NAPO PASTAZA: Tena, *Asplund 8871* (US). PICHINCHA: Santo Domingo de los Colorados, *Asplund 16416* (NY, R, US), *Acosta Solís 10883* (F, US). Junction of the provinces of Guayas, Cañar, Chimborazo, & Bolívar: near the village of Bucay, *Camp 3819* (GH, NY, US); Bucay, *Rose 22446* (NY, US). Guatemala. ALTA VERAPÁZ: near Secanquím, *Mason 3153* (US); Cubilquitz, *von Tuerckheim 7702* (US). IZABAL: Los Amates, *Kellerman 7585* (F, NY); N of Quiriguá, *Weatherwax 92* (US); near Quiriguá, *Standley 23709* (F, GH, MO, US), *24246* (GH, MO, NY, US). PETÉN: Lancandón, *Contreras 3340* (GH, US); La Libertad, *Aquilar 185* (MO, US), *Lundell 2120* (US), *2545* (GH, US); Río Pasión, 4 km NE of Puste, *Lundell 18099* (GH). QUEZALTENANGO: between Finca Pirineos and Patzulín, *Standley 86608* (F, US); El Palmar, *Kellerman 6246* (F, US). RETALHULEU: Río Coyote, *Standley 87445* (F). SANTA ROSA: La Joya de Limón, E of Cuilapa, *Standley 78309* (US); near El Molino, *Standley 78429* (F, US). TEXACAPA: 13 km al E de Lobo, *Harmond & Fuentes 1854* (MO). Honduras. ATLÁNTIDA: Cutiapa, 26 km E de Las Ceibas, *Nelson et al. 3412* (MO); Lancetilla, *Pohl & Davidse 12072* (MO). CORTÉS: along Río Lindo, N of lake Yopoa, *Morton 7894* (F). EL PARAÍSO: Pueblo de Agua Fría, *Molina 7642* (US). MORAZÁN: Río Yeguare, *Molina 1374* (MO). OLANCHO: Jutiapa forest camp, near Salamá, *Pohl & Gabel 13746* (F); vicinity of Juticalpa, *Standley 17863* (F); between Catacamas and La Presa, *Standley 18307* (F). YORO: Ciudad de Yoro y alrededores, *Nelson 1989* (MO). Mexico. CHIAPAS: Campo Experimental de Quina, *Vera Santos 2731* (US); near the junction of Río Perlas and Río Jataté at San Quintín, near Laguna Miramar, *Sohns 1652* (US), *Breedlove 33374* (F, NY). OAXACA: vicinity of Cafetal Concordia, *Morton 2374* (US); San José Chiltepec, *Schultes & Reko 527* (US); Yaveo, *Mexía 9134* (GH, MO, NY). TABASCO: Hacienda Mayito, *Rovirosa 323* (NY). VERACRUZ: Córdova, *Hitchcock 6444* (US); Valle de Córdova, *Bourgeau 1455* (GH, US). Nicaragua. CHONTALES: Santo Tomás, *Seymour 2753* (F, GH, NY); Santo Domingo, *Seymour 3382* (F, GH, NY). JINOTEGA: N of Jinotega, *Williams et al. 27411* (F). MATAGALPA: Cordillera Central de Nicaragua, 5 km N of Matagalpa, *Williams et al. 23740* (F, NY, US). ZELAYA: a lo largo del Río Grande, *Molina 2260* (F, GH, US); near El Recreo, *Standley 19570* (F). Panama. CHIRIQUÍ. San Bartolo, 19 km W de Pto. Armuellos, *Busay 610* (F, MO). COLÓN: Canal Zone, Mount Hope Cemetery, *Standley 28824* (US); Canal Zone, cerca de Culebra, *Pittier 2226* (US); near Fort Sherman, *Standley 31045* (US); Barro Colorado Island, trail at rear 8, *Croat 7436*, *13150* (MO); Canal Zone, Quebrada Bonita, *Steyermark & Allen 17157* (US); Canal Zone, between France field and Catival, *Standley 30176* (US). PANAMÁ: E of the Río Tacumén, *Standley 26554* (US); Río Tapia, *Hitchcock 22945* (F, R. US); Altos de Campana, *Méndez 179* (MO); sabana near Chepo, *Hunter & Allen 54* (GH, US); Archipiélago Perlas, San José Island, *Erlandson 170* (NY, US), *I. Johnston 1136* (GH, US), *1274* (GH). Peru. AYACUCHO: Estrella, between Huanta and Río Apurimac, *Killip & Smith 30699* (US). LORETO: Yurimaguas, *Anderson 84* (US). CUZCO: Pilcopata, Santa Inés, *Vargas 11315* (US); without locality, 5 May 1930, *Bues s.n.* (F-659976, US). Venezuela. AMAZONAS: Isla Carestía, 5 km NNW of Sanariapo, *Davidse 2862* (MO, US); edge on Isla Carestía, saltos Carestía y Gallo, 5 km N of Sanariapo, *Maguire et al. 36162* (NY, US). ANZOÁTEGUI: Fila El Guácharo, *Davidse & González 19422* (MO); cafetales al NW de Buenos Aires, 18 kms aéreos al NE de Bergantín, *Davidse & González 19632* (MO). ARAGUA: 12 km S of Alto de Choroní, *Davidse 3078* (MO); Cordillera Interior, entre el Paují y el Socorro, *Steyermark 118086* (MO). DISTRITO FEDERAL: Cotiza, *Chase 12421* (US). LARA: Distrito Jiménez, Parque Nacional Yacambú, *Davidse & González 20980* (MO, US); Terepaima, Barquisimeto, *R. Smith V186* (US). MÉRIDA: 2 km del Río Guaymaray, *Liesner & González 10623* (MO). MIRANDA: Guinand Estate, *Pittier 5975* (NY, US); Los Teques, *Chase 12303* (NY, US), *Archer 3055* (US). PORTUGUESA: between Aparición and Acarigua, *Pittier 12086* (US). SUCRE: without locality, *Tamayo 2152* (US). TÁCHIRA: Fila de Paramito, al N de Mesa del Tigre, *Davidse & González 22482* (MO); cerro Las Minas, *Steyermark et al. 119937a* (VEN). YARACUY: Cerro La Chapa, 7 km N of Nirguá, *Davidse et al. 20809* (MO).

10. **Panicum rude** Nees, Agrost. Bras. 158. 1829. TYPE: Brazil. Minas Gerais: habitat in marginibus sylvarum Districtus Adamantum prope Milho verde, *Martius s.n.* (holotype, M, not seen, fragments at BAA, US). Figure 12.

P. bambusaefolium Desv., Opusc. 83. 1831. TYPE: Brazil. Without state and locality: *Desvaux s.n.* (holotype, P; fragments at BAA, US).

P. secundum Trin., Spec. Gram. 3: pl. 324. 1836. *P. secundum* var. *secundum* (as '*subaequiglume*') Doell, in C. Martius, Fl. Bras. 2(2): 194. 1877. TYPE: Brazil. Without locality: *Riedel s.n.* (holotype, LE, not seen, fragment at US; isotypes, P, US).

P. secundum var. *inaequiglume* Doell, in C. Martius, Fl. Bras. 2(2): 194. 1877.

P. semitectum Swallen, Sellowia 18: 112. 20 Dec. 1966. Not *Panicum semitectum* Swallen, Phytologia 14: 68. 5 Dec. 1966. TYPE: Brazil. Paraná: Jaguariaiba, in woods, overhanging on bank, 25 Feb. 1946, *Swallen 8675* (holotype, US).

FIGURE 12. Panicum rude.—*a. Portion of a culm and panicle.—b. Ligule.—c. Detail of a racemose branch.—d. Spikelet, ventral view.—e. Spikelet, lateral view.—f. Spikelet, ventral view, lower lemma with glands.—g. Upper anthecium, dorsal view.—h. Upper anthecium, ventral view.—i. Caryopsis, embryo side.—j. Caryopsis, hilum side. f based on* Riedel s.n. *(US-974743); a–e, g–j based on* Sendulsky 1039 *(US).*

P. pompale Swallen, Sellowia 18: 110. 1966. TYPE: Brazil. Rio de Janeiro: top of sheer face of Corcovado, Rio de Janeiro, 11 Jan. 1925, *Chase 8165 I* (holotype, US).

P. kleinii Swallen, Sellowia 18: 111. 1966. TYPE: Brazil. Santa Catarina: Pinhal da Companhia, Lauro Muller-Urussanga, 23 Aug. 1958, *Reitz & Klein 7043 I* (holotype, US).

P. albospiculatum Swallen, Sellowia 18: 110. 1966. TYPE: Brazil. Santa Catarina: Rio Caçador, 22 Jan. 1946, *Swallen 8291* (holotype, US).

P. apricum Swallen, Sellowia 18: 112. 1966. TYPE: Brazil. Santa Catarina: Campo dos Padres, 16 Nov. 1956, *Smith, Reitz & Klein 7643* (holotype, US; isotype, NY).

Robust, cespitose, short-rhizomatous perennials. *Culms* decumbent and rooting at the lower nodes to erect or leaning among branches of trees, 60–200(–300) cm tall, usually simple, the internodes cylindric, glabrous, hollow; nodes obscure, compressed, glabrous. *Leaf sheaths* 7–20 cm long, longer than the internodes, stramineous, auriculate, striate, papillose-pilose with caducous hairs to densely or sparsely hispid with whitish and appressed hairs, otherwise completely glabrous, the margins pilose to glabrous. *Ligules* membranous-ciliate, 0.5–2.5 mm long; external ligule conspicuous, similar to the inner ligule but smaller; collar brown, pilose to glabrous. *Leaf blades* lanceolate to long-lanceolate, acuminate, flat, 15–45 cm long, 1.6–5 cm wide, cordate to subcordate basally, hispid on both surfaces with appressed short hairs to glabrous, the margins scabrous, ciliate or glabrous; *pseudopetiole* brownish, 0.5–1 cm long and with ciliate margins. *Panicles* lax, pyramidal to oblong, many-flowered, 20–65 cm long, 5–25 cm wide, with secund branches alternate to subopposite, diverging toward the base of the panicles and contracted toward the apex, the spikelets short-pedicelled and disposed in pairs in the branches; axis longitudinally ridged, scabrous to densely hispid; branches and branchlets longitudinally ridged, scabrous and long- to short-pilose, the axils of the branches brownish, shortly pilose; pedicels scabrous, sometimes with long hairs. *Spikelets* ellipsoid, 2.3–3 mm long, 0.8–1.1 mm wide, stramineous or nearly purplish, the glumes and lower lemma sparsely to densely pilose, upper glume and lower lemma subequal and longer than the upper anthecium. *Lower glume* shortly pilose on both surfaces, acute, 1.4–2.5 mm long, ½–¾ the length of the spikelet, 3(–5)-nerved, the nerves anastomosed apically, the midnerve markedly scabrous. *Upper glume* 5(–7)-nerved, acute to acuminate, scabrous, pilose toward the margins and the base or with whitish hairs on the entire surface. *Lower lemma* 5(–7)-nerved, acute to acuminate, with pubescence similar to that of the upper glume, occasionally with one pair of glands on the middle portion. *Lower palea* lanceolate to elliptic, 1.8–2.5 mm long, 0.6–0.7 mm wide, hyaline, with long-ciliate margins; male flower present or absent. *Upper anthecium* ellipsoid, 1.7–2.3 mm long, 0.6–0.8 mm wide, stramineous to brownish at maturity. *Caryopsis* ovoid, light brown, 1.4–1.7 mm long, 0.8–1 mm wide; hilum oblong. In flower September to April.

Distribution. Brazil. Common in interior or edges of forests at 0–1,900 m elevation.

Common names. Papanduva, capim-papanduva, papua, capim papua, cana-de-macaco (Smith et al., 1982); capim de anta (*Pereira 2281*).

Additional specimens examined. BRAZIL. DISTRITO FEDERAL: 10 km NW of Planaltinha, *Irwin et al. 13196* (MO, US). ESPÍRITO SANTO: Vargem Alta, San José de Fruteira, *Pereira 2281* (US). MINAS GERAIS: Serra do Gongo Socco, *Hoehne 4898* (US); Serra do Espinhaço, 12 km W of Barão de Cocais, *Irwin et al. 29321* (MO, NY); Serra de Ouro Preto, *Magalhaes Gomez 2821* (US); Serra do Espinhaço, 35 km E of Belo Horizonte, *Irwin et al. 30390* (MO, NY); Serra do Espinhaço, Pico do Itambé, *Anderson et al. 35723, 35894* (MO); Ouro Preto, *Pires & Black 3375* (US); Araponga, *L. Bailey 1094* (US); Itacolumy, *Chase 9420* (F, NY, US). PARANÁ: Curitiba, *Swallen 8594* (US); Banhado–Piroquara, *Swallen 8644* (US); Paredão da Santa, *Hatschbach 35468* (MO); Fazenda Monte Alegre, Rio Harmonía, *Hatschbach 3027* (SI); Serra Capivari Grande, *Hatschbach 22959* (NY, US); Jaguariaiva, *Dusén 13233* (NY, US), *15920* (MO); Rio Iguaçú, Salto Grande, *Hatschbach 14934* (US); Barigny, *Dusén 15765* (F, MSC); Jacareí, *Dusén 17012* (F). RIO DE JANEIRO: Corcovado, *Chase 8165 II* (NY, US); Pão de Açucar, *Chase 10043* (US). RIO GRANDE DO SUL: Cambará do Sul, Jan. 1972, *Normann et al. s.n.* (US-2635110); Cambará, serra da Pedra, *Rambo 36751* (US). SANTA CATARINA: 4 km S of Campo Alegre, *Smith & Klein 7344* (US); Pinhal da Companhia, Lauro Muller–Urussanga, *Reitz & Klein 7043 II* (US); Campo dos Padres, *Reitz 2638* (US); Azambuja, *Reitz 2213* (US); Jordão, Governador Celso Ramos, *Klein & Bresolin 9772* (US); Serra da Boa Vista, S. José, *Reitz & Klein 10197* (US); Alto Matador, Rio do Sul, *Reitz & Klein 7269* (US); Morro do Ribeirão, *Klein 6924* (US), *Klein & Bresolin 7647* (US); between Fazenda Santo Antonio and the falls of Rio Canoas, Campo dos Padres, *Smith & Klein 7871* (NY, US); Itajaí, Morro da Ressacada, *Klein 1775* (NY, US); Porto União, *Orth 2510* (US); Pilões, *Reitz & Klein 2456, 2762* (US), *3630* (NY, US); Brusque, *Reitz 3547* (F, SI); Blumenau, mata da Companhia Hering, Bom Retiro, *Reitz & Klein 9190* (NY, US), *9220* (NY); base of Morro do Funil, *Smith & Klein 15470* (R, US); Sabiá, *Klein 2252* (NY, US), *2271* (US); Pinheiral, *Smith & Reitz 8750* (US); Morro do Cambirela, *Klein & Bresolin 9714* (US); Morro da Bateia, *Reitz 1907* (US); Biturina, *L. Emygdio 693* (R). SÃO PAULO: São Paulo, Parque do Estado, grounds of the Instituto de Botânica, *Davidse 10510* (MO), *Hoehne 27202* (F, NY, US), *Sendulsky 278, 417, 1039* (SP, US), *Skvortzov 157* (SP, US); Igaratá, 1 Mar. 1939, *Gehrt s.n.* (US); Parque Estadual das Fontes do Ipiranga, *da Silva 258* (MO).

The polymorphous nature of *Panicum rude* lies behinds its numerous descriptions under different names. Its pilosity is variable on the vegetative and floral parts, with leaf sheaths, leaf blades, and inflorescences varying from densely pilose with different types of pubescence to glabrous.

The spikelets can be densely pilose on the glumes and lower lemma to glabrescent (only minutely scabrous on the glumes). The lower glume varies from ½ to about ⅘ the length of the spikelet, even in the same specimen (as for example in *Irwin et al. 29321*).

The crateriform glands on the middle portion of the lower lemma may be present or absent on the same specimen, but they are most often absent. These glands are present in the type specimens of "*P. bambusaefolium*" and "*P. secundum*," and they occur in *Irwin et al. 13196*. In the voluminous recently collected material in the Instituto de Botânica of São Paulo studied by T. Sendulsky, glands were not detected.

The illustration of *P. secundum* in Trinius (1836, pl. 324) draws attention to the peculiar one-sided position of the leaves. *Panicum rude* grows mostly at the borders of forests; when the culms develop in more or less open and uniformly lighted areas, they bear leaves distichously or alternately arranged. On the other hand, when the culms grow at forest margins and lean against dense vegetation, they receive light only from one side, which promotes unilateral arrangement of the leaves due to the twisting of the culm (Fig. 12).

Swallen (1966) treated five species closely related to *P. rude* within the Latissima group. The characters used by Swallen to separate these species were mainly pubescence of the leaf sheaths and blades and the sizes of plants and spikelets. We conclude that these characters do not justify separation of species.

Swallen cited *Chase 8165* as type of "*P. pompale*" and *Reitz & Klein 7043* as type of "*P. kleinii.*" It should be noted that these specimens are divided into two sheets each: *Chase 8165 I, Chase 8165 II, Reitz & Klein 7043 I,* and *Reitz & Klein 7043 II.* In both cases, *Chase 8165 I* and *Reitz & Klein 7043 I* contain the upper portion of a culm (including the panicle), and *Chase 8165 II* and *Reitz & Klein 7043 II* contain the vegetative part of the plant only. Consequently, *Chase 8165 I* and *Reitz & Klein 7043 I* should be considered as holotypes of the two names.

11. Panicum soderstromii Zuloaga & Sendulsky, sp. nov. TYPE: Brazil. Bahia: Município de Mucujê, 3 km ao S de Mucujê, na estrada para Jussiape, 1,000 m de alt., 13°00'S, 41°24'W, campo rupestre, 26 July 1979, *S. A. Mori, R. M. King, T. S. dos Santos & J. L. Hage 12652* (holotype, CEPEC; isotype, MO). Figure 13.

Gramen probabiliter perenne (basis non visa), 45–95 cm altum, *culmis* erectis, caespitosis, cylindricis, pilosis. *Foliorum vaginae* internodis superantie, sparse et longe pilosae, basilitex pilis papillosis instructae. *Ligula* brevissima, membranacea, arcuatae, breviter ciliata. *Foliorum laminae* anguste lanceolatae, acutae, 2–13 cm longae, utrinque breviter pilosae, basidus angustis, truncatis, marginibus rotundatis. *Paniculae* terminales, racemosae, pyramidales, effusae, 8–18 cm longae, 2–3(–4.5) cm latae; ramis adscentibus. *Spiculae* late ellipticae, plerumque hiantae, 2–2.8 mm longae, 1–1.5 mm latae, stramineae vel violaceae; *gluma inferior* ovata, ½–¾ longitudinis spiculae aequans, 3-nervis, pilis longis, albis, ad apicem, crassis; *gluma superior* acuta, spiculae subaequans, 3–5-nervis, marginibus subtiliter ciliatis. *Anthoecium inferum*: lemma ovatum, spiculam aequans, 5-nerve, marginibus subtiliter ciliatis, 2–4 glandulis crateriformibus, ocellatis, infra apicem sitis; palea acuta, ad apicem pilosa. *Anthoecium superum* ellipsoideum, stramineum, atrofuscum ad fructus maturitatem. *Caryopsis* ellipsoidea, 1.5 mm long, 1 mm lata, succinea; hilum ovatum sub-basale; embryo longitudine ca. ⅓ caryopsis aequans.

Cespitose, rather robust probable perennial, 45–70(–95) cm tall (base not seen), the lower nodes covered with small, pubescent sheaths. *Culms* erect, branching at the median and upper nodes; internodes cylindric, hard, solid or hollow, pilose, striate, the nodes

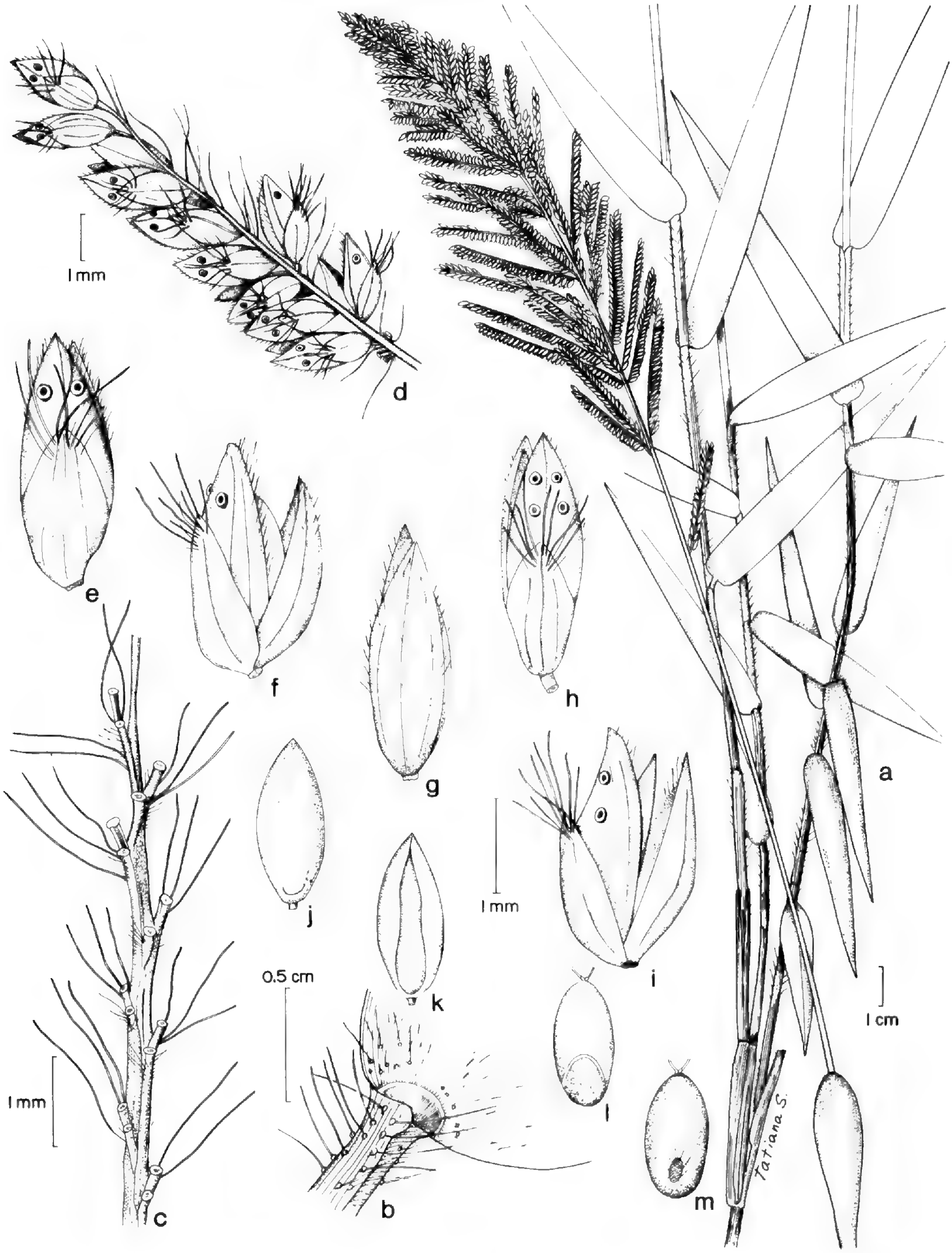

FIGURE 13. Panicum soderstromii.—*a. Leafy stems.—b. Ligule.—c. Portion of a branch showing pedicels.—d. Racemose branch.—e. Spikelet, ventral view.—f. Spikelet, lateral view.—g. Spikelet, dorsal view.—h. Spikelet, ventral view, lower lemma with two pairs of glands.—i. Spikelet, lateral view, lower lemma with two pairs of glands.—j. Upper anthecium, dorsal view.—k. Upper anthecium, ventral view.—l. Caryopsis, embryo side.—m. Caryopsis, hilum side. Based on* Mori et al. 12652 *(MO)*.

dark, constricted, pilose. *Leaf sheaths* longer than the internodes, slightly auriculate, tightly embracing the culms, with long, papillose, pilose hairs; the lower sheaths approximate, short. *Ligule* membranous-ciliate, ca. 0.5 mm long; collar area densely pubescent, dark. *Leaf blades* long-lanceolate, 2–13 cm long, 0.7–1.3 cm wide, stiff, attenuate toward the apex, a little narrowed and truncate basally, with rounded margins, velutinous on both surfaces; the midnerve not prominent; the basal leaves ca. 2–3 cm long, smaller than the uppermost leaves; *pseudopetiole* short. *Panicles* terminal, pyramidal, 8–18 cm long, 2–3(–4.5) cm wide, with numerous, many-flowered, upwardly appressed or spreading racemose branches bearing spikelets in pairs on unequal pedicels; axis glabrous, longitudinally ridged, finely hispid along the ridges; axils of the branches slightly swollen, dark brown, pilose; pedicels with 2 or 3 papillose-pilose whitish and thickened hairs, these longer than the spikelet. *Spikelets* broadly ellipsoid, 2–2.8 mm long, 1–1.5 mm wide, laterally compressed, usually gaping, stramineous or purplish. *Lower glume* ovate, acute, 3-nerved, ½–¾ the length of the spikelet, with a tuft of long, white, papillose-pilose hairs at the apex, otherwise scaberulous. *Upper glume* ovate, acute, 3–5-nerved, a little shorter than the lower lemma, finely ciliate at the margins, otherwise scaberulous. *Lower lemma* ca. 2 mm long, ca. 1 mm wide, 5-nerved, finely ciliate at the margins, otherwise scaberulous, with 2–4 crateriform, ocellate glands; the inner surface pilose. *Lower palea* acute, finely pilose at the apex and scabrid at the keels; male flower present, anthers 0.8–1.1 mm long. *Upper anthecium* ovoid, 1.1–1.4 mm long, 0.4–0.7 mm wide, stramineous or dark brown at maturity, smooth, shining. *Caryopsis* broadly ovoid, ca. 1.5 mm long, 1 mm wide, amber; hilum ovate, sub-basal; embryo ca. ⅓ the length of the caryopsis. In flower July to September.

Distribution. Brazil. Bahia, on rocks, in open and sunny habitats on "campo rupestre" at 1,000 m elevation.

Paratypes. BRAZIL. BAHIA: Serra da Jacobina, *Andrade-Lima 70-6159* (IPA, SP); Morro do Chapeu, 1,000 m, *E. Pereira 2138* (RB, US); Jacobinas, Serra do Brite, 11°09'S, 40°01'W, *H. P. Bautista & R. P. Orlandi 1000* (HRB, US).

The number of glands is generally constant for the same individual, two or four. Sometimes there is a third pair of rudimentary glands. This species is related to *P. chapadense* Swallen, from which it differs mainly by having hairs on the pedicels, pilose lower glumes (with long hairs toward the apex), and smaller spikelets.

None of the specimens was collected with its base, so it is not possible to know if cormlike bases as found in *P. chapadense* are present in the new species.

We have the pleasure of naming this species in honor of the late Dr. Thomas R. Soderstrom, our friend, colleague, and renowned North American agrostologist.

12. **Panicum stoloniferum** Poiret, Encycl. Meth. Suppl. 4: 272. 1816. TYPE: French Guiana. Cayenne: Cayenne, without collector (isotype, P, fragment at US). Figure 14.

P. frondescens G. Meyer, Prim. Fl. Esseq. 56. 1818. TYPE: Guiana: in graminosis umbrosis insulae Arcuabisch, *Meyer s.n.* (holotype not located; fragment of an isotype at US (79732)).

P. olyraefolium Raddi, Agrost. Bras. 43, pl. 1, fig. 6. 1823. TYPE: Brazil. Rio de Janeiro: in viciniis Rio Janeiro, *Raddi s.n.* (holotype, PI, not seen, fragment at US).

P. ctenodes Trin., Spec. Gram. 2: tab. 171. 1829.

P. ctenodes var. *major* Trin., Spec. Gram. 2: tab. 171a. 1829. *P. stoloniferum* var. *major* (Trin.) Kunth, Distr. Meth. Gram. 2: 389. 1831. Not Rev. Gram. 1. tab. 108. 1830.

P. trichoclados C. Reichb. ex Kunth, Enum. Pl. 1. 89. 1833. nom. nud.

P. brachyclados C. Reichb. ex Trin., Mem. Acad. Imp. Sci. Saint Petersbourg VI. 1: 251. 1834. nom. nud.

P. leprieurii Steudel, Syn. Pl. Glum. 1: 65. 1854. TYPE: French Guiana. Cayenne: Cayenne, 1835, *Leprieur s.n.* (syntype, P, fragment at US). Surinam. Without locality: *Kappler 1500* (isosyntypes, MO, US).

P. kegelii Steudel, Syn. Pl. Glum. 1: 65. 1854.

P. umbrosum Salzm. ex Steudel, Syn. Pl. Glum. 1: 65. 1854. nom. nud.

Stoloniferous perennials. *Culms* geniculate, long, decumbent, rooting and branching at the lower nodes, then becoming erect; erect portion of the culms 10–60 cm tall (reaching 1 m tall according to herbarium labels); internodes cylindric to compressed, hollow, branching at the middle and upper nodes, hispid in a longitudinal line to glabrescent, stramineous, sometimes purplish; nodes obscure, constricted, sparsely pilose to glabrous. *Leaf sheaths* splitting, striate, stramineous,

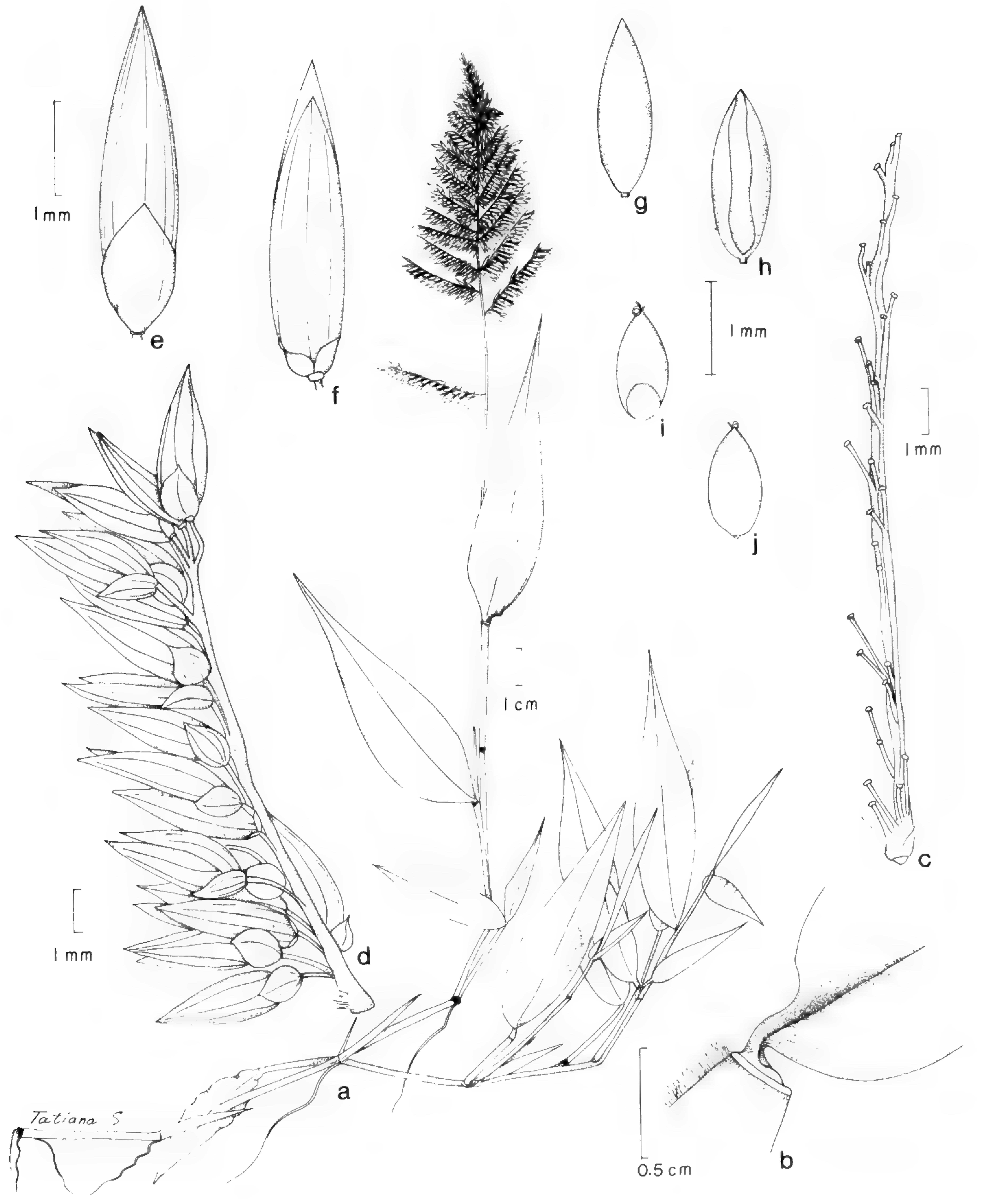

FIGURE 14. Panicum stoloniferum.—*a. Habit.—b. Ligule.—c. Racemose branch showing pedicels.—d. Racemose branch.—e. Spikelet, ventral view.—f. Spikelet, dorsal view.—g. Upper anthecium, dorsal view.—h. Upper anthecium, ventral view.—i. Caryopsis, embryo side.—j. Caryopsis, hilum side. Based on* Burkart et al. 26833 *(US)*.

shorter than the internodes, sparsely pilose to glabrous, the upper margins ciliate, the lower margins membranous. *Ligule* membranous, short, 0.2–0.4 mm long, laciniate at the apex; external ligule conspicuous, formed by a row of dense, whitish hairs. *Leaf blades* ovate-lanceolate to lanceolate, flat, 1.5–13 cm long, 0.3–3.5 cm wide, acuminate, contracted and asymmetrical basally, shortly pilose to minutely scabrid or glabrous on both surfaces (with long hairs toward the base or glabrous), the abaxial surface mostly purplish, the midnerve prominent, the lateral nerves usually anastomosing; *pseudopetiole* dark, shortly pubescent. *Panicles* exserted, (1.5–)4–9(–22) cm long, (0.8–)1.5–3(–6) cm wide, formed by numerous, dense, spikelike, alternate to subopposed racemose branches, ± divergent from the axis, the spikelets borne in pairs, densely congested along the lower side of the branches; peduncles hispid to glabrous; axis longitudinally ridged, hispid to scabrous or glabrous; axis of the branches triquetrous (one side flat), scabrous to glabrous, the axils shortly and densely pilose; pedicels short, 0.5–1 mm long, pilose to glabrous. *Spikelets* lanceolate, 2.2–3.2 mm long, 0.5–0.8 mm wide, glabrous, dark green, the upper glume shorter than the lower lemma, occasionally subequal. *Lower glume* ovate, 0.7–1.3 mm long, glabrous, ⅓ the length of the spikelet, 3-nerved, the midnerve scabrous. *Upper glume* gibbous, acute, 1.9–2.8 mm long, 5(–7)-nerved, the midnerve scabrous or glabrous apically. *Lower lemma* acuminate, 2.4–3 mm long, 5(–7)-nerved, the midnerve scabrous. *Lower palea* elliptic, 1.4–1.9 mm long, 0.3–0.5 mm wide, brownish, glabrous, the margins finely ciliate to glabrous; male flower absent. *Upper anthecium* ellipsoid, 1.3–1.9 mm long, 0.4–0.6 mm wide, stramineous, brownish at maturity; lemma 5-nerved; anthers brown, 0.5 mm long. *Caryopsis* ellipsoid, 1–1.5 mm long, 0.5–0.8 mm wide; hilum oblong. In flower all year.

Distribution. A widely distributed species found in Mesoamerica, Lesser Antilles, and South America, from Colombia to Argentina. The plants form dense and weedy ground vegetation in the moist and shaded forests at 150–1,400 m elevation.

Common names. Capim-do-Mato, capim-do-brejo (Smith et al., 1982).

Representative specimens examined. ARGENTINA. CHACO: Isla Soto, *Burkart et al. 30688* (RB, SI, US), *Schinini 16130* (MO, SI); Resistencia, *Meyer 366* (SI). ENTRE RIOS: Isla Curuzu-Chalí, *Burkart et al. 26833* (SI, US), *26851* (SI). CORRIENTES: 42 km E de Ituzaingó, Puesto de Prefectura, *Zuloaga et al. 620* (SI); Isla Apipé Grande, Puerto San Antonio, *Krapovickas et al. 23850* (CTES, US). FORMOSA. Colonia Clorinda, *Venturi 9164* (US). MISIONES: Posadas, *Ekman 623* (US); Eldorado, selva a orillas del Paraná, *Burkart 14528* (SI, US), *Cabrera et al. 28875* (SI, US); Puerto Rico, *Cabrera et al. 28803* (SI); Campo Grande, *Montes 10780* (SI); San Antonio, *Montes 7063* (SI); San Juan, *Montes 15308* (SI); Santa Ana, *Montes 15278* (MO, SI); Arroyo Piray-Guazú, *Cabrera et al. 28875* (SI); Santa Ana, *Rodriguez 676* (F, SI, US); entre Pto. Aguirre y Pto. Iguazú, *Wolffhugel & Van de Venne 37* (SI). SANTA FE: Puerto Piracuacito, *Lewis 946* (SI, US). BELIZE. EL CAYO: Retiro, *Lundell 6314* (F, NY, US). TOLEDO: Upper Jacinto Creek, *Gentle 5276* (US); beyond San Antonio, *Gentle 7552* (US). BOLIVIA. BENI: vicinity of Chacobo village Alto Ivón, *Boom 4086* (US). COCHABAMBA: Antahuacana, *Buchtien 2502* (MO, US). LA PAZ: Tipuani, Hacienda Casana, *Buchtien 7120* (MO, NY, US); between Coroico and Caranavi, *Davidson 4788* (MO); Polo-Polo bei Coroico, *Buchtien s.n.* (MO, SI, US-711096), *264* (F); San Carlos, *Buchtien 3* (US); Mapiri, *Buchtien 1172, 1173* (US). SANTA CRUZ: Buena Vista, *Steinbach 5130* (F, NY, US), *6855* (F, MO, US); Montero a Puerto Grether, *Renvoize & Cope 3962* (MO). BRAZIL. ACRE: track from km 20, road Cruzeiro do Sul to Japiim, *Prance et al. 2879* (MO). AMAPA: Rio Araguarí, *Pires et al. 51262* (NY, US); Rio Oiapoqué, *Irwin et al. 48146* (RB, US), *48150* (NY); Riozinho, 122 km NW of Porto Grande, *Mori & Souza 17604* (US). AMAZONAS: Cucuhí, Rio Negro, *Baldwin 3252* (US); Esperança, *Pires & Black 855* (US); east bank of Rio Madeira, 1 km N of Humaitá, *Prance et al. 3524* (MO, US); vicinity of Tototoví, *Prance et al. 10223* (MO, NY, US), *10282* (R, US); Rio Solimões, Rio Juruá, 10 km por encima de la boca, *Prance et al. 24494* (MO); Içana River, *Fróes 28028* (US); basin of the upper Juruá, *Fróes 45* (US). BAHIA: 22 km de la rodovía Ilheus–Itabuna, *Mori 12844* (MO); ramal a esquerda no km 13 da rodovía Valência–Guaibím, *Carvalho & Lewis 1130* (CEPEC, MO); próximo ponte sobre Rio Mucurí, na rodovía BR-101, *Mori et al. 10537* (CEPEC, MO, RB); km 22 da antiga rod. Camacã/Itaimbé, *Hage & Mattos Silva 304* (CEPEC); Mun. Ilheus, área do CEPEC, *Hage & Brito 1395* (CEPEC), *Santos 3399, 3787* (CEPEC). ESPÍRITO SANTO: Santa Bárbara do Caparão, *Mexia 4099* (NY, US). GOIÁS: Serra do Caiapó, 42 km south of Caiapônia, *Prance & Silva 59692* (F, MO, US). MARANHÃO: Rio Alto Turiaçu, Nueva Esperança, *Jangoux y Bahia 252* (RB), *266* (MO, NY). MATO GROSSO: Serra do Roncador, 55 km N de Barra do Garças, *Prance & Silva 59442* (MO, NY). MATO GROSSO DO SUL: Dourados, Colónia Agrícola Federal, *Swallen 9410* (US). PARÁ: Varadouro de Periquito a Pimental, Tapajó, *Kuhlmann 1915* (RB, US); Rio San Manuel, entre Igarapé Prata a Igarapé Preto, *Pires 3810* (US); Ingatubinha, *Black 47-2116* (US); estrada da Cachoeira Porteira, km 72, *Cid et al. s.n.*, 1 July 1980 (MO); Belém, *Pires & Black 599* (US), *Archer 8103* (F, US), *Silva 24* (F); Moju River, Rubber Estate Fábrica, *Goeldi 18* (F, US); Boa Vista, Rio Tapajós, *Swallen 3198* (R, RB, US). PARANÁ: Garuvá, *Hatschbach 3453* (BAA, SI); Ilha dos Bandeirantes, Rio Paraná, *Lindeman & Haas 4368* (US). RIO DE JANEIRO: Serra do Andaraí, *Rosa 95* (R); Parque Nacional da Tijuca, Serra dos Pretos Forros, *Martinelli 3118* (R); Cachoeira de Macau-Nova Friburgo, *Sucre & Soderstrom 9061* (R). RIO GRANDE DO SUL: Finca Peixoto, *Malme 1332* (GH); São Leopoldo, *Dutra s.n.* (US-1388850); Esteio, pr. Porto Alegre, *Rambo 38269* (US). RORAIMA: vicinity of Aguaris, *Prance et al. 9651* (F, US); Rio Jarani, *Pires et al. 14420* (US); between Maitá and Paramiterí Indian village, *Prance et al. 10560* (US). SANTA CATARINA: Mato São Pedro, *Klein 11770* (US); Braço Joaquim, Luis Alves, *Reitz & Klein 2062* (US). SÃO PAULO: Cainua, *Brade 7818* (R); Morro das Pedras, *Brade 7846* (R), *9167* (R); Ubatuba, *Costa s.n.* (US-1761194). COLOMBIA. AMAZONAS: Puerto Nariño and vicinity, along lower Río Loretoyacu, *Zarucchi 1067* (COL); Fleuve Amazona, 5 km en amont de Leticia, *Sastre & Gómez-Pompa 538* (COL); Monkey Island, a few miles up river from Leticia on the Amazon, *Gillett 16529* (COL, US); edge of Río Agua Branca about 80 km W of Leticia, Trapecio, *Schultes & Black 46-337* (US). ANTIOQUIA: 15 km W of Chiborodó, *Feddema 1968* (NY, US). CHOCÓ: bank of Río San Juan, near Andagoya, *Killip 35389* (COL); Hoya del Río San Juan, Quebrada Cunperro, abajo de Noanamá, *Forero et al. 4860* (COL); hoya del Río San Juan, arriba de Palestina, *Forero et al. 4169* (COL, MO); Muquí, alto de Buey, *Kjall von Sneidern a-26* (COL, MO); Unguía, *Forero et al. 1988* (COL, MO); hoya del Río San Juan, Quebrada La Sierpe, *Forero et al. 3973* (MO). MAGDALENA: Santa Marta, *H. H. Smith 2126* (MO, NY). META: about 20 km SE of Villavicencio, *Killip 34256* (COL, F, US); reserva de La Macarena, margen izquierda del Río Duida, 20 km de su desembocadura, *Pinto et al. 727, 773* (COL); serranía de La Macarena, orilla del Río Sansa, *Fernandez Perez & Jaramillo 5017* (COL); San Pedro de Arimena, *Haught 2820* (COL, US); boca del Caño Cabra, *Pinto & Sastre 1000* (COL). VALLE DEL CAUCA: Río Calima, región del Chocó, entre Pailón y El Coco, *Cuatrecasas 21251* (F, US); Río Calima, entre La Herradura de Ordoñez y Peña de Campo Triste, *Cuatrecasas 16673* (F, US). VAUPÉS: Río Vaupés, above raudal Yuruparí, *Schultes & Cabrera 18723* (GH, US); Caño Curuyarí, afluente izquierdo del Vaupés, selva y matorral en Zurubi, *Cuatrecasas 7215* (COL). COSTA RICA. GUANACASTE: NW of Lago Arenal, *Croat 423* (MO). LIMÓN: 10 km por ruta al S de Cahuita, *Pohl & Pinette 13188* (F); La Bomba, *Pohl & Davidse 11105* (F). PUNTARENAS: Golfo Dulce Area, vicinity of Esquinas Experimental Station, *Allen 5299* (F, MO, US); 5 km SE of Rincón, Osa Península, *Pohl & Davidse 10711* (F, MO, US). SAN JOSÉ: Basin of El General, *Skutch 4816* (US). ECUADOR. GUAYAS: Tenguel, S of Guayaquil, *T. Holmgren 86* (US). LOS RIOS: Río Palenque Biological Station, km 56 Quevedo–Santo Domingo, *Dodson 5817* (US). NAPO PASTAZA: between Tena and Arquidona, *Asplund 9171* (R, US); Tena, *Asplund 10306* (NY, US). PICHINCHA: entre Santo Domingo y Quinindé, *Acosta Solís 13926* (US); 20 km W of Santo Domingo de Los Colorados, *Cazalet 5140* (NY, US). TUNGURAHUA: valley of Río Pastaza, La Victoria, *Asplund 10058* (US). GUATEMALA. ALTA VERAPAZ: Río Santa Isabel, *Steyermark 45867* (F, US). PETÉN: Tikal National Park, Tikal, *Lundell 16484* (US). SUCHITEPEQUEZ: near Piquizate, *Steyermark 47695* (F, US). GUYANA: Yarikita, *Hitchcock 17590* (F, US); lower Saramacca River, *Maguire 23741* (F, GH, NY, RB); between Gamura and Amatuk, Potaro River, *Maguire 23008* (GH, NY); Kaieteur Plateau, *Cowan & Soderstrom 2026* (NY, US), *2120* (US); Tumatumari, *Gleason 290* (GH, NY, US); vicinity of Tumatumari, Potaro River, *Hitchcock 17410* (US); Amacura River, *de la Cruz 3478* (GH, NY, US); Pomeroon River, *de la Cruz 3220* (F, GH, US), *3166* (GH, NY, US); Kanuku mountains, in drainage of Takutu River, *A. C. Smith 3349* (GH, NY, US), *3423* (US); Barima River, *Jenmann 7115* (US), *Archer 2513* (US); vicinity of Issorora on Aruka River, *Hitchcock 17568* (MO, US); Mazaruni Station, *Archer 2431* (NY, US), *Tutin 139* (GH, US). FRENCH GUIANA: Compte River, *Mori 8932* (NY); Maripasoula, *Hoock 132* (US); Haut Itany, *Hoock 111* (US). HONDURAS. ATLÁNTIDA: Lancetilla, 10 km al SW de Tela, *Nelson 5205* (MO); vicinity of Tela, *Standley 55116* (US). GRACIAS A DIOS: alrededores del Río Plátano, *Clewell 4019* (MO). MEXICO. CHIAPAS: Libertad, *Matuda 18138* (F, US); Escuintla, *Matuda 332* (US). OAXACA: El Palmar, Zongolica, *Vera Santos 2639* (NY); Ubero, *Williams 9483* (F, US). VERACRUZ: Zacuapán, *Purpus 8070* (F, NY, US). NICARAGUA. ZELAYA: Guamil, *Molina 2225* (F), *2266, 2347* (F, US). PANAMA. BOCAS DEL TORO: Chiriquicito, 5 mi. S of Guarumo River, *Dwyer 2108* (MO); cercanías de la Laguna Chiriquí, *von Weddell 2575* (GH, MO). CHIRIQUÍ: near Puerto Armuellos, *Woodson Jr. 858* (MO). COLÓN: Trinidad basin, near Cirrí River, *Pittier 4027* (NY, US). DARIÉN: vicinity of Paya, Río Paya, *Stearn et al. 440* (MO); vicinity of Campamento Buenavista, Río Chucunaque above confluence with Río Tuquesa, *Stearn et al. 827* (MO, US), *957* (MO). PANAMÁ: east of the Río Tecumen, *Standley 26682* (US). PARAGUAY: entre el Río Apa y el Río Aquidabán, *Fiebrig 4706* (F); near Tobatí, *Archer 4843* (US); Alto Paraguay, Primavera, *Woolston G. 96* (SI); Curupaytí, Humaitá, *Bernardi 18476* (MO); Villarica, *Jörgensen 3540* (MO, US). Without locality, *Weddell 3152* (F, NY). PERU. AMAZONAS: left bank of Río Marañon, above Cascadas de Mayasi, *Wurdack 1976* (NY, US). HUANUCO: Tingo María, *Asplund 13210* (NY, US), *Allard 21662* (US); 6 km S of Tingo María, *Seibert 2258* (MO, US), *Storp 9479* (F). JUNÍN: Colonia Perené, *Hitchcock 22058* (US); Chanchamayo Valley, *Schuncke 129* (F, US); bajo Río Nanay, *Williams 189* (F); above Pongo de Manseriche, right bank of mouth of Río Santiago, *Mexia 6151* (F, US); La Merced, Hacienda Schuncke, *McBride 5646* (F, US). LORETO: Río Hueppi, *Gentry et al. 21852* (MO); Río Itaya, *Diaz et al. 653* (MO); Caño Iricahua, abajo de Jenaro Herrera, *Encarnación 25080, 25087* (US); Caño Supai, *Encarnación 25056* (US); lower Río Nanay, *Williams 589* (US). SAN MARTÍN: Quebrada de Almendras, *Schunke Vigo 4461* (F, US); Tarapoto, *Williams 5554* (F); Juan Juí, *Klug 3813* (F, GH, MO, US); San Roque, *Williams 7521* (F, US). SURINAM: Kayselberg airstrip, *Cramer 2980* (NY); Oelemari, *Wessels Boer 926* (GH); opposite Gansee, *van Doselaar 1325* (US). Without locality, *Weigelt s.n.* (US-1720223). TRINIDAD: Ortoire River, *Britton et al. 2539* (NY, US); Port of Spain, Saddle Road, *Tutin s.n.* (US-2954418); 3 mi. W of Tabaquite, *Soderstrom 1074* (US); El Tucuche Mountain, *Soderstrom 1048* (US). VENEZUELA. T. F. AMAZONAS: Isla Sebastián, Río Casiquiare, *Liesner & Clark 8945* (MO); Sierra Parima, *Steyermark 107022* (MO, NY), *Cardona 1346, 1478* (US); 5 km E of San Fernando de Atabapo, *Davidse et al. 17164* (MO). BARINAS: Reserva Forestal de Ticoporo, *Aristeguieta 7005* (MO), *Breteler 3710* (NY). BOLÍVAR: Guayapo, Bajo Caura, *Williams 11999* (F, US); Río Paragua, between Guaiquinima and Río Torono, *Killip 37425* (NY, US), *37527* (US), *37480* (NY, US); Caño Pablo, *Liesner & Morillo 13943* (MO); El Dorado, *Curet 213* (US); Salto de Chalimano en el Río Paramichi, *Steyermark 90706* (US); selva al lado del Río Nichare, *Steyermark 95673* (MO, NY, US). DELTA

AMACURA: 33 km al E de El Palmar, *Steyermark 93096* (US); a lo largo del Caño Araguao, *Steyermark et al. 114792* (MO); 73 km al SE de Piacoa, *Davidse & González 16466* (MO). LARA: near Barquimiseto, *Saer 284* (NY, US). MIRANDA: along Río Grande del Tuy, above Paparo, *Pittier 6328* (US). MONAGAS: 1.5 km N of La Hormiga, *Wurdack & Monachino 39527* (RB, NY, US); 2 km N of Santa Inés, *Pursell et al. 9167* (US). SUCRE: Península de Paria, entre Los Pocitos de Santa Isabel y Roma, *Dumond et al. 7659* (NY). ZULIA: 3 km E of Río de Oro, *Davidse et al. 18784* (MO); alrededores de Casigua El Cubo, *Bunting 7815* (MO); intersección del Río Catatumbo y la ruta entre Maracaibo y La Fría, *Davidse et al. 18838* (MO); Quebrada Tayaya, *Davidse et al. 18493* (MO).

Hitchcock & Chase (1910, 1915) distinguished *P. stoloniferum* from *P. frondescens* by the sizes of the plants and the panicles and by the length of the upper glume compared with the lower lemma. Abundant material showed a complete gradation in these characters. Therefore, we are treating *P. frondescens* as a synonym of *P. stoloniferum*.

13. Panicum venezuelae Hackel, Oesterr. Bot. Z. 51: 368. 1901. *Brachiaria venezuelae* (Hackel) Henrard, Blumea 3: 435. 1940. TYPE: Venezuela. Without locality: *Eggers 13471* (holotype, W, not seen, fragment at US). Figure 15.

P. ineptum A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 17: 509. 1915.

P. berteronianum Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 5. 1921. Not *P. berteronianum* Schultes, 1854. TYPE: Venezuela. Federal District: La Guayra, *Zollner s.n.* (holotype, B, not seen, fragment at US).

Stoloniferous, densely and freely branching perennials, with very long, slender, prostrate stolons. *Culms* decumbent to ascending, densely branching mostly at the lower nodes, 40–80 cm tall; internodes 3–8 cm long, cylindric to compressed, hollow, sparsely pilose to glabrous; nodes densely pilose, with long whitish, usually retrorse hairs. *Leaf sheaths* 1–4 cm long, usually shorter than the internodes, stramineous, striate, sparsely to densely pilose with long, whitish hairs, the margins ciliate. *Ligule* membranous-ciliate, ca. 0.5 mm long, with long hairs toward the back at the base of the blade; collar stramineous, pilose. *Leaf blades* ovate-lanceolate to lanceolate, acuminate, flat, 3–9 cm long, 0.5–1 cm wide, cordate basally, densely to sparsely hirsute; the margins long-ciliate toward the base, otherwise ciliate to scabrous, cartilaginous; midnerve inconspicuous; *pseudopetiole* short, ca. 0.2 cm long. *Panicles* lax, long-exserted, 2–11 cm long, 1–3 cm wide, formed by 4–10 distant, alternate, short branches, these divergent from the axis and racemose, with cleistogamous spikelets in pairs arranged along either side of a ventral septum; chasmogamous spikelets occasionally present; axis longitudinally ridged, long-hirsute, the axils of the branches densely pilose, axis of the branches triquetrous, densely hirsute; pedicels short. Axillary panicles similar to the terminal panicle, but short-exserted and few-flowered. *Spikelets* ellipsoid, 2.5–3 mm long, 1.1–1.3 mm wide, stramineous to greenish, the glumes and lower lemma sparsely to densely hirsute. *Lower glume* ovate, 1.5–1.7 mm long, ½ or more the length of the spikelet, 3-nerved, the midnerve scabrous. *Upper glume* 2.6–2.9 mm long, gibbous, 5(–7)-nerved, with thick, papillose hairs over the entire surface or only toward the apex, 2 glands occasionally present on the middle portion of the outer surface, the inner surface scabrous. *Lower lemma* larger than the upper glume, the apex ± inflated, with a few thick hairs, the middle portion flattened and glabrous, the margins inrolled toward the apex, 5-nerved, the lateral nerves remote from the midnerve, 2 glands sometimes present on the middle portion of the outer surface. *Lower palea* elliptic to obovate, 1.6–1.8 mm long, 0.7 mm wide, hyaline, shortly pilose toward the upper margins, glabrous over the rest of the surface; male flower absent. *Upper anthecium* ellipsoid to obovoid, obtuse, 1.6–1.8 mm long, 0.8–1.1 mm wide, stramineous; lemma 5-nerved, strongly convex; anthers 3, those of the cleistogamous spikelets small, 0.2–0.3 mm long; anthers of the chasmogamous spikelets 0.9 mm long. *Caryopsis* 1.3 mm long, 1 mm wide; hilum punctiform. In flower all year.

Distribution. This species occurs in Guatemala, Honduras, Cuba, Haiti, the Dominican Republic, and Venezuela to northern

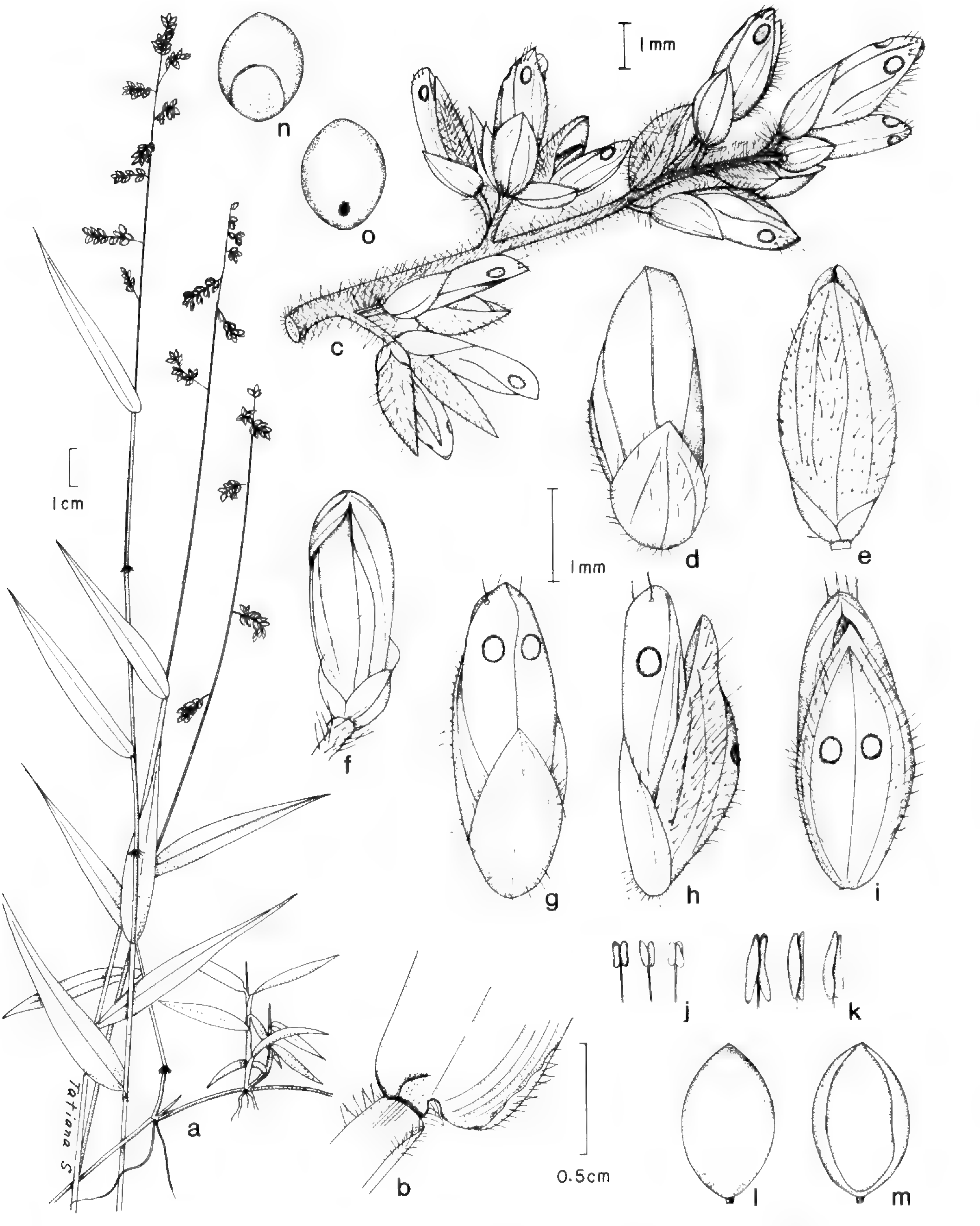

FIGURE 15. Panicum venezuelae.—*a. Habit.*—*b. Ligule.*—*c. Racemose branch.*—*d. Spikelet, ventral view.*—*e. Spikelet, dorsal view.*—*f. Lower lemma.*—*g. Spikelet, ventral view, lower lemma with glands.*—*h. Spikelet, lateral view, upper glume and lower lemma with glands.*—*i. Spikelet, dorsal view, upper glume with glands.*—*j. Anthers of cleistogamous flower.*—*k. Anthers of chasmogamous flower.*—*l. Upper anthecium, dorsal view.*—*m. Upper anthecium, ventral view.*—*n. Caryopsis, embryo side.*—*o. Caryopsis, hilum side. Based on* Pinto 307 *(US)*.

Brazil in humid and shady places at 100–1,200 m elevation.

Representative specimens examined. BRAZIL. ALAGOAS: Tapera, *Pickel s.n.* (US-1645543), *2469* (US). BAHIA: Alagoinhas, *Chase 8135* (US); camino de Santa Inés a Rio Bahia, *Pinheiro 7855* (MO); Espigão Mestre, 6 km S of Cocos, *Anderson et al. 37036* (F, MO); Serra do Itiuba, 6 km E of Itiuba, *Harley et al. 16203* (MO, US); Santa Terezinha, *Bondar 2609* (SP, US); Paraguaçú-valley, Muritiba, *Pinto 307* (US); Feira de Santana, *Chase 8066* (F, RB, US), *8070* (US); Cachoeira, vale dos rios Paraguaçú e Jacuipé, *Pedra do Cavalo 475* (CEPEC); basin of the upper São Francisco River, just beyond Calderão, ca. 32 km NE from Bom Jesus de Lapa, *Harley 21497* (CEPEC); rodovía Sta. Inés a Rio Bahia aos 10 km, *Pinheiro 1855* (CEPEC, US). CEARÁ: Serra de Baturité, morro de Ceu, *Eugenio 278* (RB). PARAÍBA: Moreno, *Pickel 3848* (RB); Areia, *Coelho de Moraes 850* (P). PERNAMBUCO: Garanhuns, *Chase 7786, 7789* (F, US); Pesqueira, *Pickel 1663* (US); Fazenda Recreio, Mun. de Rio Grande, *Faria 2495* (RB). RIO GRANDE DO NORTE: Nova Cruz de Montanhas, *Swallen 4813* (RB, US). CUBA. ORIENTE: Barbí, Loma del Gato, Sierra Maestra, *Ekman 15661* (US); Loma del Gato, S of Loma San Juán, *Leon et al. 10190* (US). GUATEMALA. GUATEMALA: near Fiscal, Standley *59580, 80411, 80463* (F, US), *80630* (F). HONDURAS. EL PARAÍSO: Quebrada de El Muro, between Las Mesas and Yuscarán, *Standley 29263* (US); road to Yuscarán, *Swallen 11329, 11333* (US). MORAZÁN: near El Jicarito, *Standley 20874, 21640* (F), *27498* (US), *Swallen 11377* (US); trail from La Quince, El Zamorano, *Standley 14567, 21272* (US); campus of Escuela Agrícola El Zamorano, *Pohl & Davidse 12458* (MO); 8 km S of La Venta by road, *Davidse & Pohl 2155a* (MO). SANTO DOMINGO. MONTE CRISTI: near Arroyo Seco, *Ekman 12608, 13085* (US); Puerto Plata, Bajabonico, *Ekman 14499* (US). SANTIAGO: San José de las Matas, *Ekman 14602* (US), *Jiménez 950* (US). VENEZUELA. DISTRITO FEDERAL: Colinas de Yaguará, *Tamayo 1449* (F); Antimano, *Pittier 12581* (US); entre Caracas y La Guayra, *Burkart 17013* (SI). FALCÓN: Serranía de San Luis, Fila Las Playitas, *Ruiz 2543* (MO). LARA: en cerros arriba del caserío Simara, *Burandt Jr. v0192* (MO); Loma de León, Iribarre, *Tamayo 3743* (MO); Hacienda Sosa, *Badillo s.n.* (US-1760677).

Henrard (1940) transferred *P. venezuelae* to *Brachiaria* without explanation. Previously, when describing *P. ineptum*, Hitchcock & Chase (1915) did not refer it to any of the groups of *Panicum*. Brown (1977) pointed out that this species, being a C_3 plant, is not actually a *Brachiaria*, since the genus *Brachiaria* is totally C_4 or Kranz. Sendulsky (1978), in her treatment of *Brachiaria* for Brazil, called attention to the size of the anthers and to the unusual form, for *Brachiaria*, of the long-winged lodicules. She suggested retention of this species in *Panicum*.

The panicle, habit, and spikelets (which bear glands on the lower lemma and occasionally on the upper glume also) suggest inclusion of *P. venezuelae* in sect. *Stolonifera*. However, this is the only species in the section with cleistogamous spikelets, a feature otherwise only found in *Panicum* in species of subg. *Dichanthelium* A. Hitchc. & Chase. Also, the glands differ from those in other species of sect. *Stolonifera*; in *P. venezuelae* the glands are bigger and depressed, not crateriform.

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Appendix I

List of taxa and informal groups. Species listed in italics are accepted. Those listed in roman are not accepted.

Brachiaria venezuelae (Hackel) Henrard
Dichanthelium, subg.
Eriochloa pulchella (Raddi) Kunth
Hymenachne leptostachya (J. S. Presl) Fourn.
Ichnanthus gardneri Mez
Latissima, group
Laxa, sect.
Lophatherum gracile Brongn.
Lorea, sect.
Megista, sect.
Molinia caerulea (L.) Moench
Monticola, sect.
Panicum L.
P. albospiculatum Swallen
P. andreanum Mez
P. apricum Swallen
P. bambusaefolium Desv.
P. berteronianum Mez
P. biglandulare Scribner & Smith
P. bipustulatum Schldl.
P. blepharophorum Mez
P. blepharophorum J. S. Presl
P. boliviense Hackel
P. brachyclados Reichb.
P. brachystachyum Trin.
P. bresolinii L. B. Smith & Wassh.
P. bulbosum Kunth
P. chapadense Swallen
P. crateriferum Sohns
P. ctenodes Trin.
P. ctenodes var. major Trin.
P. frondescens G. Meyer
P. ineptum A. Hitchc.
P. irregulare Swallen
P. kegelii Steudel
P. kleinii Swallen
P. latissimum Mikan ex Trin.
P. leprieurii Steudel
P. leptachne Doell
P. leptostachyum J. S. Presl
P. macrophyllum Raddi
P. olyraefolium Raddi
P. paucifolium Swallen
P. piauiense Swallen
P. pilosum Swartz
P. pirineosense Swallen
P. pompale Swallen
P. pulchellum Raddi
P. quadriglume (Doell) Henrard
P. rude Nees
P. secundum Trin.
P. secundum var. inaequiglume Doell
P. secundum var. subaequiglume Doell
P. semitectum Swallen
P. soderstromii Zuloaga & Sendulsky
P. stoloniferum Poiret
P. umbrosum Salzm. ex Steudel
P. venezuelae Hackel
Parvifolia, sect.
Parviglumia, sect.
Phanopyrum, sect.
Phanopyrum, subg.
Pseudechinolaena Stapf
Puelia ciliata Franch
Sarmentosa, sect.
Sarmentosum, subg.
Stolonifera, group
Stolonifera, sect.
Sucrea sampaiana (A. Hitchc.) Soderstrom
Verrucosa, sect.

A REVISED TREATMENT OF BORAGINACEAE FOR PANAMA[1]

James S. Miller[2]

ABSTRACT

The Boraginaceae known from Panama now number 52 species compared with the 33 that were recognized the last time the family was treated. Eight of these are described as new species, five in the genus Cordia *and three in* Tournefortia. *Among the new records for Panama is* Moritzia lindenii, *the genus being previously unknown in the country. Most genera of Panamanian Boraginaceae are South American in origin. More than half of the species are widespread in the Neotropics, but the remainder show stronger affinities with the rest of Central America than with South America or with the West Indies.*

The Panamanian species of Boraginaceae have been treated numerous times since the turn of the century. Standley's floras of the Canal Zone (1928) and Barro Colorado Island (1933) predate Ivan Johnston's studies of the family, and many of the names Standley used were later placed in synonymy by Johnston, who published extensively on the family from the 1920s to the 1950s. Johnston's book *The Botany of San José Island* (1949b) treated another island flora, but unfortunately all of the works up to this time essentially describe the flora of the Canal Area. Thomas B. Croat's *Flora of Barro Colorado Island* (1978) provides an excellent treatment of the species on the island.

The Boraginaceae of Panama were treated for the entire country by Nowicke (1969) in the *Flora of Panama*. Subsequently, the number of collections from Panama increased, especially from regions then poorly known. Floristic studies in other Central American countries have altered taxonomic concepts of some Panamanian species. Examination of collections while preparing a revision of *Cordia* for Mexico and Central America (Miller, 1985) and of floristic treatments for Nicaragua (Miller, in press) and Mesoamerica (Miller, in prep.) revealed nine previously unrecorded species as well as eight undescribed species for Panama, a significant increase from 33 to 52 species.

Five subfamilies are currently recognized within the Boraginaceae (Johnston, 1951; Cronquist, 1981): Cordioideae, Ehretioideae, Heliotropioideae, and Boraginoideae, all of which have representatives in Panama, and the Wellstedioideae, which consists of two African species. The Cordioideae and Ehretioideae have sometimes been treated together as a separate family, Ehretiaceae (Lindley, 1830; Airy Shaw, 1973; Hutchinson, 1973). They are, however, clearly related to the other three subfamilies and are tied to them by

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[1] *W. G. D'Arcy suggested this project and provided encouragement throughout. C. W. Hamilton and K. Krager helped during my visit to Panama. J. K. Myers provided the illustrations, J. D. Dwyer helped with the Latin descriptions, M. J. Huft sent information regarding collections at the Field Museum, and W. G. D'Arcy, P. P. Lowry II, and W. D. Stevens read portions of the manuscript. G. D. McPherson and J. W. Nowicke provided valuable review comments and I thank them for their help. The staff of the Missouri Botanical Garden assisted in many ways and their help is greatly appreciated. I also thank the curators of the following herbaria for lending specimens and for hospitality: A, AAU, ARIZ, ASU, B, BM, BR, C, CAS, CFMR, CHAPA, CR, DS, DUKE, ENCB, F, FHO, G, GB, GH, HAL, HNMN, IND, INIF, K, L, LE, LL, MEXU, MICH, NMC, NY, P, PMA, POM, RSA, SCZ, SD, SLPM, TEX, U, UC, US, USJ, WIS. My wife, Leslie, provided encouragement and accompanied me during field studies in Panama.*

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intermediate genera. Recent authors (e.g., Cronquist, 1981) have generally accepted their inclusion in a broadly defined Boraginaceae. Recognition of one family with five subfamilies also provides more information about relationships.

PHYTOGEOGRAPHIC RELATIONSHIPS OF PANAMANIAN BORAGINACEAE

The Boraginaceae of Panama make up an assemblage of species derived from different regions. In order to assess their phytogeographic relationships, the distributions of the constituent genera and species were determined. The genera *Borago* and *Cynoglossum* were excluded from the generic analysis, as both are not indigenous. The remaining seven genera are listed in Table 1 with their presumed centers of origin.

Four of the seven genera are clearly South American in origin. All three species of *Moritzia* occur in South America, with only one ranging north as far as Costa Rica. Although *Cordia*, *Heliotropium*, and *Tournefortia* are pantropical in distribution, they are strongly centered in South America.

Bourreria and *Hackelia* clearly originated in North America. The majority of the species of *Bourreria* occur in Mexico, with an additional group centered in the Greater Antilles; only a few species range south to southern Central America and South America. *Hackelia* is distributed widely in north temperate regions with the greatest concentration of species in the western United States (Gentry & Carr, 1976).

Ehretia is more problematic but certainly seems to be of Old World origin. Most of its species occur in Africa but it is well represented in tropical and subtropical Asia. Whether or not this strong African representation indicates that *Ehretia* originated there or radiated there as the climate became drier at the end of the Oligocene (Raven & Axelrod, 1974) is not clear. Regardless, *Ehretia* is poorly represented in the New World, with only three species, and the southern limit of distribution is in Chiriquí Province of western Panama. The presence of *Ehretia* in Panama, then, probably results from southward migration.

From this it seems clear that the generic affinities of Panamanian Boraginaceae are predominantly South American. Four of the seven genera that account for all but four of the native Panamanian Boraginaceae are centered in South America. *Hackelia* and *Bourreria* are North American in origin and, at least in the New World, so is *Ehretia*. The strong South American tie agrees with other analyses at familial or generic levels. Gentry (1985) reported that 84% of the plant species in Panama were members of Gondwanaland families, and Karr (1985) reported that at least 50% of the bird species in Panama were members of families that were South American in origin.

Distributions of Panamanian species of Boraginaceae are summarized in Table 2 following Davidse's (1985) format. Distributional data were derived from herbarium specimens and literature (Gentry & Carr, 1976; Gibson, 1970; Johnston, 1924, 1927, 1928, 1930, 1935, 1940, 1949a, c, 1950; Miller, 1985, in press; Nash & Moreno, 1981; Nowicke, 1969). Each species was scored for presence in North America, Central America, South America, and the West Indies. In addition, presence in the Old World or cultivated status was noted.

INTRODUCED SPECIES

Two introduced species of Boraginaceae are known from Panama. *Borago officinalis* L. is widely cultivated throughout the world and occasionally is found naturalized, although these populations do not appear to persist for long. *Cynoglossum amabile* Stapf & J. R. Drumm. is a native of China originally imported as an ornamental and has become established in numerous localities at high elevations in the Neotropics.

COSMOPOLITAN SPECIES

Two species, *Heliotropium curassavicum* L. and *H. indicum* L., are widespread in the

TABLE 1. *Native genera of Panamanian Boraginaceae and presumed centers of origin.*

Genus (Number of Species)	Number of Species in Panama	% of Panamanian Species	Center of Origin
Bourreria (50)	2	4	North America
Cordia (300+)	27	54	South America
Ehretia (50)	1	2	Paleotropics
Hackelia (45)	1	2	North America
Heliotropium (150)	4	8	South America
Moritzia (3)	1	2	South America
Tournefortia (150)	14	28	South America

New World and have become widespread in the Old World as introduced weeds (Nowicke & Miller, in press).

NORTHERN SPECIES

Seven species of borages reach their southern limits in Panama. A single species each of *Bourreria* and *Ehretia*, both genera probably northern in origin, are included in this group. Five Central American species of *Cordia* make up the remainder of this group, of which four are Central American species of lowland wet forests. *Cordia diversifolia* Pavón ex A. DC. and *C. megalantha* S. F. Blake range north to Veracruz in southern Mexico; *C. lucidula* I. M. Johnston and *C. porcata* Nowicke range only as far north as Nicaragua. These four belong to Central American species groups. The fifth, *Cordia inermis* (Miller) I. M. Johnston, reaches from Panama north to Sinaloa, Mexico in dry disturbed areas. It is a member of a group of about eight species that is widespread in the Neotropics of which *Cordia foliosa* Martens & Galeotti is the only other species restricted to Central America.

NORTHERN–SOUTHERN SPECIES

Twenty-seven species, comprising slightly more than half of the Boraginaceae known from Panama, range widely in the Neotropics. With two exceptions, all of these are truly widespread species that indicate no particular geographic affinity. The genus *Moritzia* consists of three species and is entirely restricted to South America except for *M. lindenii* (A. DC.) Gürke ex Benth., which ranges north to Costa Rica. *Hackelia* is a northern genus, but *H. mexicana* (Schldl. & Cham.) I. M. Johnston is widespread in Central America

TABLE 2. *Distributions of Panamanian Boraginaceae.*

Category[1]	Number of Species	Combined Categories	Number of Species	% of Flora
1. Cultivated	1	Introduced	2	4
2. Alien Weeds	1			
3. Cosmopolitan[2]	2	Cosmopolitan	2	4
4. CA & WI & NA	0	Northern	7	13
5. CA & WI	0			
6. CA & NA	0			
7. WI & NA	0			
8. CA	7			
9. SA & WI	0	Southern	0	0
10. SA	0			
11. CA & SA & WI & NA	3	Southern–Northern Combination	27	52
12. CA & SA & WI	11			
13. CA & SA & NA	0			
14. CA & SA	13			
15. Panama	7	Endemic Element	14	27
16. Panama & Costa Rica	4			
17. Panama & Colombia	3			

[1] Abbreviations: CA = Central America (Costa Rica–Tropical Mexico); NA = North America (United States to Subtropical Mexico); SA = South America; WI = West Indies.

[2] Includes all native American species distributed on at least one Old World continent.

TABLE 3. *Endemic elements among the Boraginaceae of Panama and distributions.*

Species	Distribution[1]	Elevation (m)
Cordia anisophylla	CN, DA, PA, SB	0–1,000
Cordia correae	CC, PA, VE	800–1,000
Cordia croatii	CC, VE, Costa Rica	800–1,200
Cordia lasiocalyx	BT, CA, CC, DA, PA	0–800
Cordia leslieae	PA	800–1,000
Cordia protracta	SB, Colombia	sea level
Cordia tacarcunensis	DA, Colombia	100
Tournefortia brenesii	VE, Costa Rica	800–1,350
Tournefortia johnstonii	CH, VE, Costa Rica	1,000–1,300
Tournefortia longispica	BT, CH, CC, VE	600–1,500
Tournefortia multiflora	CN, VE	400–900
Tournefortia ramonensis	BT, CH, Costa Rica	2,000–3,000
Tournefortia tacarcunensis	DA, Colombia	1,500
Tournefortia urceolata	CH, CN, SB	400–2,300

[1] Abbreviations for provinces: BT = Bocas del Toro; CA = Canal Area; CH = Chiriquí; CC = Coclé; CN = Colón; DA = Darién; PA = Panamá; SB = San Blas; VE = Veraguas.

and the Andes. *Cordia* and *Tournefortia* contain 22 of the widespread species, all of which are found in most of Central America, but only about one-third of them range as far south as southern Brazil and Argentina. The majority have southern limits of distribution in northern South America or extend south only in the Andes.

ENDEMICS

Fourteen species of Panamanian borages, all species of *Cordia* and *Tournefortia*, are known only from Panama and adjacent Colombia or Costa Rica. Seven are known only from Panama (Table 3); three range slightly into Colombia, and four others extend into Costa Rica. All are relatively rarely collected. Eight are described as new in this paper. All of the species of *Tournefortia* and three of *Cordia* occur at mid to high elevations, while the widespread taxa generally inhabit lowlands.

More than half of the Panamanian species of Boraginaceae are widespread or introduced and are not helpful in indicating geographic affinity. The pattern of the lowland Panamanian flora being composed primarily of South American elements has been reported for other groups (Davidse, 1985; Raven & Axelrod, 1974, 1975). Hammel (1986) found a similar pattern for a subset of the flora of La Selva in lowland Costa Rica. The fourteen endemic elements indicate that the Panamanian flora is old enough to have become distinct from that of surrounding areas. The relationships of the endemics are poorly understood but the majority are probably with species of Colombia and Ecuador. Seven species have distributions extending to the north, and many are members of species complexes restricted to Mexico and Central America. These species, and the absence of southern elements, indicate that Panamanian borages have a stronger relationship at the species level with Central America than with South America. Although most of the species belong to originally South American genera, a significant portion of these seem to have reached Panama from the north, perhaps as a result of secondary radiations of *Cordia* and *Tournefortia* in Mexico and northern Central America.

SYSTEMATIC TREATMENT

Boraginaceae Juss., Gen. Pl. 128. 1789.

Trees, shrubs, lianas, vines, or herbs, often conspicuously pubescent, the hairs often with a basal cystolith. Leaves estipulate, simple, alternate or rarely opposite. Inflorescence cymose to paniculate, the branches often scorpioid, helicoid, or reduced and capitate to glomerate. Flowers perfect or imperfect, usually 5-merous; calyx usually persistent, tubular to campanulate, usually 5-lobed; corolla gamopetalous, usually 5-lobed; stamens usually as many as the corolla lobes and alternate with them; ovary superior, 2-carpellate but often becoming falsely 4-locular; ovules usually 4, anatropous; style 1, terminal or gynobasic, simple or branched; stigmas 1–4. Fruits drupaceous and 1–4-seeded, sometimes dry at maturity, or of 4 nutlets.

The Boraginaceae are worldwide in distribution and comprise about 100 genera with approximately 2,000 species. Nine genera are known from Panama containing 52 species. Although no collections of the genus *Borago* are known from Panama, the European species *Borago officinalis* L. is often cultivated in gardens in other parts of Tropical America and is included here as it undoubtedly occurs in Panama.

KEY TO THE GENERA OF BORAGINACEAE IN PANAMA

1a. Plants trees or shrubs; stigmas 2 or 4; fruits fleshy at least when young.
  2a. Style twice divided into 4 stigmas .... *Cordia*
  2b. Style once divided into 2 stigmas.
    3a. Calyx lobes valvate; corolla fleshy, longer than 8 mm .... *Bourreria*
    3b. Calyx lobes imbricate or open in bud; corolla thin, shorter than 5 mm .... *Ehretia*
1b. Plants herbs, lianas, vines, or clambering shrubs, rarely small trees; stigma 1; fruits dry except in *Tournefortia*.
  4a. Fruits entire to shallowly 4-lobed; style terminal; corolla white, green, or yellow-green, rarely purple.
    5a. Plants woody; fruits fleshy .... *Tournefortia*
    5b. Plants herbaceous; fruits dry .... *Heliotropium*
  4b. Fruits deeply 4-lobed, consisting of 4 separate nutlets or the nutlets solitary by abortion in *Moritzia*; style gynobasic; corolla blue.
    6a. Calyx campanulate to rotate.
      7a. Nutlets with glochidiate spines; calyx lobes less than 4 mm long.
        8a. Cauline leaves clasping at base; nutlets spreading, the spines ca. 0.5 mm long .... *Cynoglossum*
        8b. Cauline leaves cuneate to decurrent but not clasping at base; nutlets erect, the spines 1–4 mm long .... *Hackelia*
      7b. Nutlets lacking spines, shallowly ribbed; calyx lobes more than 10 mm long .... *Borago*
    6b. Calyx cylindrical .... *Moritzia*

Borago L., Sp. Pl. 137. 1753; Gen. Pl. ed. 5. 67. 1754. TYPE: *Borago officinalis* L., Sp. Pl. 137. 1753.

Annual or perennial herbs, the stems hirsute. Leaves alternate, the basal ones petiolate, the cauline ones sessile. Inflorescence a corymbose group of racemes, bracteate. Flowers bisexual; calyx with 5 lobes, these free to nearly the base; corolla broadly campanulate to rotate, the 5 lobes imbricate, the tube short, appendaged in the throat; stamens 5, exserted, the filaments broad, the anthers linear; ovary 4-lobed, the ovules 4, the style gynobasic, filiform, the stigma emarginate. Nutlets 4, obovoid or oblong, the gynobase flat or nearly so.

Borago comprises three species from southern Europe and the Mediterranean region, one of which, *Borago officinalis*, is widely cultivated.

Borago officinalis L., Sp. Pl. 137. 1753. TYPE: without locality or collector (holotype, LINN (Savage Catalog number 188.1), not seen; microfiche, MO).

Annual herb, 30–60 cm tall, the stems coarsely hirsute. Basal leaves petiolate, obovate to oblong, 6–12 cm long, 2–6 cm wide, the apex acute to obtuse, the base cuneate and decurrent along the petiole, the margin entire to irregularly undulate, the adaxial surface hirsute to scabrous, the veins prominent, the lower surface pubescent with most of the hairs restricted to the veins, the uppermost leaves sessile, lanceolate. Inflorescence loosely racemose, bracteate, the rachis hirsute. Flowers borne on pedicels 1–5 cm long; calyx rotate, with 5 lanceolate lobes to 10–18 mm long, 2–3 mm wide, hirsute; corolla blue, yellow in the throat, rotate, 18–22 mm long, the 5 lobes ovate to lanceolate, 8–11 mm long, the tube to 3 mm long; stamens 5, the filaments to 2 mm long, broad, the anthers lanceoloid, 5–7 mm long, with an appendage to 3 mm long at the base; ovary ca. 2 mm broad, the 4 lobes globose, the style 5.5–7.5 mm long. Fruits with the calyx and style persistent, the 4 nutlets obovoid, 4–6 mm long, 2–3 mm broad, finely ribbed, tuberculate at the apex.

Distribution. *Borago officinalis* is native in Europe, north Africa, and adjacent Asia but is widely cultivated and occasionally becomes naturalized.

Although *Borago officinalis* has not been collected in Panama, it seems almost certain that it is present in Panamanian gardens. It is often cultivated as a culinary or medicinal herb and is known from most neotropical countries, often as an adventive.

Bourreria P. Browne, Civ. Nat. Hist. Jamaica. 168. 1756; nom. cons. TYPE: *Bourreria succulenta* Jacq., Enum. Syst. Pl. 14. 1760; Select. Stirp. Amer. Hist. 44. 1763.

Trees or shrubs. Leaves alternate, petiolate, the margin usually entire. Inflorescences terminal cymes. Flowers bisexual, actinomorphic; calyx campanulate, 2–5-merous, the lobes valvate in bud; corolla relatively large, salverform, white to yellow in the Central American species, usually 5-merous, the lobes imbricate in bud; stamens 5, the filaments adnate to the base of the tube, the anthers ovate to oblong; ovary 4-locular, the style terminal, bifid; stigmas 2, flattened. Fruits drupaceous, enclosing 4 bony nutlets, the endosperm carnose, the cotyledons flat.

Bourreria has been considered to comprise about 50 species (Airy Shaw, 1973); however, Gibson's (1970) estimate of 15–20 species is probably more realistic. This poorly understood genus needs revision. Numerous species have been published based upon minor variations in leaf shape and indument—resolution of the problems this has created will necessitate field study of these characters. *Bourreria* ranges from Mexico and southern Florida through the West Indies and Central America to northern South America, with the majority of the species occurring in Mexico and the West Indies. About seven species are known from Central America, although only two have been found in Panama. Despite considerable confusion about delimitation of species, the two known from Panama are among the most distinct and easily recognized members of the genus.

De Candolle (1845) placed the species currently recognized as belonging to *Bourreria* in *Ehretia* sect. *Bourreria* (P. Browne) DC. All recent authors have, however, accepted *Bourreria* as distinct generically on the basis of its valvate calyx lobes and corollas that are larger and more fleshy than those in *Ehretia*. Miers (1869) pointed out that *Bourreria* has fruits that dry at maturity and separate into four single-seeded pyrenes with an apical attachment, whereas species of *Ehretia* have drupaceous fruits that usually remain entire at maturity, probably until they are dispersed. They later divide into two 2-seeded pyrenes.

KEY TO THE SPECIES OF *BOURRERIA* IN PANAMA

1a. Corollas 28–48 mm long; most leaf blades greater than 12 cm long .... *B. costaricensis*
1b. Corollas 8–12 mm long; most leaf blades less than 12 cm long .... *B. oxyphylla*

Bourreria costaricensis (Standley) A. Gentry, Phytologia 26: 67. 1973. *Schlegelia costaricensis* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1128. 1938. TYPE: Costa Rica. Alajuela: cataratas de San Ramón, Mar. 1931, *A. M. Brenes 13570* (holotype, F 857116; isotype, NY).

Bourreria superba var. *glabra* Schery, Ann. Missouri Bot. Gard. 29: 366. 1942. *Bourreria panamensis* I. M. Johnston, J. Arnold Arbor. 29: 229. 1948. TYPE: Panama. Bocas del Toro: Chiriquí Lagoon, Isla Colón, 3 June 1941, *H. von Wedel 2472* (holotype, MO, not seen).

Tree 10–15 m tall, the twigs glabrous. Leaves persistent; petioles 10–25 mm long, glabrous; leaf blade elliptic to obovate, 6.5–

23.5 cm long, 3.7–10.5 cm wide, the apex obtuse to rounded and sometimes mucronate, the base acute to cuneate, the margin entire, the adaxial and abaxial surfaces glabrous. Inflorescence a small terminal cyme. Flowers sessile, bisexual; calyx campanulate, 13–18 mm long, 10–18 mm wide at the mouth, glabrous, the 5 lobes triangular; corolla white, broadly funnelform, 2.8–4.8 cm long, 5-merous, the lobes depressed ovate; stamens 5, the filaments 18–20 mm long, the upper 14–18 mm free, slightly puberulent at the point of insertion, the anthers narrowly ellipsoid, 4 mm long. Fruits green, globose, 2–2.5 cm diam.

Distribution. This species occurs in wet to moist forests from sea level to 1,700 from Nicaragua to Panama. In Panama it is known from Bocas del Toro and Colón.

This is one of the most distinctive species of *Bourreria* with its large, funnelform corollas more than 2.5 cm long. It is quite similar to *Bourreria superba* I. M. Johnston of western Mexico in general appearance but is widely separated geographically and grows in a very different habitat. *Bourreria costaricensis* differs further from *B. superba* by having glabrous twigs, leaves, and staminal filaments.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Chiriquí Lagoon, Isla Colón, *Wedel 2974* (MO). CHIRIQUÍ: Fortuna Dam area, 1,200 m, *McPherson 6782* (MO); Fortuna Dam Region, near forestry experimental station, S of lake, 1,150 m, *McPherson 7873* (MO). COLÓN: Santa Rita Ridge Road, near junction of Transisthmian Highway, *D'Arcy et al. 15554* (MO).

Bourreria oxyphylla Standley, Trop. Woods 16: 40. 1928. TYPE: Belize. El Cayo: San José, Nov. 1927, *J. B. Aitken 4* (holotype, F 572622).

Beureria wagneri Standley in Yuncker, Publ. Field Mus. Nat. Hist., Bot. Ser. 9: 328. 1940. TYPE: Honduras. Atlántida: foothills back of La Ceiba, 23 July 1938, *T. G. Yuncker, J. M. Koepper & K. A. Wagner 8608* (holotype, F 941533).

Shrub or small tree to 5(–15) m tall, and ca. 1 m diam., the twigs glabrous to puberulent or sparsely strigillose. Leaves persistent, the petioles 7–17 mm long, glabrous to puberulent, the blades elliptic to elliptic-oblong, 4.5–10.5 cm long, 2–5 cm wide, the apex acute to obtuse and often abruptly short acuminate, the base acute to obtuse, the margin entire, the adaxial surface glabrous, the abaxial surface essentially glabrous but sparsely puberulent along the major veins. Inflorescence terminal, cymose, to 9 cm broad, the branches sparsely to evenly strigillose to puberulent. Flowers sessile, bisexual; calyx narrowly campanulate, 5–6 mm long, strigillose to puberulent, the 3–5 lobes deltate and often bifid at the apex; corolla white to pale green, tubular with spreading lobes, 8–12 mm long, 5-merous, the lobes oblong-obovate, 5–6 mm long, the tube 5–6 mm long; stamens 5, exserted, the filaments 3–4 mm long, glabrous, the anthers oblong, 2–3 mm long; ovary ovoid, 1.5–2 mm long, the disc annular, the style 6–8 mm long, the stigmas discoid. Fruits yellow to orange and later turning black, ovoid to subglobose, 6–12 mm long, 5–11 mm broad.

Distribution. *Bourreria oxyphylla* is known from southern Mexico through Belize to Nicaragua with a single collection from San Blas in Panama and a few collections from Colombia. It occurs in wet forests, where it ranges from sea level to nearly 800 m in elevation.

Bourreria oxyphylla is distinctive and is one of only two members of the genus in Central America with glabrous, elliptic leaves; the other, *Bourreria costaricensis*, is readily separated by its larger leaves, some to 10.5 cm wide, and corollas more than 2.8 cm long. *Bourreria wagneri* was described from a population in Honduras with slightly more puberulent twigs but is otherwise identical to other populations and is not recognized as distinct. The southern populations from Panama and Colombia have slightly larger, less lustrous leaves than the populations from northern Central America, but the differences are slight and they do not seem to warrant taxonomic recognition.

Additional specimens examined. PANAMA. SAN BLAS: island of Soskatupu, west end, *Kirkbride 195* (MO).

Cordia L., Sp. Pl. 190. 1753; Gen. Pl. ed. 5. 87. 1754. TYPE: *Cordia sebestena* L., Sp. Pl. 190. 1753.

Trees or shrubs. Leaves alternate, deciduous or persistent, petiolate, the petioles usually adaxially canaliculate. Inflorescence cymose, paniculate, spicate, capitate, or glomerate. Flowers perfect, or unisexual by abortion, with the plants then dioecious; calyx 3–5(–10)-lobed or rarely circumscissile; corolla funnelform, campanulate, or tubular with reflexed or spreading lobes, (4–)5(–18)-lobed, or sometimes the lobes nearly lacking and the corolla apically undulate to frilled or nearly truncate; stamens as many as corolla lobes, the lower part of the filaments adnate to corolla tube, often with hairs at or near insertion, the anthers oblong to ellipsoid; ovary entire, falsely 4-locular; disc annular to crateriform; style terminal, twice bifid, the 4 stigma lobes clavate, filiform, or discoid. Fruits borne with the calyx persistent, variable, dry with a fibrous wall and capped by the persistent, cartilaginous base of the style (sect. *Gerascanthus*), dry and bony-walled (sect. *Rhabdocalyx*), or with a thin exocarp, juicy to mucilaginous mesocarp, and bony endocarp (sects. *Varronia*, *Myxa*, and *Cordia*), usually 1-locular and 1-seeded, the endosperm lacking, the cotyledons plicate.

The pantropical genus *Cordia* is the largest in the family: there are about 300 species, mostly neotropical. Species of *Cordia* are found in a wide variety of habitats, but, although many species can be found in wet forests, those found in dry, disturbed areas are a more important component of the vegetation.

Cordia is the only Panamanian genus of the Cordioideae. The South American genera, *Auxemma* Miers and *Patagonula* L., differ from *Cordia* in the unusual form of their fruiting calyces and by having short styles and monomorphic flowers. Although clearly related to *Cordia*, they seem to represent a distinct lineage. *Cordia*, however, is a very diverse assemblage, and a number of authors have suggested dividing it into 3–12 segregate genera (Mez, 1890; Friesen, 1933; Nowicke & Ridgway, 1973). Nevertheless, *Cordia* sensu lato appears to be a distinct monophyletic group and its division into narrowly defined genera seems unwarranted. Johnston (1930, 1940, 1949a, b, 1950, 1951) treated the genus in a broad sense and recognized five to seven sections in his various works. Recent authors (Nowicke, 1969; Gibson, 1970; Nowicke & Ridgway, 1973; Opler et al., 1975; Miller, 1985) have recognized five sections. Twenty-seven species in four of the sections are known from Panama.

KEY TO THE SPECIES OF *CORDIA* IN PANAMA

1a. Corolla bright red-orange; fruit drupaceous and totally enclosed in the accrescent calyx at maturity (sect. *Cordia*) .... *C. sebestena*
1b. Corolla white to yellow; fruit not totally enclosed by the calyx at maturity or if enclosed, then not drupaceous.
  2a. Corolla marcescent; fruit with a fibrous wall (sect. *Gerascanthus*).
    3a. Ant domatia present at the base of the inflorescences; leaves and twigs with stellate hairs; corolla lobes oblong .... *C. alliodora*
    3b. Ant domatia absent; leaves and twigs glabrous; corolla lobes deltate or ovate .... *C. megalantha*
  2b. Corolla deciduous; fruit with a bony wall.
    4a. Trees or shrubs with few stems; leaf margin entire or denticulate; inflorescences cymose to paniculate, branching more than twice; fruits generally asymmetrical (sect. *Myxa*).
      5a. Corolla yellow to almost white; calyx circumscissile and striate .... *C. dentata*
      5b. Corolla white; calyx opening with valvate lobes or if circumscissile than not striate.
        6a. Calyx costate; leaf margin with short, filiform teeth toward the apex or entire .... *C. diversifolia*

6b. Calyx smooth or striate, not costate; leaf margin entire.
7a. Ovary and fruit strigillose ..... *C. bicolor*
7b. Ovary and fruit glabrous.
8a. Adaxial leaf surface evenly strigillose or scabrous to strigose; plants usually dioecious.
9a. Corolla tube 1.5–3.9 mm long; fruits ovoid, 6–10 mm long.
10a. Stems and peduncles with simple hairs; the larger leaves generally 6.5–13.5 cm wide ..... *C. panamensis*
10b. Stems and peduncles with echinate hairs; the larger leaves generally 11.2–20.4 cm wide ..... *C. cymosa*
9b. Corolla tube ca. 10–12 mm long; fruits ellipsoid, 8.5–16.5 mm long ..... *C. anisophylla*
8b. Adaxial leaf surface glabrous or nearly so; plants usually with bisexual flowers, these usually distylous, dioecious only in *C. collococca* and *C. tacarcunensis.*
11a. Leaf margin distinctly revolute.
12a. Stems sub-alate; abaxial leaf surface glabrous; leaves not bullate ..... *C. leslieae*
12b. Stems not winged or ridged; abaxial leaf surface velutinous; leaves bullate ..... *C. dwyeri*
11b. Leaf margin not or only slightly revolute.
13a. Corolla campanulate ..... *C. eriostigma*
13b. Corolla tubular, with reflexed or spreading lobes.
14a. Calyx distinctly 5-lobed.
15a. Inflorescences axillary, numerous on a single stem; plants dioecious ..... *C. tacarcunensis*
15b. Inflorescences terminal or subterminal, few per stem; plants with bisexual flowers.
16a. Fruits white; leaf blades falcate ..... *C. protracta*
16b. Fruits red or orange; leaf blades flat, not falcate ..... *C. correae*
14b. Calyx (2–)3(–4)-lobed, circumscissile or dehiscing irregularly.
17a. Plants hermaphroditic; leaves persistent; flowers borne on current season's growth.
18a. Apex of the leaf caudate, the caudex 1–3.5 cm long ..... *C. lasiocalyx*
18b. Apex of the leaf acuminate.
19a. Leaf blade elliptic to elliptic-ovate, less than 5 cm wide, usually less than 8 cm long ..... *C. croatii*
19b. Leaf blade ovate to narrowly elliptic or lance-elliptic, usually more than 5 cm wide, usually more than 8 cm long.
20a. Fruit red, the stone not rostrate; anthers 1.1–1.2 mm long; calyx 3–4 mm long ..... *C. lucidula*
20b. Fruit white, the stone not rostrate; anthers 1.9–2.3 mm long; calyx 5.2–6.5 mm long ..... *C. porcata*
17b. Plants dioecious; leaves deciduous; flowers usually borne below the current season's growth ..... *C. collococca*
4b. Shrubs, usually multistemmed; leaf margin serrate to minutely denticulate; inflorescences condensed, spicate, capitate, or if cymose, then less than 2.3 cm broad, dichotomous, and branching only twice; fruits symmetrical or nearly so (sect. *Varronia*).
21a. Inflorescences spicate.
22a. Leaf blade lanceolate; inflorescences terminal ..... *C. curassavica*
22b. Leaf blade ovate; inflorescences axillary, the peduncle adnate to the petiole ..... *C. spinescens*
21b. Inflorescences cymose or capitate.
23a. Inflorescence branched, cymose ..... *C. bifurcata*
23b. Inflorescence capitate.
24a. Calyx lobes with prolonged filiform tips.
25a. Peduncles 0.5–2 cm long; corolla 5–10 mm long ..... *C. globosa*
25b. Peduncles 3–7 cm long; corolla 3–6 mm long ..... *C. bullata*
24b. Calyx lobes acute to acuminate but lacking prolonged tips.
26a. Inflorescences terminal or internodal ..... *C. inermis*
26b. Inflorescences axillary ..... *C. linnaei*

Cordia alliodora (Ruíz Lopez & Pavón) Oken, Allg. Naturgesch. 2(2): 1098. 1841. *Cerdana alliodora* Ruíz Lopez & Pavón, Fl. Peruv. 2: 47, pl. 184. 1799. TYPE: Peru. Huanuco: Pozuzo, *Hipólito Ruíz & José Pavón* (holotype, B, not seen; photo, MO).

Tree to 20(–25) m tall, the twigs stellate-pubescent when young, ending in obovoid ant domatia. Leaves deciduous; petioles (5–)8–28(–35) mm long, stellate-pubescent; blade elliptic to narrowly elliptic or slightly obovate, (3.5–)5–17(–20.5) cm long, (1.4–)2–7(–8.5) cm wide, the apex acuminate or acute, the base acute to obtuse, the adaxial surface glabrous to sparsely stellate-pubescent, the abaxial surface sparsely to densely stellate-pubescent. Inflorescence terminal, usually arising from an obovoid ant domatium, paniculate, to 25(–30) cm broad, the branches usually densely stellate-pubescent. Flowers borne on short spurs to 1.5 mm long, bisexual, monomorphic; calyx tubular, (4–)4.5–5.5(–6.5) mm long, 10(–12)-ribbed, stellate-pubescent, with (4–)5(–6) small teeth; corolla marcescent, white, (8.5–)9.5–12(–14) mm long, (4–)5(–6)-merous, the lobes oblong, (4.5–)5–7(–8.5) mm long, the tube (3.5–)4.5–6(–8.5) mm long; stamens (4–)5(–6), the filaments 9–12 mm long, the upper (3.5–)5.5–7.5 (–9) mm free, sparsely pubescent at insertion, the anthers oblong, 1.5–2(–2.5) mm long, borne at the same height or above the stigmas; ovary ovoid to very broadly ovoid, (0.7–)1–2(–2.5) mm long; disc depressed obovoid to very broadly obovoid, 0.5–1 mm tall; style 4.5–6.5 mm long, the stigma lobes clavate. Fruits enclosed by the persistent corolla and calyx, ellipsoid, (4.5–)5–7(–8) mm long, (1–) 2–2.5 mm broad, the wall thin, fibrous.

Distribution. *Cordia alliodora* occurs in dry to wet forests from sea level to 1,100 m in elevation and ranges from Mexico to South America and to the West Indies. This species is known from all provinces in Panama.

Cordia alliodora is the widest-ranging species of the genus. Its ant domatia and stellate indument are distinctive. It is also one of only two homostylous species in sect. *Gerascanthus*, the other being *Cordia trichotoma* (Vell.) Arráb. ex Steudel of southern South America (Gibbs & Taroda, 1983). This condition is derived in the section, and these two species form a monophyletic group further characterized by stellate hairs on the stems and leaves and by flowers considerably smaller than those of their relatives. The flowers of *Cordia alliodora* vary from short-style to forms with the stigmas and anthers borne at about the same height, but individual plants appear to be constant in the ratio of anther and stigma height. No plants have been found with styles exceeding the stamens considerably.

Cordia alliodora is valued as a timber tree and, for this reason, there has been a great deal of interest recently in establishing plantations of it throughout Central America (Stead, 1980). Flowering occurs at the onset of the dry season with fruits maturing and being dispersed during mid dry season. Common names include Laurel, Laurel Blanco, and Laurel Negro.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Almirante region, *Cooper & Slater 22* (CFMR, F, US); Changuinola Valley, *Dunlap 291* (F, GH, US); vicinity of Chiriquí Lagoon, Old Bank Island, *Wedel 1877* (MO, US). CANAL AREA: Summit Area, *Avilla 302* (MO); U.S. Army Tropic Test Center, Fort Clayton, vicinity Gorgas Hospital, *Blum 2210* (MO, SCZ); between Gatún and Bohio, *Christopherson 118* (US); Barro Colorado Island, *Croat 4799* (F, SCZ); *7694* (MO); *8104* (F (3), MO, NY, SCZ); *8164* (MO); 8401 (F, MO); Gaillard Highway, 2 mi. NW of Summit Garden, *Croat 14048* (MO); Barro Colorado Island, *D'Arcy 3931* (C, MO, TEX); Albrook, U.S. Army Tropic Test Center Site, *Dwyer & Robyns 56* (BR, MO); Barro Colorado Island, *Foster 719* (F, MICH); Curundu, *Harvey 5249* (F); in government forest along Las Cruces trail, 75 m, *Hunter & Allen 449* (BR, F, G, MO, NY, P, UC, US); near Gamboa, along edge of Canal, dump 4 area, along shore side, *Kennedy & Steiner 2453* (C, CAS, ENCB, F, L, MO, NY, US); vicinity of Culebra, *Maxon 4901* (C, F, NY, US (2)); roadside near RR along Panama Canal, 1½ km W of Gamboa, *Nee & Mori 3596* (CFMR, MO); near Gamboa, *Piper s.n.* (GH (2)); Chiva-Chiva Trail, *Piper 5755* (GH, NY, US); vicinity of Ancon, *Piper 6007* (US); Barro Colorado Island, *Shattuck 780* (GH, MO), *789* (MO (2)); along the old Las Cruces trail, between Fort Clayton and Corozal, *Standley 29229* (US); between France Field, Canal Zone, and Catival, province of Colón, *Standley 30200* (US); Fort Clayton, Cardenas Creek Area, *Tyson 3473* (MO, SCZ); vicinity of Fort Clayton, *Walker 1* (UC); Ancon, *Wheeler & Zetek s.n.* (GH (2)); Barro Colorado Island, *Wilson 80* (F, MO); *Woodworth & Vestal 590* (F, MO). CHIRIQUÍ: 1 km carretera a Los Citricos, *Barrera 46* (MO); vicinity of San Felix, 0–120 m, *Pittier 5279* (US). COCLÉ: Penonomé and vicinity, 50–1,000 ft., *Williams 326* (NY (2), US), *327* (NY). COLÓN: Juan Mina, Río Chagres, 25 m, *Allen 4198* (G, MO); entres Brazo sawmill, Icacal which is in between Salud y Boca de Río Indio, *Howell 27* (MO). DARIÉN: Battelle Memorial Institute, sea level, Canal Bioenvironmental Program, *Duke 8145* (MO); near mouth of Río Paya on Río Tuira, *Gentry 4349* (MO); Quebrada "Camachimuricate" cerca casa de Bartolo, *Kennedy 2870* (MO). HERRERA: vicinity of Ocú, hill above the cantera of Sr. Joaquin Carrizo, limestone area, *Stern et al. 1721* (MICH, MO, US). LOS SANTOS: Los Toretos, *Dwyer 2430* (MO, US); vicinity of Tonosi, Guanico, 117 ft., *Stern et al. 1856* (MICH, MO, US). PANAMÁ: Río Las Lajas, 20 m, *Allen 1607* (F, MO, NY, US); Island of Taboga, *Barclay 981* (F, US); a orillas del Río Aguacate cerca de Nuevo Arraijan, *Cedeno 13* (F, MO); en El Jobo, San Carlos, *Gonzalez 19* (F, MO); Isla Taboga, *Hjerting & Rahn 617* (C, US); San José Island, *Johnston 570* (GH); near Chepo, *Kluge 3* (CFMR, US); Isla Tabogo, *Macbride 2822* (F, GH, US); Chepo, *Paul 326* (US). SAN BLAS: Permé, *Cooper 649* (CFMR, DS, F, US); mainland opposite Ailigandi, from mouth of Ailigandi River to 2.5 mi. inland, *Lewis et al. 154* (MO). VERAGUAS: border of Veraguas, Coclé, and Herrera provinces along the Río Santa María near bridge of Panamerican Highway, 16 km SW of Aguadulce, 0–50 m, *Knapp et al. 3348* (MO).

Cordia anisophylla James S. Miller, sp. nov. TYPE: Panama. Colón: Santa Rita Ridge Road, 9 km from Boyd–Roosevelt Highway, 350 m, Premontane Wet Forest, 15 Mar. 1975, *S. Mori & J. Kallunki 5076* (holotype, MO 2664952; isotypes, MO, US). Figure 1.

Arbor ad 8 m alta. Folia persistentia, petiolis (4–)6–12 mm longis; laminae anisophyllae, foliis maioribus ovatis ad lanceolato-ovatis, 10.5–21(–26) cm longis, (3–)5–12.5 cm latis, minoribus ovatis ad cordatis, (3.5–)7.5–8.5 (–13.5) cm longis, 4.5–7.3(–14) cm latis, apice acuminatis ad acutis, basi obtusis, superficie strigillosa, pagina inferiore strigillosa ad pilosa. Inflorescentiae terminales in axillis ramorum dispositae, cymosae. Flores heterostyli; calyx tubuliformis, 7–9 mm longus; corolla alba, tubuliformis, 10–12 mm longa, 5-lobata; stamina 5, antheris oblongis. Fructus drupaceus, putamine inaequilateraliter ovoideo, 8.5–16.5 mm longo, 6–7.5 mm lato.

Small erect tree or large shrub to 5(–8) m tall, the bark brown, smooth, lateral branching dichotomous in a horizontal plane, the twigs strigillose to pilose. Leaves persistent; petioles (4–)6–12 mm long, canaliculate adaxially, strigillose to pilose; blades anisophyllous, the larger ones ovate to ovate-lanceolate, 10.5–21(–26) cm long, (3–)5–12.5 cm wide, the smaller ones orbicular, (3.5–) 7.5–8.5(–13.5) cm long, 4.5–7.3(–14) cm wide, the apex acuminate, the base subobtuse to obtuse, the margin entire, the adaxial surface evenly strigillose, the abaxial surface strigillose to unevenly pilose. Inflorescences terminal or borne in the axils of branches, rarely internodal, loosely branched cymes, the peduncle 5–10(–13.5) cm long, strigillose to nearly pilose. Flowers sessile, distylous; calyx tubular, 7–9 mm long, 3 mm wide at mouth, the 5 lobes ± deltate, 1.8 mm long, ribs absent, strigillose, densely pilose on interior surface; corolla white, tubular with reflexed lobes, ca. 10–12 mm long, 5-merous, the lobes 2.7 mm long, 1.8 mm wide, the tube 9.3 mm long; stamens 5, the filaments 10.5 mm long, the upper 2.6 mm free, villose at and above insertion, the anthers oblong, 2 mm long; ovary oblong, 1.8 mm long, 1.1 mm broad, glabrous; disc small, not evidently distinct from the base of the ovary; style 5.3 mm long, the stylar branches 0.9 mm long, the stigma lobes clavate. Fruits seated in the cupulate calyx, drupaceous, glabrous, the stone slightly inequilaterally ovoid, 8.5–16.5 mm long, 6–7.5 mm broad, the endocarp bony.

Distribution. *Cordia anisophylla* occurs in wet forests from sea level to 1,000 m in elevation and is known only from Panama in the provinces of Colón, Darién, Panamá, and San Blas.

Cordia anisophylla is closely related to *C. panamensis* and to *C. cymosa* but differs from them by having corollas more than 10 mm long and fruits more than 8.5 mm long. This species is also one of only two distylous Central American members of sect. *Myxa*, the other being *C. dentata*. While the *Cordia panamensis* species complex is one of the most taxonomically confusing within sect. *Myxa*, *Cordia anisophylla* is probably the most distinctive species of the group in its elongate, distylous flowers and ellipsoid fruits.

Additional specimens examined. PANAMA. COLÓN: Santa Rita Ridge, *Croat 13895* (MO); Santa Rita lumber

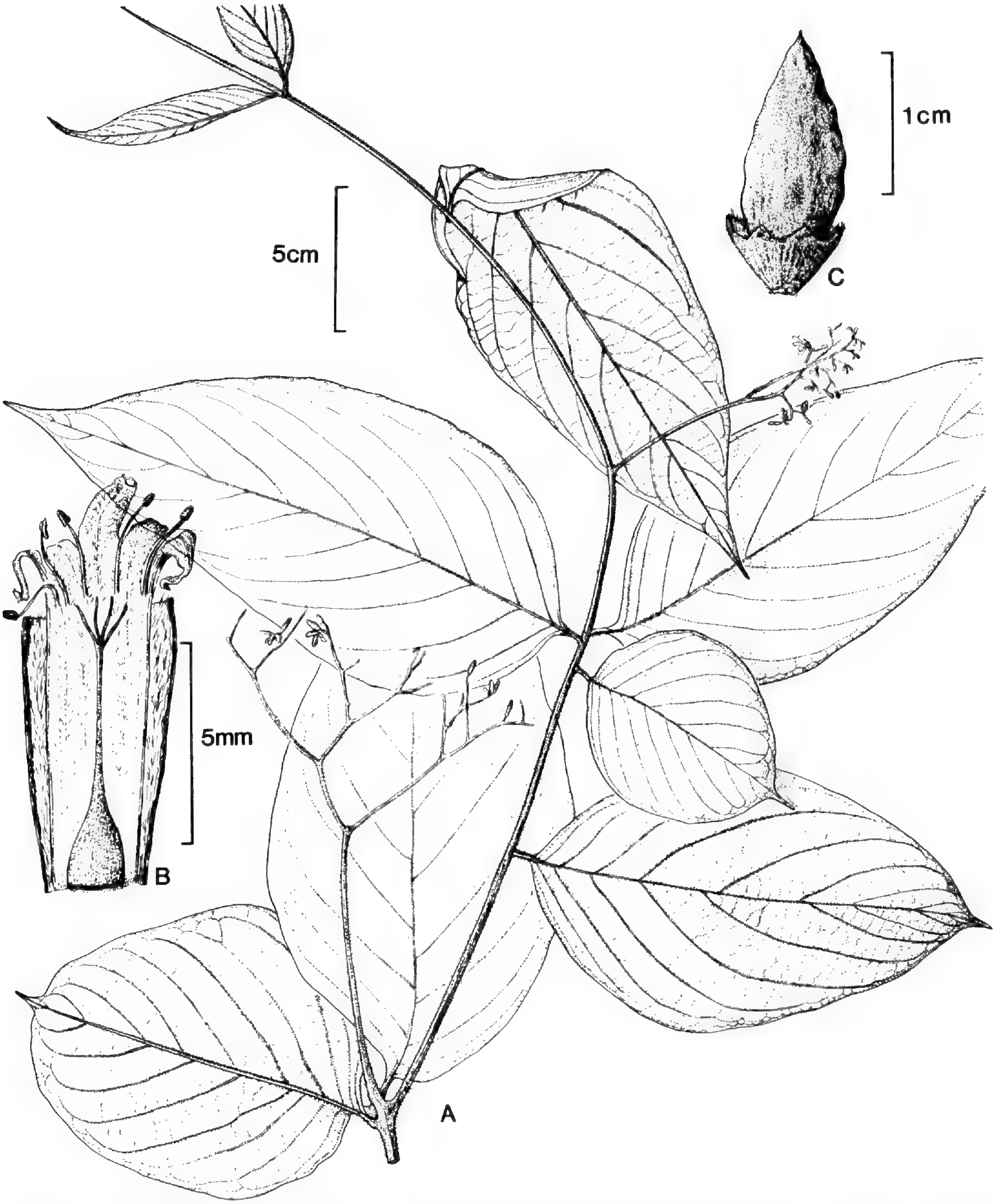

FIGURE 1. Cordia anisophylla.—*A. Flowering branch.—B. Flower with corolla opened.—C. Fruit. A, B from* Mori & Kallunki 5076 *(MO), Colón, Panama; C from* Mori & Kallunki 6373 *(MO), Panamá, Panama.*

road, ca. 15 km E of Colón, *Dressler 3799* (DUKE, F (2), MO (2)); Santa Rita Ridge Road, ca. 8 mi. E of the Transisthmian Highway, along trail N of road, 350–440 m, *McPherson & Merello 8244* (MO). DARIÉN: along Río Chucanaque between El Real and Río Canalones, *Duke 4979* (MO). PANAMÁ: region of Cerro Jefe, 1,000 m, *Correa et al. 1589* (MO); El Llano–Carti Road, 20.7 km from Interamerican Highway, 350 m, *Mori & Kallunki 5114* (MO); 5–10 km NE of Altos de Pacora on trail at end of road, 700–800 m, *Mori & Kallunki 6057* (DUKE); El Llano–Carti Road, 12.2 km from Interamerican Highway, *Mori & Kallunki 6373* (MO, SCZ, US); El Llano–Carti Road, ca. 9 mi. from Pan-American Highway along newly cut by-pass, 300–400 m, *Sytsma 4127* (MO). SAN BLAS: near Nusigandi on Llano–Carti Road, 300–350 m, *McPherson 10796* (MO).

Cordia bicolor A. DC. in DC., Prodr. 9: 485. 1845. TYPE: Surinam: *Hostmann 406* (holotype, G-DC, not seen; microfiche, MO; isotype, P).

Cordia trichostyla Pittier, Contr. U.S. Natl. Herb. 18(6): 252. 1917. TYPE: Guatemala. Alta Verapaz: vicinity of Secanquim, 550 m, 30 Apr. 1905, *H. Pittier 189* (holotype, US 472845).

Cordia belizensis Lundell, Amer. Midl. Naturalist 29: 488. 1943. TYPE: Belize. Toledo: Monkey River, in high ridge between Swacey Branch and Wahaleaf Creek, 5 July 1942, *P. H. Gentle 4045* (holotype, MICH; isotypes, GH, NY).

Tree to 20 m tall, the young twigs velutinous to puberulent. Leaves persistent; petioles (2–)3–8(–16) mm long; blades elliptic to ovate or narrowly elliptic, (8–)10–19(–22) cm long, (3.3–)4–9(–11.5) cm wide, the apex acuminate, the base obtuse to rounded, the margin entire, the adaxial surface sparsely strigillose to scabrous, the abaxial surface pale, puberulent to strigillose. Inflorescence terminal or borne in the axils of branches, cymose, to 13(–20) cm long, 14(–28) cm broad, the branches velutinous. Flowers sessile, bisexual, monomorphic with the stamens as long or longer than the stigmas; calyx tubular-campanulate, (3.3–)3.6–4.3(–4.9) mm long, ribs absent, densely strigillose, the 5 lobes deltate to attenuate; corolla white, tubular with reflexed lobes, 6.2–7 mm long, 5-merous, the lobes oblong, (2.3–)2.7–3(–3.8) mm long, the tube (2.5–)3.6–4.6(–5) mm long, pubescent in the mouth; stamens 5, the filaments (3.8–)4.8–6(–6.4) mm long, the upper (1–)1.8–3 mm free, pubescent at the point of insertion, the anthers oblong, 1–1.6 mm long; ovary ellipsoid, 0.8–1.6 mm long, strigillose; disc crateriform, 0.3–1 mm tall; style 3–3.7 mm long, the stigma lobes discoid to broadly clavate. Fruits seated in the cupulate calyx, white, drupaceous, the stone inequilaterally ovoid, (7.3–)10.5–13 mm long, (4.5–)7.5–9.5 mm broad, the exocarp densely strigillose, the endocarp bony.

Distribution. *Cordia bicolor* occurs in wet forests from sea level to 500 m in elevation and ranges from Mexico to South America. In Panama this species is known from the Canal Area, Chiriquí, Colón, Darién, Panamá, and Veraguas.

Cordia bicolor is perhaps most closely related to the *C. panamensis* complex in that it also has dichotomous lateral branching, anisophyllous leaves, and similar indument. However, it differs from the other Central American species in its strigillose fruits, a relatively rare character found in several unrelated South American species. *Cordia toqueve* Aubl. of South America is the only other species of this complex that shares this trait.

Additional specimens examined. PANAMA. CANAL AREA: Barro Colorado Island, *Aviles 21* (F); *Croat 5630* (DUKE, F, MO, NY, SCZ), *5823* (DUKE, F, NY, SCZ (2)), *7705* (DUKE, F, MO, NY), *8004* (F, MO, NY, SCZ), *8804* (DUKE, MO), *8809* (F (2), DUKE, MO, NY), *9447* (MO), *14855* (MO, SCZ, UC); *Duke 8379* (NY); without definite locality, *Epplesheimer s.n.* (F (2)); Barro Colorado Island, *Foster 1778* (DUKE, F); area W of Limón Bay, Gatún Locks and Gatún Lake, *Johnston 1588* (A); Barro Colorado Island, *Kenoyer 656* (US); Pipeline Road between mile marker 0 and 11.1 ca. 16 mi. N of Gamboa, *Lewis et al. 5446* (F, MO, NY); near Fort Randolph, *Maxon & Harvey 6520* (US); Barro Colorado Island, *Oppenheimer 252* (MO); near old Fort Lorenzo, mouth of Río Chagres, *Piper 5964* (US). CHIRIQUÍ: at Monte Rey above Boquete, *Croat 15770* (NY). COLÓN: near radio tower at the end of turnoff to Santa Rita Ridge Road, 200–300 m, *Miller & Miller 910* (MO). DARIÉN: ca. 1 mi. NE of Nura, 200 m, *Duke 10081* (MO, US). PANAMÁ: San José Island, *Erlanson 256* (G, NY, US); *Johnston 417* (GH), *545* (GH, MO, U, US), *618* (DUKE, GH, LL), *620* (GH, U, US), *621* (DUKE, GH, LL, U), *785* (GH, US), *963* (GH), *1076* (GH (2)); Altos del Río Pacora, 2,500 ft., *Lewis et al. 2267* (MO, UC). VERAGUAS: above Santa Fe on slopes of Cerro Tute below Agricultural School, *Gentry 6204* (MO); NW of Santa Fe near entrance to school, *Mori & Kallunki 4888* (AAU, MO, US).

Cordia bifurcata Roemer & Schultes, Syst. Veg. 4: 466. 1819. *Varronia dichotoma* Ruíz Lopez & Pavón, Fl. Peruv. 2: 23, t. 146. 1799, not *Cordia dichotoma* G. Forster, Fl. Ins. Austr. 18 n. 110. 1786. TYPE: Peru. Huánuco: Chacahuasi, *Hipólito Ruíz & José Pavón s.n.* (holotype, B-W, not seen; microfiche, MO).

Shrub to 3 m tall, the twigs sparsely strigillose, the hairs shorter than 0.5 mm, appressed, white translucent. Leaves deciduous, on short spurs 1.5–2 mm long; petioles 2–8 mm long, sparsely strigillose; blade ovate to lanceolate, (2.5–)3.7–9(–12) cm long, (0.8–)1.2–4(–4.7) cm wide, the apex acuminate, the base acute, the margin slightly serrate to entire, the adaxial surface sparsely puberulent with short, erect hairs, the abaxial surface sparsely pubescent. Inflorescence terminal or lateral, a small forking cyme with 4 or more branches, 0.8–2.3 cm broad, the peduncle 1.4–6 cm long, strigillose. Flowers sessile, distylous; calyx short-tubular, 2–2.7 mm long, strigillose, the 5 lobes deltate to shallowly deltate; corolla white, tubular, (2.7–)3.2–3.7 mm long, truncate at the apex, canescent in the middle of the tube; stamens 5, the filaments (2.2–)2.7–3.5 mm long, the upper 0.6–1(–1.3) mm free, canescent at insertion, the anthers broadly ellipsoid, 0.5–0.6 mm long; ovary very broadly obovoid to broadly depressed obovoid, 0.6–1 mm long; disc thin, cuplike, nearly completely adnate to the ovary; style (2.2–)3–3.5 mm long, the stigma lobes flattened. Fruits drupaceous, ⅓–½ enclosed in the slightly accrescent calyx, bright red, the stone ovoid, 4–4.5 mm long, 2.2–3 mm broad, the endocarp bony.

Distribution. Cordia bifurcata occurs in wet forests from sea level to 600 m in elevation and ranges from southern Nicaragua south to Peru. In Panama this species is known from the provinces of Bocas del Toro, Colón, and Darién.

Cordia bifurcata is distinctive in its small, shrubby habit and small, cymose inflorescences and has no close relatives in Panama. It is a member of a taxonomically difficult group of mostly South American species that are all similar in general aspect. The only other member of this group found in Central America is *C. foliosa* Mart. & Gal. of southern Mexico and Guatemala, which differs from *C. bifurcata* in its elliptic, firm-textured leaves with a scabrous upper surface, apiculate flower buds, and acuminate calyx lobes. Two other species of Central America, *C. inermis* and *C. linnaei*, are also closely related to this group, but neither of these has a branched inflorescence.

Additional specimens examined. PANAMA. BOCAS DEL TORO: region of Almirante, *Cooper 83* (F, NY); Changuinola Valley, *Dunlap 90* (GH). COLÓN: vicinity of San Juan near Cement Plant Lake, *Blum & Tyson 537* (MO). DARIÉN: on trail from Punta Guayabo Grando to Río Jaqué, 50–200 m, *Antonio & Hahn 4415* (MO); vicinity of Paya, Río Paya, *Stern et al. 268* (G, MO, US).

Cordia bullata (L.) Roemer & Schultes, Syst. Veg. 4: 462. 1819. *Varronia bullata* L., Syst. ed. 10: 916. 1759. TYPE: Jamaica, *P. Browne s.n.* (holotype, LINN, not seen (Savage Catalog number 255.2); microfiche, MO).

Cordia bullata var. *angustata* DC., Prodr. 9: 496. 1845. TYPE: Guadalupe, 1818, *Krause s.n.* (holotype, G-DC, not seen; microfiche, MO).

Cordia asperrima DC., Prodr. 9: 498. 1845. *Varronia asperrima* (DC.) Friesen, Bull. Soc. Bot. Genève, Ser. 2, 24: 155, t. 1, f. 5. 1933. TYPE: Jamaica, 1822, *Bertero ex herb. Balbis* (holotype, G-DC, not seen; microfiche, MO).

Shrub to 1(–3) m tall, the twigs hirsute to hirtellous, the hairs erect to spreading. Leaves deciduous, on short spurs to 1 mm long; petioles 2–7(–10) mm long, shallowly canaliculate to flattened adaxially, hirsute to hirtellous, the hairs erect to spreading; blade ovate to narrowly ovate, (1.5–)2–8(–9.2) cm long, (0.8–)1.2–4.7(–6.3) cm wide, the apex acute to slightly attenuate, the base subobtuse to obtuse or acute and abruptly decurrent along the petiole, the margin serrate, usually unevenly so, the teeth usually sharp and often short-apiculate, the adaxial surface usually bullate, strigose, the lower surface coarsely pubescent, the hairs ± restricted to the veins. Inflorescence internodal or less commonly subterminal or terminal, a dense, often slightly ellipsoid head, 8–12(–15) mm broad, the peduncle (1.5–)3–6.5(–13.5) cm long, hirsute, the hairs erect to spreading. Flowers distylous, sessile; calyx campanulate, (2–)2.5–3.3(–3.8) mm long, (2–)2.5–3.5 mm wide at the mouth, ribs absent, strigillose, the 5 lobes deltate to triangular, 0.5–1 mm long, with a prolonged filiform tip 1–3(–3.5) mm long; corolla white, tubular, 3–5.3(–6) mm long, undulate, the lobes scarcely distinct, the tube 1.2–2.8 (–3.2) mm long; stamens 5, the filaments (3.3–) 3.8–4.3(–5) mm long, the upper 1–1.7(–2) mm free, puberulent in a ring in the mouth of the corolla tube, the anthers ellipsoid, 0.6–1 mm long; ovary ovoid, 1–1.8 mm long, glabrous; disc usually indistinct from the base of the ovary; style 0.6–4.3 mm long, the stylar branches 0.4–1 mm long, the stigma lobes clavate to discoid. Fruits drupaceous, red, the stone ovoid, 3.7–5.3 mm long, 2.5–3.2 mm broad, the mesocarp thin, the endocarp bony.

Distribution. *Cordia bullata* occurs in dry forests from sea level to 1,400 m in elevation. It is known from Nicaragua to southern Mexico, northern South America, the Greater Antilles, and a single collection from the province of Veraguas in Panama.

Cordia bullata is closely related to and often confused with *C. globosa* (Jacq.) Kunth but differs by having peduncles greater than 3 cm long and corollas less than 6 mm long. Both are common in northern Central America, and populations with interspecific hybrids are known from Nicaragua and Honduras.

Additional specimens examined. PANAMA. VERAGUAS: El Cuchillo, near Cerro Tute, up from Santa Fe, 1,300 m, *Hamilton et al. 1203* (MO).

Cordia collococca L., Sp. Pl. ed. 2. 274. 1762; excluding *Cordia glabra* L. = *Bourreria succulenta* Jacq.; I. M. Johnston, J. Arnold Arbor. 21: 345. 1940. TYPE: without definite locality, collector unknown (holotype, LINN, not seen (Savage Catalog number 253.8); microfiche, MO).

Cordia micrantha Sw., Prodr. 47. 1788. TYPE: "habitat in Jamaica," not seen.

Small tree to 8(–15) m tall, the twigs sparsely to evenly strigillose, later waxy. Leaves deciduous; petioles 5–12(–15) mm long, sparsely strigillose; blade oblong-obovate to elliptic or obovate, (4.7–)5.5–14(–15.2) cm long, (2.5–)3–6.5(–7) cm wide, the apex acute, often with short-acuminate tip, rarely acute, the base cuneate to acute, the margin entire, the adaxial surface glabrous or nearly so but with numerous small papillae, the abaxial surface evenly strigillose to hirtellous. Inflorescence terminal, borne on old wood just before the new vegetative shoots appear, or axillary, cymose, (6–)7–14(–18) cm broad, the branches sparsely strigillose. Flowers sessile, unisexual by abortion, the plants dioecious; female flowers with small, nonfunctional anthers; male flowers with shortened, reduced styles; calyx cupulate, (1.7–)2–2.6 (–3) mm long, ribs absent, evenly strigillose, circumscissile or unevenly 3-lobed; corolla white, tubular with reflexed lobes, (4.5–)4.8–6.3(–6.9) mm long, 5-merous, the lobes oblong-ovate to ovate, (2.3–)2.8–3.7(–4) mm long, the tube 1.7–2.9(–3.3) mm long; stamens 5, the filaments 2.5–5 mm long, the upper (0.8–)1.7–2.2 mm free, puberulent to pubescent below insertion, the anthers oblong to ellipsoid, 0.5–1.6 mm long; ovary ovoid to oblong, 0.8–1.2 mm long, glabrous; style 0.4–2 mm long, the stigma lobes clavate to filiform. Fruit borne with the small calyx persisting at the base, bright red, drupaceous, glabrous, the stone inequilaterally ovoid, 7.5–9.3 mm long, 5.5–7.3 mm broad, the endocarp bony.

Distribution. *Cordia collococca* occurs in dry forests from sea level to 200(–900) m in elevation from Mexico south to northern South America and the West Indies. In Panama this species is known from Bocas del Toro, Canal Area, Chiriquí, Colón, Herrera, Los Santos, Panamá, and San Blas.

Cordia collococca is a relatively common species throughout much of its range, although it has not been collected frequently in Panama. It is easily confused with *Cordia eriostigma* but can be distinguished by being a smaller tree with an even indument of short appressed hairs on its abaxial leaf surface, deciduous leaves, and flowers that are unisexual by abortion. *Cordia collococca* is generally found at elevations below 200 m in dry forests, while *C. eriostigma* usually grows at 600–1,400 m in moist forests.

Cordia micrantha is clearly a synonym of *C. collococca*, but Swartz specified no type other than "habitat in Jamaica," and the choice of a lectotype will require study of material in European herbaria. The name *Cordia glabra* has been improperly applied to this species; Johnston (1940) showed that this name should be considered a synonym of *Bourreria succulenta.*

Additional specimens examined. PANAMA. BOCAS DEL TORO: Almirante, *Cooper 406* (CFMR, F, NY, US); on lower Changuinola River, *Stork 273* (UC, US). CANAL AREA: between Farfan beach and Vera Cruz, *Duke 11733* (MO). CHIRIQUÍ: Progresso, *Cooper & Slater 300* (CFMR, F, US); without definite locality, *Cooper & Slater 307* (CFMR, F, NY, US). COLÓN: Santa Rita Ridge, 500 m, *McPherson 8456* (MO). HERRERA: carretera a Pesé, *Lao 585* (MO). LOS SANTOS: Punta Mala, *Croat 9756* (DUKE), *9763B* (MO (2)). PANAMÁ: vicinity of Pacora, 0–20 m, *Allen 3455* (BM, BR, F, G, MO); cerca del Río Chame, *Moron 28* (MO). SAN BLAS: Permé, *Cooper 235* (NY, US).

Cordia correae James S. Miller, sp. nov. TYPE: Panama. Coclé: La Mesa, 4 km north of El Valle, disturbed tropical wet forest and roadside, 875 m, 3 Jan. 1974, *M. Nee & J. D. Dwyer 9164* (holotype, MO 2414635; isotype, DUKE). Figure 2.

Arbor vel frutex ad 8 m alta, ramunculis glabris ad strigillosis. Folia persistentia, petiolis 5–10(–14) mm longis, strigillosis; laminae anisophyllae, coriaceae, foliis maioribus ovatis ad anguste ovatis, 10.3–17.6 cm longis, 4.8–8.8 cm latis, apice acuminatis, basi rotundatis ad obtusis, superficie sparsim strigillosa, pagina inferiore minute strigillosa. Inflorescentiae internodales vel axillares, cymosae, ad 5.5 cm latae. Flores sessiles; calyx urceolatus, 5.6 mm longus, rufostrigillosus. Fructus drupaceus, aurantiacus, putamine inaequilateraliter ovoideo, 8.4–13 cm longo, 6.2–9 mm lato, ruminato.

Tree or shrub 4(–8) m tall, the twigs nearly glabrous to strigillose. Leaves persistent; petioles 5–10(–14) mm long, canaliculate adaxially, unevenly and often sparsely strigillose; blades anisophyllous, coriaceous, the larger ones ovate to narrowly ovate, 10.3–17.6 cm long, 4.8–8.8 cm wide, the smaller ones ovate, 7–8 cm long, 4–5.5 cm wide, the apex acuminate, the base rounded to obtuse or rarely acute, the margin entire, the adaxial surface with widely scattered appressed hairs, the abaxial surface minutely strigillose. Inflorescences subterminal, internodal or axillary, few per stem, cymose, to 5.5 cm broad, expanding somewhat in fruit, peduncle 1.8–5.3 cm long, strigillose, the hairs brown. Flowers sessile; calyx urceolate, 5.6 mm long, 3 mm wide at the mouth, the 5 lobes deltate, 0.7–1.4 mm long, ribs absent, rufous-strigillose; corolla white, tubular with reflexed lobes, 8.5 mm long, 5-merous, the lobes oblong, 3.6 mm long, 1.9 mm wide, the tube 7.8 mm long; stamens 5, the filaments 10.5 mm long, the upper 6 mm free, glabrous, the anthers oblong, ca. 1 mm long; ovary ovoid, glabrous; style ca. 4 mm long, the stylar branches 2.3 mm long, the stigma lobes clavate. Fruits borne in the slightly expanded, saucer-shaped calyx, orange at maturity, drupaceous, glabrous, the stone inequilaterally ovoid, 8.4–13 mm long, 6.2–9 mm broad, ruminate, the endocarp bony.

Distribution. Cordia correae occurs in wet forests from 800 to 1,000 m in elevation and is known only from Panama in the provinces of Coclé, Panamá, and Veraguas.

Cordia correae is known from only a few collections from Panama in the region of El Valle and from Cerro Jefe. Its closest relative is probably *C. protracta* I. M. Johnston, a species of low elevations along the Atlantic coast of San Blas and adjacent Colombia. The two species share similar habits of growth, branching patterns, anisophyllous leaves, and distinctly five-lobed calyces. The fruits of *C. correae,* however, are orange, subglobose, and have a ruminate surface, while those of *C. protracta* are white, elongate, and ridged longitudinally. *Cordia correae,* which is endemic to Panama, is named in honor of Profesora Mireya D. Correa A., who has done much to advance the study of Panamanian plants.

Additional specimens examined. PANAMA. COCLÉ: La Mesa above El Valle, along road which ends in pasture, 810 m, *Croat 25310* (MO, NY); vicinity of La Mesa, N of El Valle, 1,000 m, *Gentry 6813* (AAU, MO, NY); Cerro Pilón, El Valle Site Area of WEPCOR, *Kirkbride 1071* (NY); La Mesa, 4 km N of El Valle, 850–875 m, *Nee & Dwyer 9214* (MO (2), NY). PANAMÁ: along road, 18.9 km N of Cerro Azul, *Mori & Kallunki 4998* (AAU, DUKE, NY, (2)). VERAGUAS: vicinity of Cerro Tute, forested slopes along trail to summit, 850–1,000 m, *McPherson 10684* (MO).

Cordia croatii James S. Miller, sp. nov. TYPE: Panama. Verguas: 5 mi. west of

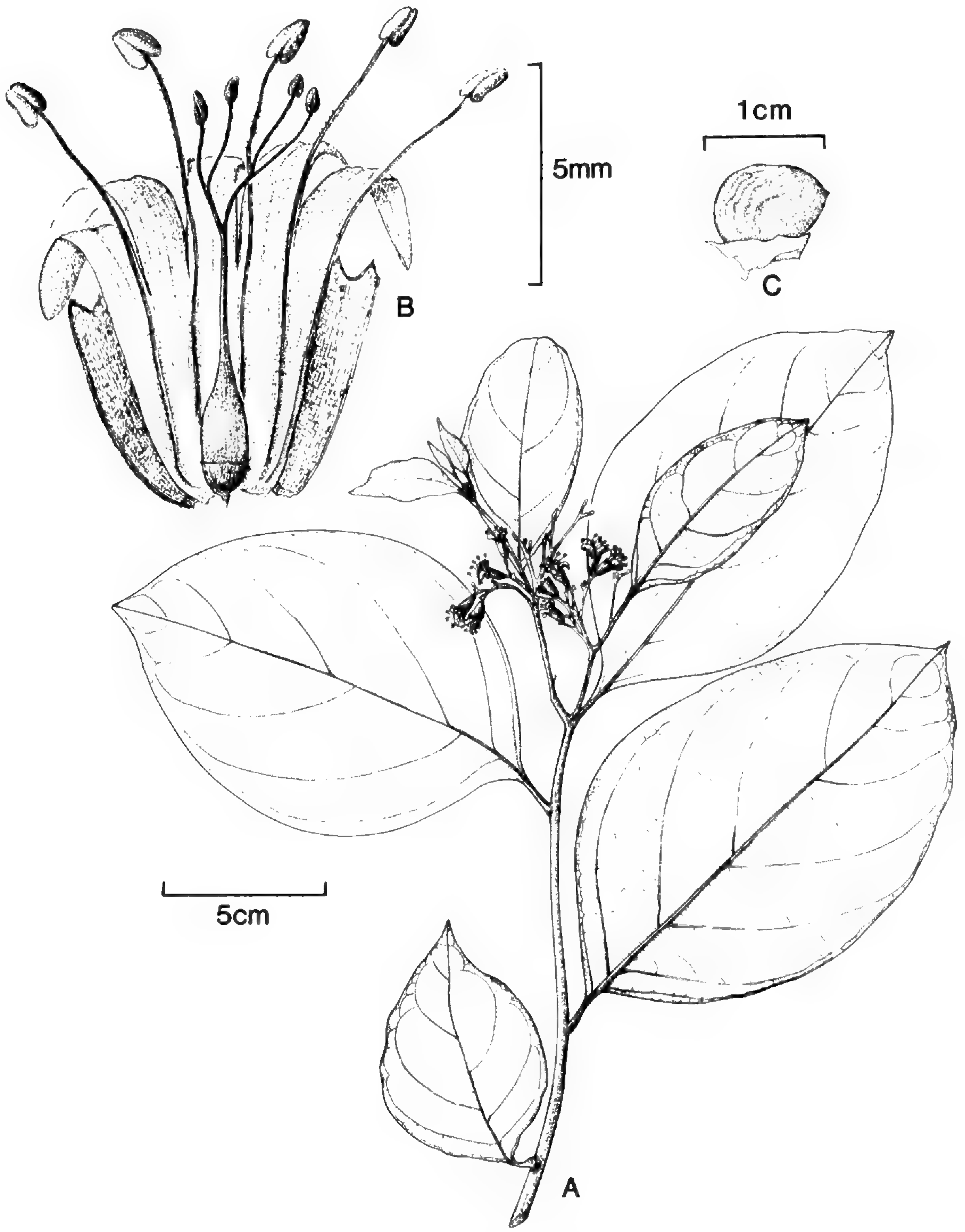

FIGURE 2. Cordia correae.—*A. Flowering branch.—B. Flower with calyx and corolla opened.—C. Dried fruit. A, B from* Nee & Dwyer 9164 *(MO), Coclé, Panama; C from* Mori & Kallunki 4998 *(NY), Panamá, Panama.*

Santa Fe on road past Escuela Agricola Alto Piedra on Pacific side of divide, 800–1,200 m, *T. B. Croat 23059* (holotype, MO 2198065; isotypes, AAU, BR, C, CAS, CR, DUKE, F, L, LL, MEXU, NY, RSA, US, WIS). Figure 3.

Arbor ad 20 m alta, ramunculis glabris ad strigillosis. Folia persistentia, petiolis 6–12 mm longis, laminae ellipticae ad elliptico-ovatae, (4.5–)5.7–8.2(–11.2) cm longae, (2–)3–4.3(–4.8) cm latae, apice acuto ad leviter acuminato, basi acuta ad obtusa. Inflorescentiae terminales, cymosae (3–)8–12(–15) cm latae. Flores bisexuales; calyx campanulatus, 3–4.3 mm longus, glaber, 3(–4)-lobatus; corolla alba, tubularis, 5–7.2 mm longa, 5-lobata, lobis reflexis, ovatis; stamina 5, filis 4–6.5 mm longis, villosis, antheris oblongis, 1.1 mm longis. Fructus drupaceus, putamine inaequilateraliter ovoideo, 8–11 mm longo, 6–8(–11) mm lato.

Tree to 20 m tall, the twigs nearly glabrous to sparsely strigillose, often with considerable waxy deposits. Leaves persistent; petioles 6–12 mm long, deeply canaliculate adaxially, nearly glabrous to sparsely strigillose; blades

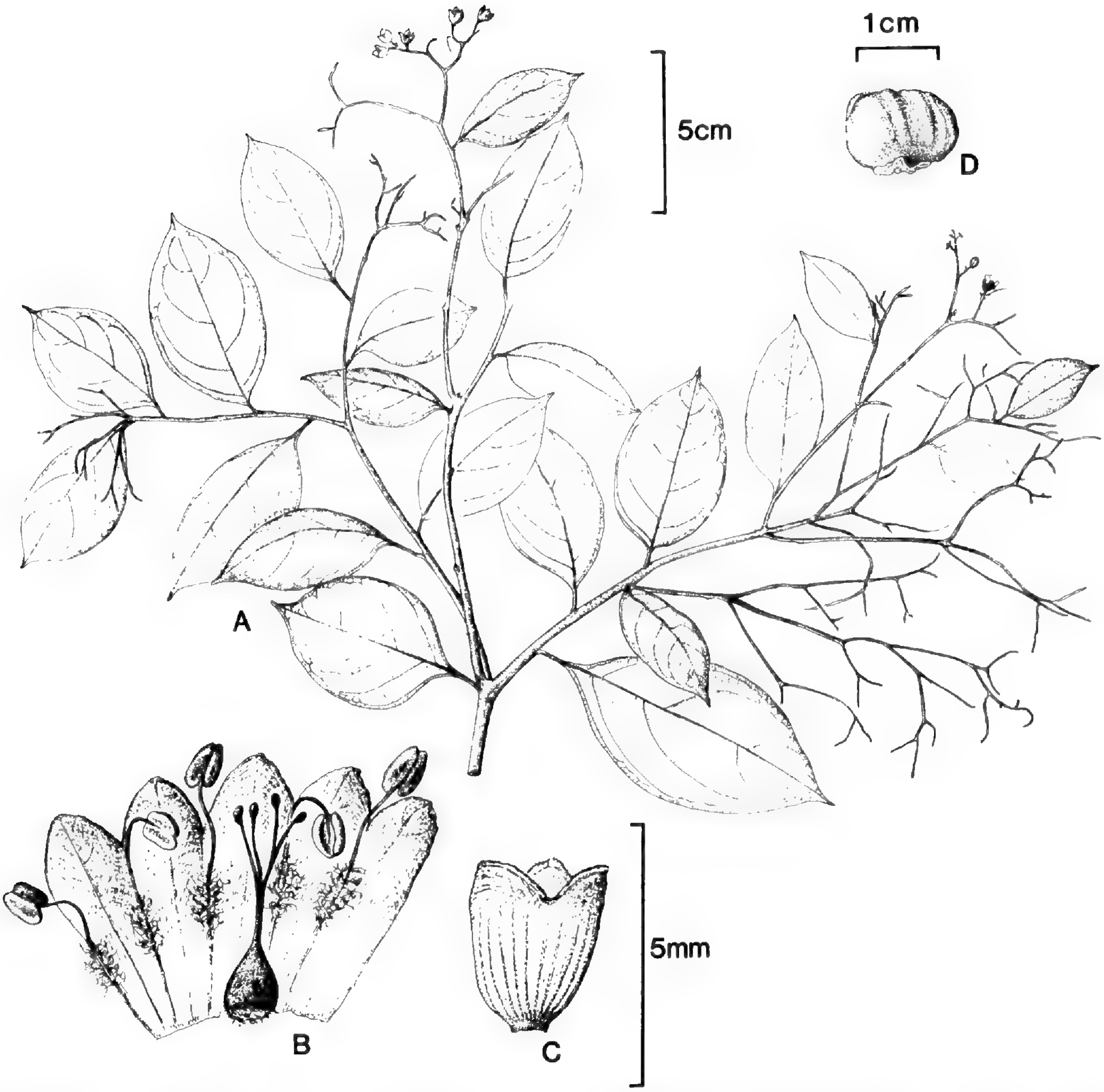

FIGURE 3. Cordia croatii.—*A. Flowering branch.—B. Flower with corolla opened.—C. Calyx.—D. Dried fruit.—A–C from* Croat 23059 *(MO), Veraguas, Panama; D from* Tonduz 12520 *(US), Alajuela, Costa Rica.*

elliptic to elliptic-ovate, (4.5–)5.7–8.2(–11.2) cm long, (2–)3–4.3(–5) cm wide, the apex acute to slightly acuminate, the base acute or less commonly obtuse and slightly decurrent, the margin entire, the adaxial surface glabrous to papillose with widely scattered appressed hairs, the abaxial surface glabrous. Inflorescence terminal, cymose (3–)8–12 (–15) cm broad, the branches sparsely brown-strigillose to ferruginous-puberulent. Flowers sessile, monomorphic, the stamens longer than style; calyx campanulate, 3–4.3 mm long, 3.4–4 mm wide at mouth, the 3(–4) lobes ovate, rounded at apex, 1–1.8 mm long, ribs absent, glabrous; corolla white, tubular with reflexed lobes, 5–7.2 mm long, 5-merous, the lobes ovate, 2–4.3 mm long, 1.5–3 mm wide, the tube 2.2–3 mm long, glabrous; stamens 5, the filaments 4–6.5 mm long, the upper 2–2.5 mm free, villous along the lower free portion, the anthers oblong, 1.1 mm long; ovary ovoid to conical, 1–1.6 mm long, 1–1.4 mm broad, glabrous; disc crateriform, 0.4–0.5 mm tall, 1–1.1 mm broad, glabrous; style 2–2.3 mm long, the stylar branches 1.7–2.5 mm long, the stigma lobes discoid. Fruits borne in the saucer-shaped calyx, drupaceous, glabrous, the stone inequilaterally broadly ovoid, 8–11 mm long, 6–8(–11) mm broad, the endocarp bony.

Distribution. *Cordia croatii* occurs in cloud forests from 800 to 1,200 m in elevation and is known from the San Ramón region of Costa Rica and the provinces of Coclé and Veraguas in Panama.

Cordia croatii is distinct in its small elliptic leaves. It is known only from a few Panamanian collections and several from the San Ramón region of Costa Rica, although further collecting efforts may reveal it in cloud forests in between. This species is somewhat unusual in sect. *Myxa* in that it occurs at relatively high elevations, unlike the majority of its relatives, which are usually found in lowland wet forests. *Cordia croatii* shares a three-lobed calyx with *Cordia lasiocalyx* Pittier, *C. lucidula* I. M. Johnston, and *C. porcata* Nowicke and is probably closely related to these species. *Cordia croatii* is named in honor of Dr. Thomas B. Croat who collected the type material and has contributed greatly to the study of Panamanian botany.

Additional specimens examined. PANAMA. COCLÉ: Cerro Pilón, 2,900 ft., *Lallathin 1F* (MO); *1-1* (MO).

Cordia curassavica (Jacq.) Roemer & Schultes, Syst. Veg. 4: 460. 1819. *Varronia curassavica* Jacq., Enum. Syst. Pl. 14. 1760. TYPE: Curassao, *Jacquin* (not seen).

Cordia obliqua Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 74. 1818. *Cordia peruviana* var. *mexicana* DC., Prodr. 9: 491. 1845. TYPE: Mexico. Campeche: *collector unknown* (holotype, P, not seen; microfiche, MO).

Cordia brevispicata Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(2): 331. 1844. TYPE: Mexico. Puebla: Tehuacán, Apr. 1840, *Galeotti 7192* (holotype, BR; isotypes, BR, G, K).

Cordia linearis A. DC., Prodr. 9: 493. 1845. TYPE: Mexico: *Herb. Pavón* (holotype, G-DC, not seen; microfiche, MO).

Cordia hispida Benth., Bot. Voy. Sulphur 139. 1845. TYPE: Honduras: Gulf of Fonseca, *Sinclair s.n.* (holotype, K).

Cordia palmeri S. Watson, Proc. Amer. Acad. Arts 24: 62. 1889. TYPE: Mexico. Sonora: Guaymas, 1887, *E. Palmer 281* (holotype, GH; isotypes, C, K, NY, UC, US (3)).

Cordia socorrensis Brandegee, Erythea 7: 5. 1899. TYPE: Mexico. Colima: Socorro Island, Mar.–June 1897, *Anthony 384* (holotype, UC 78381; isotypes, DS, F, GH, K, MEXU, MO, POM, SD, US).

Cordia brevispicata var. *hypomalaca* Greenman, Publ. Field Columbian Mus., Bot. Ser. 2: 338. 1912. TYPE: Mexico. Oaxaca: Cerro San Filipe, 1,700 m, 30 June 1907, *Conzatti 1831* (lectotype, here designated, F 225986; isolectotypes, F, GH). In describing this variety Greenman designated Conzatti's collection at the Field Museum as the type and listed two accession numbers (225986 and 246873). Neither sheet had been clearly marked as holotype by Greenman, and the better of the two specimens is selected as a lectotype here to rectify this situation.

Cordia imparilis J. F. Macbr., Contr. Gray Herb. 49: 16. 1917. TYPE: Mexico. Michoacán or Guerrero: 1 Aug. 1898, *E. Langlasse 265* (holotype, GH; isotypes, G (2), K, US).

Cordia chepensis Pittier, Contr. U.S. Natl. Herb. 18: 253. 1917. TYPE: Panama. Panamá: Chepo, 60 m, Oct. 1911, *H. Pittier 4511* (holotype, US 679672; isotype, US).

Cordia littoralis Pittier, Contr. U.S. Natl. Herb. 18: 253. 1917. TYPE: Costa Rica. Limón: Porto Limón, 27 May 1911, *H. Pittier 3641* (holotype, US 678699; isotype, GH).

Cordia mollis Pittier, Contr. U.S. Natl. Herb. 18: 294. 1917. TYPE: Guatemala: between Chiguin and Trapiche Grande, 900 m, 19 Apr. 1905, *H. Pittier 134* (holotype, US 472788).

Shrub to 2(–4) m tall, the twigs glabrous to strigillose or puberulent or rarely hirsute but always with small, globose wax particles. Leaves deciduous, on short spurs to 1 mm long; petioles 1–8(–21) mm long, strigillose or puberulent to hirsute; blades lanceolate to narrowly elliptic or elliptic-ovate, (1–)2–9.4(–16) cm long, 0.5–4(–7.3) cm wide, the apex acute, the base cuneate to acute and sometimes decurrent, the margin serrate, occasionally merely undulate, the adaxial surface scabrous to papillose, the abaxial surface strigillose with most hairs restricted to the major veins, or tomentulose. Inflorescence terminal, spicate, 1.5–8.8(–15) cm long, the peduncle 1.8 cm long, puberulent or strigillose to nearly glabrous. Flowers sessile, distylous; calyx campanulate, 2–3.2(–3.8) mm long, the 5(–6) lobes deltate; corolla white, tubular with reflexed to spreading lobes, (3.8–)4.8–6.8 (–8.2) mm long, 5(–6)-merous, the lobes ovate to depressed ovate, 1.2–1.8(–2.8) mm long, the tube 2.4–3.4 mm long; stamens 5, the filaments 3.2–5(–6) mm long, the upper 0.8–2 mm free, the free portion glabrous, puberulent to pubescent beneath the point of insertion, the anthers ellipsoid, (0.3–)0.7–1 mm long; ovary ovoid to broadly ovoid, (0.8–)1–1.2(–1.6) mm long; disc crateriform, 0.4–0.6(–0.8) mm tall; style (1.4–)2–4(–5.7) mm long, the stigma lobes clavate. Fruits drupaceous, red, ½–¾ enclosed in the slightly accrescent calyx, the stone ovoid, (3.7–)4–4.5 (–6) mm long, 2.2–3 mm broad, the endocarp bony.

Distribution. *Cordia curassavica* is common in a wide variety of habitats but is found most often in disturbed or dry areas from sea level to 2,000 m in elevation. This species ranges from Sonora and Baja California in northern Mexico south to northern South America and east to the West Indies. It is known from all of the provinces in Panama.

Cordia curassavica is extremely variable, and many of its variants have been recognized as taxonomically distinct by previous authors. Much of the variation throughout the range of *C. curassavica* is in overall size of the plants, size of leaves, and size of inflorescences. Individuals from populations in Baja California and Socorro Island are quite small in stature with leaves much reduced in size; the synonym *C. socorrensis* Brandegee is based on a collection of this sort. The most diminutive plants occur in populations from the Tehuacán region of Puebla, Mexico, the area from which the type of another synonym, *Cordia brevispicata* Martens & Galeotti, was collected.

The other extreme variant of *Cordia curassavica* occurs along the Atlantic coast of Central America, and only in Panama can it be found on the Pacific slope. These plants are more robust and differ from other populations in being larger in all aspects as well as in having broader leaves. Also, the pubescence of the upper leaf surface differs from what is seen in other populations; the hairs are represented only by the persistent bases, lacking shafts. *Cordia chepensis*, based on a type collection from Chepo, and *Cordia littoralis*, based on a population from the Atlantic coast of Costa Rica, are synonyms of this sort. These were referred to as "typical *Cordia curassavica*" by Johnston (1949a), who felt that with further study, several segregate species would be recognized. Numerous collections from all portions of the range indicate that there are no clear morphological discontinuities.

Although populations of *Cordia curassavica* vary over its geographic range, a much greater component of this variation appears to be due to phenotypic response to local climate rather than genetic differences between the populations. While collections made in the field from different regions often vary widely in appearance, most of these differences are not evident in the plants that have been raised in the greenhouse from seed collected in Mexico, Nicaragua, and Panama. Adult plants raised from seed under uniform conditions from morphologically and geographically diverse populations are often virtually indistinguishable.

Cordia curassavica hybridizes with *C. spinescens* L. and with *C. bullata* (L.) Roemer & Schultes and probably hybridizes with several additional species (Miller, in prep.). Observations made on numerous hybrids show that they vary in pollen stainability according to the parentage, but even if sterile, they are capable of persisting by spreading rhizomatously. As a result, these hybrids are represented in herbarium collections, leading to confusion and the long list of synonyms associated with this species. Although interspecific hybridization appears to be relatively uncommon, it may be adding to the variability of populations through rare backcrossing to parent plants.

Data indicate that *Cordia curassavica* is best treated in a broad sense, as much of the variability between populations is phenotypic. While there are considerable differences between the extremes, none of the intermediates exhibit any significant reduction in pollen stainability. Despite this variability, *Cordia curassavica* is a well-marked species easily distinguished from *C. spinescens* by having lanceolate leaves and elongate, terminal, spicate inflorescences. *Cordia curassavica* differs from *Cordia guanacastensis* Standley, the other Central American species with which it could be confused, by having much more elongate spikes generally less than 8 mm broad and by having the peduncles nearly glabrous or puberulent to strigillose rather than hispid as in *C. guanacastensis.*

Additional specimens examined. PANAMA. BOCAS DEL TORO: Santa Catalina River bank and beach, *Blackwell et al. 2710* (MO, SCZ, UC); vicinity of Almirante, Changuinola Canal, *Blum 1389* (MO, SCZ); Chiriquí Lagoon, Isla Colón, 0–120 m, *Wedel 562* (GH, MO, U), *2478* (MO, NY, US); Chiriquí Lagoon, Columbus Island, *Wedel 2608* (MO, US); Chiriquí Lagoon, Isla Colón, *Wedel 2923* (MO, NY, US). CANAL AREA: Ancon Hill, *Bartlett & Lasser 16312* (GH, MICH, MO); Fort Sherman area, *Blum et al. 386* (MO, SCZ); Gamboa Navy Pipe Line along main dirt road, *Correa & Haines 541* (MO); road S-10, north of Escobal, *Croat 12447* (F, MO); near beach at Fort Kobbe, *Duke 4196* (MO (2)); near Coco Solo Weather Station, *Duke 4284* (MO); Summit Gardens, *Dwyer 7190* (MO); Fort San Lorenzo, *Ebinger 457* (F, MEXU, MO); Ancon Hill, 100–200 m, *Killip 12059* (GH, NY, US), *12106* (US); near Fort Randolph, *Maxon & Harvey 6506* (US); low woods E of Bella Vista, a suburb of Panama City, *Maxon & Valentine 6945* (US); Toro Point near Fort Sherman, *McDaniel 4996* (MO); Fort San Lorenzo, bluff above Chagres River, *McDaniel 5179* (MO); Curundu, 30–40 m, *Miller 1033, 1034, 1035, 1036, 1037, 1038, 1039, 1040, 1041, 1042, 1043, 1044* (MO); along Fort Sherman road (S2 or 82), *Mori & Kallunki 2712* (MO); Ancon Hill, *Standley 25207* (US); Balboa, *Standley 25552, 27152* (US); near Fort Randolph, *Standley 28604* (US); Mount Hope Cemetery, *Standley 28786* (US); vicinity of Fort Sherman, *Standley 31220* (US); Fort Sherman near road to Gatún, *Tyson & Dwyer 1206* (MO, SCZ); Howard Air Force Base near Red Devil drop zone, *Tyson 1865* (MO); Fort Clayton, *Tyson et al. 2304* (NY); vicinity of Miraflores Lake, just outside Naval reserve, *White 244* (MO, NY). CHIRIQUÍ: along trail north of Cerro Punta, *Croat 10477* (MO, NY). COCLÉ: vicinity of El Valle, 800–1,000 m, *Allen 100, 753* (F, MO); hills S of El Valle de Antón, 700 m, *Allen 2510* (US (2)); Río Hato Airstrip, *Blum & Dwyer 2474* (AAU, SCZ); *Burch et al. 1148* (K, MO, UC, US); 10 km W of Agua Dulce on the Interamerican Highway, *Correa 87* (MO, SCZ); 3 mi. NE of Antón, *Croat 9618* (MO, SCZ); road from Pan-American Highway to El Valle, 100–1,000 m, *D'Arcy & Sytsma 14647* (MO); savannas near El Valle, *Duke & Mussell 6615* (MO); Penonomé, *Dwyer 2000* (MO (2)); along El Valle de Antón, 1 km up road toward La Mesa near first waterfall, *Folsom & Kauke 2753* (MO); W of Río Guias, *Gentry 5845* (MO); E facing slopes of the crater around El Valle de Antón, about 2 mi. W of town, 1,000 m, *Luteyn 1245* (F, GH, MO); along the road to El Valle between the Pan-American Highway and El Valle, 400 m, *Miller et al. 773* (MO); Agua Dulce, *Pittier 4860* (NY, US); Río Grande en Coclé, *Rosario 20* (F); El Valle de Antón and vicinity, 500–700 m, *Seibert 439* (F, MO); 3–6 km SE of El Valle de Antón, *Wilbur & Luteyn 11765* (DS, GH, LL, MICH, MO, NY, RSA, US); between Agua Dulce and Antón, 15–50 m, *Woodson et al. 1207* (F, MO, NY); between Las Margaritas and El Valle, *Woodson et al. 1293* (F, MO, NY). COLÓN: vicinity of Camp Pina, 25 m, *Allen 3586* (F, G, NY, U, US); 1 mi. E from Puerto Pilón along road to María Chiquita, *Correa & Haines 235* (F, MO (2)); vicinity of San Miguel de la Borda, *Croat 9867* (MO); between Bellas and Salud, near sea level, *Croat 36870* (MO); along ocean trail between Río Indio and Miquel de la Borda, sea level, *Croat 36913* (MO); María Chiquita, E of Río Piedras towards Portobelo, *Dwyer & Kirkbride 7775, 7788* (MO, UC); road to Portobelo between Río Piedras and Portobelo, roadside near ocean, *Elias & Kirkbride 1648* (MO, UC); without definite locality, *Kuntz s.n.* (NY (2)); Salud, *Lao & Holderidge 246* (MO); Nuevo Chagres, beach and adjacent roadside, *Lewis et al. 1856* (MO, US); mouth of Río Piedras, beach and adjacent areas, *Lewis et al. 3166* (MO, SCZ, UC); coastal thickets between Río Guanche and Río Buenaventura, 7.5 mi. SW of Portobelo, *Webster 16778* (MO); along roadside between 5–7 mi. SW of Portobelo towards María Chiquita, *Wilbur & Weaver 11177* (F, MICH, MO, NY, US); 6 mi. SW of Portobelo on the very edge of the Caribbean, *Wilbur & Luteyn 11665* (DS, F, GH, LL, MICH, MO, NY, US). DARIÉN: coastal thicket near Jaqué, *Duke 10668* (MO); near Yaviza, 50 m, *Gentry & Mori 13500* (MO). HERRERA: alrededores de Ocú, *Diaz 48* (F, MO); road between Las Minas and Pesé, (U. of Fla. site #4), ca. 600 ft., *Duke 12318* (MO (2)); Ocú, *Ebinger 1050* (F, MO, US); 10 mi. S of Ocú on Las Minas Road, 300 m, *Graham 251* (GH, MICH); 12.5 mi. S of Ocú, 1,200 ft., *Lewis et al. 1633* (ENCB, MO); 1 mi. N of Chupampa on the road to Ocú, *Wilbur et al. 12108* (DS, F, GH, LL, MICH, MO). LOS SANTOS: 1–2 mi. W of Candelaria, *Duke 12435* (MO (2)); N of Río Caldera near Punta Mala, *Stimson 5291* (F, GH, NY, SCZ, UC); Los Asientos, *Wendehake 37* (MO). PANAMÁ: vicinity of Río Pacora, savannas along Panama National Highway E of Panama City, *Bartlett & Lasser 16476* (GH, MICH, MO); 1.5 mi. above Interamerican Highway on road to Cerro Campana, *Croat 12040* (MO); open area near the sea, E side of town, Isla Taboga, *D'Arcy & D'Arcy 6806* (MO (2), US); Cerro Campana, *D'Arcy 9600* (MO); near beach at Nueva Gorgona, *Duke 4514* (MO (2)); Cerro Campana, 2,400–2,700 ft., *Duke 8674, 10721* (MO); along road from Panamerican Highway to Coronado Beach, *Duke 11805* (MO); Bar Mouth, Changuinola valley, *Dunlap 132* (F); Río Mar, near beach, *Dwyer 1798* (MO); Tocumen, *Dwyer 1860* (MO); Cerro Campana, ¾ of the way to the summit from Panamerican Highway, *Dwyer et al. 4849* (MO, SCZ); between Río Pacora and Chepo, roadside savanna, *Dwyer et al. 5125* (MO, SCZ, UC); La Campana, Cerro Campana, *Ebinger 370* (F, MO); Playa near Río Mar, *Ebinger 502* (F, MO); Chagres, *Fendler 130* (GH, F, US); 1 km E of Chorrera city limits, *Folsom 3463* (MO); Taboga Island, hill behind beach on main island, near sea level, *Gentry 5732* (F, MO, NY); Taboga Island, *Killip 3168* (US); next to bridge over small stream 10.6 mi. W of San Carlos on the Panamerican Highway, *Luteyn & Foster 1401* (ENCB, F, MO); along the road to Cerro Campana, 600 m, *Miller et al. 735* (MO); alrededores de Chame, *Moron 42* (MO); Punta Paitilla, *Piper 5398* (US); near Old Fort Lorenzo, mouth of Río Chagres, *Piper 5925, 5932* (US); Las Sabanas, *Standley 25857* (US); near Punta Paitilla, *Standley 26282* (US); vicinity of Juan Franco Race Track near Panama, *Stand-*

ley 27795 (US); Taboga Island, *Standley 28021* (US); Tumba Muerto Road, near Panama, *Standley 29785* (US); Nuevo San Francisco, *Standley 30738* (US); dirt road to Ojos de Agua where it branches off the carretera transisthmica (between Panama City and Colón) about 5 mi. N of Panama City, *Stimson et al. 5055* (GH, SCZ, UC); on lower Changuinola River, *Stork 132* (UC, US); Goofy Lake, SW facing slope, 500 m, *Sullivan 78* (MO); W slope of Cerro Campana, 2,300 ft., *Tyson 4038* (MO, SCZ); slopes of Cerro Jefe beyond Cerro Azul between 4–8 mi. in mostly heavily wooded slopes, *Wilbur & Weaver 11345* (DS, GH, MICH, MO); weedy roadsides within 1 mi. of Chepo, *Wilbur & Luteyn 11807* (DS, GH, MICH, MO); Isla Taboga, ca. 0–186 m, *Woodson et al. 1485* (F, MO, NY). SAN BLAS: vicinity of Puerto Obaldía, *Croat 16880* (MO); Isla Soskatupu, *Duke 8945, 10191* (MO); Ailigandi, San Blas Islands, *Dwyer 6809* (MO, TEX); Island of Soskatupu, on the only hill on the island, 150 ft., *Kirkbride 187* (MO, NY); on trail to inland village of Armila, 3–8 km SW of Puerto Obaldía, *Mori et al. 6804* (MO, US). VERAGUAS: ca. 5 mi. N of Santiago, vicinity of Santa María River, *Blum & Tyson 624* (MO, SCZ); 15 mi. W of Santiago, *Croat 10734* (MO); roadside savanna 2–4 mi. E of Santiago, ca. 30 m, *Duke 12366* (MO (2)); Santiago, 12 mi. from Santiago toward divisa on Transisthmian Highway, *Dwyer & Kirkbride 7449* (MO); Santiago, 2 mi. W of Santiago on Transisthmian Highway, *Dwyer et al. 7550* (MO, UC); Río Gatu at intersection with highway from Santiago to Santa Fe, *Folsom 3085* (MO); mouth of Río Concepción, beach, cliffs, and adjacent swamp, *Lewis et al. 2849* (MO, NY, SCZ); road between Laguna La Yeguada and Calobre, *Luteyn 1472* (MO); Projecto Agro-forestal Alto Guarumo, N of Santiago, S of San Sebastian, 300–400 m, *Meijer & Lao 362* (MO); road to Santa Fe, 15 km from Santiago, 150 m, *Sullivan 409* (MO).

Cordia cymosa (J. D. Smith) Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., 18: 981. 1938. *Cornutia cymosa* J. D. Smith, Bot. Gaz. (Crawfordsville) 40: 10. 1905. TYPE: Costa Rica. Alajuela: Paturages de la Palma, 1,460 m, 19 Nov. 1898, *A. Tonduz 12555* (holotype, US 1323323; isotypes, K, US (2)).

Tree to 15(–30) m tall, the twigs ferruginous-tomentulose with scattered echinate hairs. Leaves persistent; petioles 15–41 mm long, shallowly canaliculate adaxially, ferruginous-tomentulose with scattered echinate hairs; blades dimorphic, the larger ones elliptic or elliptic-ovate, (15–)18–32(–37.5) cm long, (7.5–)11–20.5(–26) cm wide, the smaller ones orbicular to circular, 9.5–16 cm long, 8.5–17 cm wide, the apex obtuse or less commonly rounded or acute, the base obtuse or less commonly acute, the margin entire, the adaxial surface strigillose, the abaxial surface soft-pubescent, with most of the the hairs restricted to the veins. Inflorescence terminal, cymose, (14.5–)17–29 cm long, 18.5–31 cm broad, the peduncle (1–)3.5–8.2(–11.2) cm long, ferruginous-tomentulose with scattered echinate hairs. Flowers sessile, unisexual by abortion, the plants dioecious, the male flowers with reduced styles, the female flowers with small, nonfunctional anthers. Female flowers with a tubular calyx ca. 3.7 mm long; corolla white, tubular with reflexed lobes, 4.6–5.3 mm long, 5-merous, the lobes oblong-ovate, 2–2.2 mm long, 1–1.2 mm wide, the tube 2.4–3.3 mm long; stamens 5, nonfunctional, the filaments ca. 3.5 mm long, the upper 0.5–1.8 mm free, glabrous or nearly so, the anthers ellipsoid, shriveled, 0.2–0.4 mm long; ovary ellipsoid to ovoid, 1.5 mm long, 0.8–0.9 mm broad, glabrous; disc small, crateriform or indistinct from the base of the ovary; style 2.5–3.5 mm long, the stylar branches 1.2–2 mm long, the stigma lobes clavate to discoid. Male flowers with a campanulate calyx, 2.2–3 mm long, 2–3 mm wide at mouth, strigillose to puberulent, the 3–5 lobes depressed-ovate to deltate, ca. 0.8 mm long; corolla white, tubular-campanulate with reflexed lobes, 3.8–4.7 mm long, the 5 lobes oblong-ovate, 1.9–2.1 mm long, 1–1.4 mm wide, the tube 2–2.7(–3.8) mm long; stamens 5, the filaments (2.5–)4–5 mm long, the upper 1.6–2.4 mm free, pubescent at and just above the point of insertion, the anthers ellipsoid to oblong, 0.8–1 mm long; ovary ovoid, 0.6–1 mm long, 0.4–0.6 mm broad, glabrous; disc crateriform, 0.3–1 mm tall, 0.6–1.2 mm broad, or occasionally not distinct from the base of the ovary, glabrous; style 0.7–1(–1.8) mm long, the stylar branches 0.3–0.5(–1) mm long, the stigma lobes filiform to clavate. Fruits seated in the cupulate calyx, white, drupaceous, glabrous, the stone inequilaterally ovoid, 7.3–10 mm long, 4.8–9 mm broad, endocarp bony, 1-locular.

Distribution. *Cordia cymosa* ranges from Costa Rica south through Panama and

Colombia to Ecuador, mostly in cloud forests and rarely at low elevations in wet forests. In Panama it is known from Bocas del Toro, Canal Area, Coclé, and Panamá.

Cordia cymosa is a member of the *C. panamensis* group, one of the taxonomically most complex species groups of sect. *Myxa.* It is probably most closely related to *C. panamensis* but differs by having larger stature. *Cordia cymosa* is easily distinguished from the other members of the complex by its scattered echinate hairs on the stems, petioles, and peduncles.

Additional specimens examined. PANAMA. CANAL AREA: Mt. Lerio, *Christopherson 152* (US (2)). BOCAS DEL TORO: region of Cerro Colorado, 4.3 mi. above Camp Chami, 1,500 m, *McPherson 9595* (MO). COCLÉ: El Valle de Antón, *Alston 8809* (US). PANAMÁ: Cerro Campana, *Folsom et al. 2312* (MO); Cerro Campana, trails just inside entrance to Parque Nacional, 850 m, *Miller & Miller 998* (MO); along the Panamerican Highway 6.5 mi. E of highway checkpoint at turnoff to Chepo, *Miller et al. 1018* (MO).

Cordia dentata Poiret, Encycl. 7: 48. 1806. TYPE: Curasao: *Von Rohr 1799* (holotype, P in herb. Jussieu, not seen; microfiche, MO).

Cordia calyptrata Bertero ex Sprengel, Syst. Veg. 1: 649. 1825. *Varronia calyptrata* (Bertero ex Sprengel) DC., Prodr. 9: 469. 1845. TYPE: Mexico, Veracruz: near Vera Cruz, 1,000 ft., 1839, *J. J. Linden 284* (holotype, BR; isotypes, K, MICH).

Cordia tenuifolia Bertol., Rendiconto Sess. Ordinarie Accad. Sci. Ist. Bologna 1860–1861: 63. 1860; Mem. Reale Accad. Sci. Ist. Bologna, 11: 199, t. 11. 1861. TYPE: Guatemala: In Volcano d'acqua a Valasquezio (not seen).

Cordia leptopoda K. Krause, Bot. Jahrb. Syst. 37: 628. 1906. TYPE: Colombia: in planitiebus ad flumen Magdalena, prope Purificacion, 200–500 m, *Lehmann 7347* (not seen).

Cordia ovata Brandegee, Univ. Calif. Publ. Bot. 10: 187. 1922. TYPE: Mexico. Veracruz: Remudadero, *C. A. Purpus 8937* (holotype, UC; isotypes, GH, MO, NY, US).

Tall shrub or tree to 7(–10) m tall, the twigs puberulent to nearly glabrous. Leaves semideciduous; petioles 8–20 mm long; blades elliptic to widely elliptic or ovate, occasionally obovate, 4.6–10 cm long, 3–7 cm wide, the apex obtuse, or less commonly acute or rounded, the base obtuse to rounded, rarely acute, the margin entire or slightly denticulate, the adaxial surface strigillose to scabrous, the hairs arising from a distinct cystolith, the abaxial surface nearly glabrous to puberulent with dense tufts of curly hairs in the axils of the major veins. Inflorescence terminal, cymose-paniculate, 15–20 cm broad, the branches puberulent to sparsely strigillose. Flowers sessile, distylous; calyx campanulate, 3–3.8 mm long, circumscissile and tearing open somewhat unevenly, faintly 10(–12)-ribbed; corolla yellow to almost white, campanulate, 9–12 mm long, 5(–6)-merous, the lobes depresssed ovate, 1.8–4 mm long; stamens 5(–6), the filaments 4.7–9.4 mm long, puberulent at the point of insertion, the anthers ellipsoid to oblong, 1.2–2 mm long; ovary ellipsoid to globose, 1–1.5 mm long; style 3.5–5.3 mm long, the stigma lobes clavate. Fruits borne in the saucer-shaped calyx, translucent white, drupaceous, the stone ellipsoid, symmetrical or nearly so, 9–11 mm long, 5.5–7.2 mm broad, the endocarp bony.

Distribution. Cordia dentata occurs in dry forests from sea level to 400(–1,400) m in elevation from Mexico to northern South America and the West Indies. In Panama this species is known from the Canal Area and the provinces of Chiriquí, Herrera, Los Santos, Panamá, and Veraguas.

Cordia dentata is the most distinctive member of sect. *Myxa* in Central America. It is the only species with a yellow corolla that is relatively large, campanulate, and rather showy, and it is often cultivated for this reason, as well as for its sweet, edible fruits. It differs further from most other members of the section by having a circumscissile calyx. The unusual calyx and corolla of *C. dentata* suggest that it is not closely related to any of the other Panamanian members of sect. *Myxa*, and its relationships with species from other geographic regions are obscure. Johnston (1940) stated that the type of *C. dentata* was collected by Von Rohr, but the only sheet in the Jussieu herbarium is labeled as a Vahl collection. It was apparently collected by Von Rohr, and the sheet at Paris is a duplicate that Poiret received from Vahl.

Cordia dentata is common throughout

much of Mexico, Central America, the West Indies, and northern South America but has been only rarely collected in Panama. While most species of sect. *Myxa* occur in wet forests, *C. dentata* occurs in drier regions, often in second-growth and disturbed areas. It is frequently found growing along roadside ditches and fencerows from Costa Rica northward.

Additional specimens examined. PANAMA. CANAL AREA: Monte Lirio, *Christopherson 125* (US); between Gorgona and Mamei, 10–30 m, *Pittier 2236* (NY, US). CHIRIQUÍ: vicinity of David, *Pittier 2820* (GH, NY, US); vicinity of San Felix, 0–120 m, *Pittier 5448* (GH, NY), *5458* (US). HERRERA: Pesé, ca. 20 m, *Allen 805* (MO, NY (2), US); Chitré, *Carrasquilla 314* (F, MO); ca. 2 mi. E of Chitré, *D'Arcy & Croat 4190* (MO, SCZ); outskirts of Chitré, *D'Arcy & Antonio 13481* (MO); Las Minas, 350 m, *Lao 45* (MO). LOS SANTOS: Las Tablas, *Dwyer 1167* (MO (2)); Monagre Beach, *Dwyer 4165* (MO); road from Macaracas to Chitré Highway, *Tyson et al. 3156* (MO, SCZ). PANAMÁ: near Chepo, *Kluge 52* (CFMR, F, US). VERAGUAS: 5 mi. E of Santiago, *Tyson et al. 4289* (MO, SCZ).

Cordia diversifolia Pavón ex A. DC. in DC., Prodr. 9: 474. 1845. TYPE: Nueva España, *Pavón s.n.* (holotype, G-DC, not seen; microfiche, MO; isotype, G).

Cordia johnstonii Cuf., Arch. Bot. Sist. 10: 41. 1934. TYPE: Costa Rica. Atlantida: 28 mi. from Puerto Limón, *Cufodontis 365* (not seen).

Cordia petenensis Lundell, Wrightia 4: 49. 1968. TYPE: Guatemala. Petén: Remate, 26 Apr. 1960, *E. Contreras 894* (holotype, LL; isotypes, F, K).

Shrub to slender tree to 5(–10) m tall, the twigs hispid to hirsute. Leaves persistent; petioles 5–19 mm long, hispid to hirsute; blades narrowly elliptic or sometimes lanceolate or oblanceolate, 10.5–19 cm long, 3.2–6.8 cm wide, the apex acuminate to acute, the base acute, the margin with few, short, filiform teeth toward the apex or entire, the adaxial surface strigose, the abaxial surface soft strigose, the hairs mostly restricted to the veins. Inflorescence terminal, paniculate, 5.5–11 cm broad, the branches hispid to villous. Flowers sessile or on short spurs to 2(–4) mm long, unisexual by abortion, the plants dioecious, the male flowers lacking styles, the female flowers with small, nonfunctional anthers; calyx tubular, 4.5–5.5 mm long, 10-ribbed, 3–4(–5)-lobed; corolla white, tubular with reflexed lobes, 8–9.5 mm long, 5-merous, the lobes oblong to obovate; stamens 5, in male flowers the filaments 7.7–9(–10.7) mm long, the upper (3–)4.5–5.3 mm free, glabrous or the lower free portion pubescent, the anthers oblong, 0.4–1.8 mm long, in female flowers the stamens much reduced, the anthers 0.4–0.7 mm long; ovary ovoid, 0.4–1.2 mm long; disc widely depressed obovoid, 0.5–1 mm tall, style 7–8.5 mm long, absent in male flowers, the stigma lobes filiform. Fruits borne in the expanded, saucer-shaped calyx, white, drupaceous, the stone ovoid to ellipsoid, 7–9 mm long, 4–6 mm broad, the endocarp bony.

Distribution. *Cordia diversifolia* occurs in wet forests of the Atlantic coast from sea level to 600 m in elevation from Mexico to Panama. In Panama this species is known from Bocas del Toro and the Canal Area.

Cordia diversifolia is an uncommon species of Atlantic lowland forests in Central America but is apparently quite common in lowland Bocas del Toro. It is distinctive in its narrowly elliptic to lanceolate leaves, leaf margins with short, filiform teeth, costate calyx, and filiform stigma lobes. This is the most widespread member of a small complex of closely related Central American species that is defined by the presence of denticulate leaf margins, costate calyces, and consistent dioecy. The group also includes *C. cordiformis* I. M. Johnston, *C. salvadorensis* Standley, and *C. skutchii* I. M. Johnston, all of which occur from Nicaragua northward.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Almirante, out along the road to the "Bomba," *Blum 1314* (MO, SCZ); Lincoln Creek, *Carleton 40* (NY, US); Changuinola Valley, *Cooper & Slater 61* (CFMR, F), *112* (CFMR, F, US); region of Almirante, *Cooper 342* (CFMR, F (2), NY, US); Changuinola, *Croat 16309* (F, MO, NY); Changuinola Valley, *Dunlop 175* (F, US); Changuinola to 5 mi. S at junction of ríos Changuinola and Terebe, 100–200 ft., *Lewis et al. 795* (MO, UC, US), *937* (K, MO, US), *938A* (MO), *946* (F, MO, NY, UC, US); Chiriquí to 5 mi. S along Río Guarumo, *Lewis et al. 1994* (F, MO (2), US); Almirante, near road to Chiriquí, *McDaniel 5077* (MO); Shepherd Island, *McDaniel 5077*, *5161* (MO); on lower Changuinola River, *Stork 284* (UC, US); Almirante region, *Taylor & Slater 61* (US); Chiriquí Lagoon, Water Valley, *Wedel 632* (MO); Chiriquí Lagoon, *Wedel 1070* (MO); Chiriquí Lagoon, Old Bank Island, *Wedel 1894* (GH, MO, US), *2051* (MO, US); Chiriquí Lagoon, Pumpkin River, *Wedel*

2580 (MO, US); Chiriquí Lagoon, *Wedel 2595* (MO, US); vicinity of Nievecita, ca. 0–50 m, *Woodson et al. 1824* (F, MO, NY); Río Cricamola, between Finca St. Louis and Konkintoe, ca. 10–50 m, *Woodson et al. 1895* (MO, NY). CANAL AREA: Gamboa Naval Reservation, *Ebinger 482* (BR, ENCB, F, GH, MO).

Cordia dwyeri Nowicke, Phytologia 18: 419. 1969. TYPE: Panama. Colón: Santa Rita Ridge, 19 km from the Transisthmian Highway, 28 Jan. 1968, *J. D. Dwyer 8857* (holotype, MO 2518567; isotypes, F, GH, MO).

Sparsely branched tree to 10(–20) m tall, the twigs reddish-brown villous. Leaves persistent; petioles (2–)4–8(–14) mm long, thick, villous; blades coriaceous, bullate, ovate to elliptic, (9–)19–35(–60) cm long, (5–)8–16 (–25) cm wide, the apex acuminate to acute, the base rounded to obtuse or rarely subcordate, the margin entire, revolute, the adaxial surface distinctly bullate, often drying with a silver cast, nearly glabrous with a few scattered, appressed hairs, the abaxial surface brown pubescent to densely brown pilose. Inflorescence axillary or terminal, cymose, 4–15(–23) cm broad, the branches densely velutinous to tomentose, the hairs reddish brown. Flowers sessile, bisexual, monomorphic; calyx cupulate, 6–7 mm long, ribs absent, densely strigillose, with 2–3 unevenly deltate lobes; corolla white, cupulate with reflexed lobes, 8–9.5(–10.6) mm long, 5-merous, the lobes ovate to widely elliptic, 3–4 mm long, the tube 4.5–7 mm long; stamens 5, the filaments (5–)8–11(–13) mm long, the upper (2–)4.5–6.5 mm free, densely pubescent just above the point of insertion, the anthers ellipsoid to oblong, 1.4–1.8 mm long; ovary ovoid to conical, 1–1.7 mm long, glabrous; disc transversely oblong, 0.4–0.8 mm long; style 5–7.4 mm long, the stigma lobes clavate. Fruits half enclosed in the slightly accrescent calyx, white, drupaceous, inequilaterally ovoid, the stone ca. 1.7 cm long, ca. 1.3 cm broad, the endocarp bony, pebbled on the surface.

Distribution. *Cordia dwyeri* occurs in wet forests from sea level to 450 m in elevation and ranges from southern Nicaragua to northern South America. In Panama this species is known from the provinces of Bocas del Toro, Colón, and Panamá.

Cordia dwyeri appears to have no close relatives in Central America and is very distinctive in its habit of growth and in its extremely large, bullate leaves. Its closest relative is probably *C. trichoclada* DC. of South America, a species that has large bullate leaves but differs in having a costate calyx. *Cordia dwyeri* is apparently common throughout lowland wet forests of Costa Rica and Panama, although it is not often collected. This may be due to relatively rare flowering or may relate to the difficulty of preparing specimens from such bulky plants.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Palo Blanco, *Gordon 95c* (MO). COLÓN: East Santa Rita Ridge, *Correa & Dressler 663* (MEXU, MO); Santa Rita Ridge, *Croat 13856* (MO). PANAMÁ: El Llano-Carti Highway, about 8 km N of El Llano, *Dressler 4573* (ENCB, F, MO); forest and roadside between 6–12 km N of El Llano on Carti Road, 1,200 ft., *Hammel 866* (MO); El Llano–Carti Road, 7.9 km from Interamerican Highway, 400 m, *Miller et al. 872* (MO); El Llano–Carti Road, 7.9 km from Interamerican Highway, 350 m, *Mori & Kallunki 5608* (AAU, MO, NY); along El Llano–Carti Road, 7 km N of Pan-American Highway at El Llano, 450 m, *Nee 10402* (MEXU, MO, US); El Llano–Carti Road, ca. 9 mi. from Pan-American Highway along newly cut bypass, 350–400 m, *Sytsma 4145* (MO).

Cordia eriostigma Pittier, Contr. U.S. Natl. Herb. 18: 251, fig. 101. 1917. TYPE: Colombia. Cauca: El Paso de la Balsa, on the Cauca River, near Jamundi, 480 m, 10 Feb. 1906, *H. Pittier 1489* (holotype, US 531695).

Tree to 15(–30) m tall, the twigs minutely brown strigillose, later waxy. Leaves persistent; petioles (7–)10–24(–30) mm long, sparsely strigillose; blade elliptic or slightly ovate or obovate, occasionally narrowly elliptic, (5–)6–16(–22.5) cm long, (2.4–)4.3–7.5(–11) cm wide, the apex usually obtuse and acuminate at the very tip, occasionally acute or rounded, the base obtuse to acute, the margin entire, the adaxial surface glabrous or nearly so, usually with small papillae, the abaxial surface with few, small, scattered hairs, some attached medianly. Inflorescence terminal, cymose, 8–13(–17) cm broad, the branches brown strigillose. Flowers sessile, bisexual, monomorphic; calyx cupulate to campanulate, 2.8–3.5(–4.7) mm long, ribs absent, evenly strigillose, opening without distinct lobes or unevenly 3–5-lobed; corolla white, campanulate, 5.7–6.3(–7.3) mm long, 5(–6)-merous, the lobes deltate to shallowly deltate, (2.5–)3–4.3 mm long, the tube 2.4–3.4 mm long; stamens 5(–6), the filaments (4–)5–5.5 mm long, the upper (1.4–)2–2.5 (–3) mm free, puberulent below insertion, the hairs often spreading onto corolla tube; anthers oblong to ellipsoid, 1–1.7 mm long; ovary ovoid to broadly ovoid, 1.3–2 mm long, glabrous or with short bristles on the upper portion; disc crateriform, small; style 1.5–2.6 mm long, the stigma lobes spatulate to discoid. Fruit borne in the saucer-shaped calyx, red to orange at maturity, drupaceous, glabrous, the stone inequilaterally ovoid, 6–7 mm long, 3.5–5.5(–6) mm broad, the endocarp bony.

Distribution. *Cordia eriostigma* occurs in moist to wet forests at 200–1,200 m in elevation and ranges from Mexico to Colombia. In Panama this species is known only from the province of Coclé.

Cordia eriostigma is uncommon and is often confused with *C. collococca*, from which it can be distinguished by having persistent leaves with nearly glabrous abaxial surfaces, bisexual flowers, campanulate corollas, valvate calyx lobes, and ovaries with distinct bristles on the upper portion. *Cordia eriostigma* differs further from *C. collococca* in usually being found above 600 m in elevation.

Additional specimens examined. PANAMA. COCLÉ: El Valle site area of WEPCOR, Cerro Pilón, *Kirkbride 1071* (MO, US); El Valle de Antón, *Lao 281* (F, MO).

Cordia globosa (Jacq.) Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 76. 1818; *Varronia globosa* Jacq., Enum. Syst. Pl. 14. 1760. TYPE: not seen.

Varronia humilus Jacq., Enum. Syst. Pl. 14. 1760. *Cordia humilus* (Jacq.) D. Don, Gen. Hist. 4: 383. 1838. *Cordia globosa* var. *humilus* (Jacq.) I. M. Johnston, J. Arnold Arbor. 30: 98. 1949. TYPE: not seen.

Cordia jacmeliana K. Krause, Bot. Centralbl. 32: 344. 1914. *Varronia jacmeliana* (K. Krause) Friesen, Bull. Soc. Bot. Genève, Ser. 2, 24: 177. 1933. TYPE: Haiti. Ouest: near Jacmel, *Krause 11808* (not seen).

Varronia humilus var. *mexicana* Friesen, Bull. Soc. Bot. Genève, Ser. 2, 24: 162, t. 1, f. 4. 1933. *Varronia mexicana* Friesen, Bull. Soc. Bot. Genève, Ser. 2, 24: 162. 1933. TYPE: Mexico. Morelos: near Cuernavaca, 5,000 ft., 22 June 1896, *C. G. Pringle 6346* (holotype, G; isotypes, BR, CAS, ENCB, F, K, L, LE, MEXU (2), MO, NY, US (3)).

Shrub to 3(–4) m tall, the twigs strigillose. Leaves deciduous, on short spurs to 1 mm long; petioles (2–)3–12(–25) mm long, strigillose, the hairs appressed to spreading; blades ovate to lance-ovate, (1.3–)2–5.7(–9) cm long, (0.7–)1–2.7(–5) cm wide, the apex acute, the base subobtuse to acute and decurrent along the petiole for a short distance, the margin serrate, usually unevenly so, the teeth usually blunt, occasionally short-apiculate, the adaxial surface usually ± smooth, occasionally slightly bullate, strigose to strigillose, or scabrous, the abaxial surface strigillose to strigose, most of the hairs restricted to the veins, rarely nearly tomentose. Inflorescence subterminal, a dense, globose head, 8–14(–16) mm broad, the peduncle 0.5–1.5 (–3.6) cm long, strigillose. Flowers sessile, distylous; calyx campanulate, (2.3–)3–4(–4.2) mm long, ribs absent, the 5 lobes deltate to triangular with prolonged filiform tips 2–4 mm long; corolla white, tubular, (5–)6–8 (–10) mm long, undulate to shallowly lobed, the lobes scarcely separate to transversely elliptic-oblong, the tube (2.4–)3–4(–4.5) mm long; stamens 5, the filaments (4.5–)5–8(–9) mm long, the upper (1.3–)2–3(–4) mm free, puberulent in a ring in the mouth of the corolla tube, the anthers ellipsoid, 0.8–1.1 mm long; ovary ovoid, 1–1.5(–1.8) mm long; disc crateriform, 0.5–1 mm tall; style (3–)4.5–7 (–7.5) mm long, the stigma lobes filiform to clavate. Fruits drupaceous, red, the stone ovoid, 3.5–4.8 mm long, (1.5–)2–3.8 mm broad, the endocarp bony.

Distribution. *Cordia globosa* occurs in dry to moist forests from sea level to 600 m in elevation and ranges from southern Florida and Mexico to northern South America and the West Indies. This species is known in Panama from one collection.

Cordia globosa is a common weedy shrub throughout Central America, the West Indies, and parts of northern South America, but apparently rare in Panama. *Cordia globosa* is most closely related to *C. bullata*, which ranges from Costa Rica to Mexico and the West Indies, but the former differs in having corollas more than 5 mm long and peduncles less than 3.6 cm long. The leaves of *C. globosa* are also generally smaller and have a less prominent indument. Nevertheless, these two species are often difficult to separate, and interspecific hybridization appears to occur in some populations in Nicaragua, Honduras, and Yucatán (Miller, in prep.).

Jacquin did not specify a type when he published the names *Varronia globosa* and *V. humilus*. None of his collections of this species seem to be present in the Willdenow or Linnaean herbaria. There may be a specimen at BM (Stafleu, 1967), but Johnston (1949c) stated that no type was preserved. Proper lectotypification will have to await examination of specimens in European herbaria. An odd situation exists with *Varronia humilus* var. *mexicana* and *Varronia mexicana*, two names published by Friesen based on the same type for either a new species or a new variety. Friesen did not indicate at which rank he felt it should be treated.

Additional specimens examined. PANAMA. PANAMÁ: Punta Paitilla, *Standley 26268* (US).

Cordia inermis (Miller) I. M. Johnston, J. Arnold Arbor. 30: 95. 1949. *Lantana inerma* Miller, Gard. Dict. ed. 8, 1768. TYPE: Mexico. Veracruz: *Houston s.n.* (holotype, BM, not seen).

Cordia cana Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11: 331. 1844. TYPE: Mexico. Oaxaca: Bois de la late Pacifique, 1840, *Galeotti 7140* (holotype, BR).

Cordia insularis Greenman, Proc. Amer. Acad. Arts 33: 482. 1898. TYPE: Mexico. Nayarit: Tres María Islands, 3–25 May 1897, *E. W. Nelson 4296* (holotype, GH; isotype, US).

Erect shrub to 2(–3) m tall, the twigs strigillose to puberulent when young, later glabrous and lenticellate. Leaves deciduous; petioles (2–)4–12(–22) mm long, strigillose to puberulent; blades elliptic-ovate to narrowly elliptic or elliptic-lanceolate, (2–)3.5–10(–14) cm long, (0.7–)1–3.5(–6.8) cm wide, the apex acuminate to acute, the base attenuate, the margin serrate, the adaxial surface strigillose to strigose, the abaxial surface strigillose. Inflorescence internodal or terminal, a small globose head, (3–)4–7(–10) mm broad, the peduncle (0.7–)1–5(–9) cm long, strigillose to puberulent. Flowers sessile, appearing unisexual, the plants subdioecious, the male flowers with reduced styles, the female flowers smaller than the males, with small nonfunctional anthers; calyx campanulate, 1.8–3 mm long, ribs absent, strigillose, the (4–)5 lobes deltate, 0.5–1 mm long; corolla white to greenish white, 2.5–3.5(–3.8) mm long, truncate to undulate but lacking distinct lobes, puberulent to pubescent in the middle of the tube; stamens 4–5, in male flowers the filaments (3.3–)3.5–4 mm long, the upper 1–1.6 mm free, puberulent at insertion, the anthers oblong, 0.7–1 mm long, in female flowers the filaments 2–2.5 mm long, the upper 0.3–0.5 mm free, puberulent at insertion, the anthers ellipsoid, ca. 0.3 mm long; ovary ovoid to nearly spherical, 0.5–1 mm long; disc crateriform, 0.2–0.6 mm tall; style in male flowers 0.7–1 mm long, the stigma lobes much reduced, filiform to slightly flattened, the style in female flowers 2–3.5 mm long. Fruits drupaceous, (3–)4–5.5(–6.5) mm long, 2–3(–3.2) mm broad, ⅓–⅔ enclosed in the slightly accrescent calyx, the calyx and fruit bright red at maturity, the stone ovoid, the endocarp bony.

Distribution. Cordia inermis occurs in disturbed areas from sea level to 1,100 m in elevation and ranges from Mexico to Panama. In Panama this species is known from the Canal Area, Chiriquí, and Panamá.

Cordia inermis is one of the most common weedy species of the genus in Central America. It reaches its southern limit in Panama where it is known from relatively few collections. In Panama, *C. inermis* can be confused with *C. linnaei*, from which it differs in having terminal or internodal rather than axillary inflorescences.

Cordia inermis has been described as dioecious (Opler et al., 1975). The female flowers have small nonfunctional anthers, and the male flowers have reduced styles and stigmas. The pollen from anthers of female flowers is small, deformed, and completely nonstainable. The female flowers appear to be 100% male sterile, but there is no indication of complete female sterility in male flowers, even though the gynoecium is reduced. In fact, some collections of male plants have both flowers and fruits on the same branch, and this species is probably subdioecious.

Additional specimens examined. PANAMA. CANAL AREA: Quarry Heights, hilltop, *Dwyer 2610* (MO (2), NY, US). CHIRIQUÍ: 1 mi. W of airport at Puerto Armuelles, near sea level, *Croat 22531* (F, MO); Río San Cristobal, 2 mi. W of David, 150 ft., *Tyson 912* (MO, RSA). PANAMÁ: Taboga Island, *Standley 27039* (US); *Woodson et al. 1478* (F, MO, NY).

Cordia lasiocalyx Pittier, Contr. U.S. Natl. Herb. 18: 251. 1917. TYPE: Panama. Darién: open field around Garachine, sea level, 12 Feb. 1912, *H. Pittier 5694* (holotype, US 715984; isotype, F).

Shrub or small tree to 5(–10) m tall, the branching pattern divaricate, the twigs glabrous. Leaves persistent; petioles (3–)4–7 (–10) mm long, canaliculate adaxially, glabrous; leaf blades elliptic-oblong to slightly obovate, (6–)9–13(–16) cm long, (2–)2.6–5(–5.4) cm wide, the apex abruptly caudate, the caudex (1–)2–3(–3.5) cm long, the base acute and slightly decurrent, the margin entire, the adaxial surface glabrous, the abaxial surface sparsely and minutely strigillose. Inflorescence terminal, cymose, 2.5–6.5(–10) cm broad, the peduncle 2.5–5 cm long, glabrous or with a few widely scattered hairs. Flowers sessile, monomorphic, the stamens exceeding the style; calyx cupulate to campanulate, 3.8–5 mm long, 3.6–4 mm wide at the mouth, ribs absent, glabrous or nearly so, the 3 lobes deltate, 1–2 mm long; corolla white, tubular, 7.6–10 mm long, 5-merous, the lobes oblong, 3.3–4.6 mm long, 2–2.5 mm wide, the tube 4.3–6 mm long; stamens 5, the filaments 6–9.5 mm long, the upper 2.6–3 mm free, pubescent at insertion, the anthers oblong, ca. 1.3 mm long; ovary ovoid to broadly ovoid, 1.3–1.8 mm broad, glabrous; style 3.5–5 mm long, the stylar branches 1.6–2.2 mm long, the stigma lobes clavate. Fruits borne in the cup-shaped calyx, white, drupaceous, glabrous, the stone strongly inequilaterally ovoid, 10–11 mm long, 6.4–9 mm broad, ruminate, the mesocarp mucilaginous, endocarp bony, 1-locular.

Distribution. *Cordia lasiocalyx* occurs in moist forests from sea level to 800 m in elevation and is known only from Panama, where it occurs in Bocas del Toro, the Canal Area, Coclé, Darién, and Panamá.

Cordia lasiocalyx is a member of a taxonomically difficult species complex that is characterized by glabrous leaves, a three-lobed calyx, and white fruit. Its caudate leaf apex readily separates it from its closest Central American relatives, *C. croatii*, *C. lucidula*, and *C. porcata*, all of which have acuminate leaf apices. *Cordia lasiocalyx* is probably most closely related to *C. lomatiloba* I. M. Johnston, a species of Amazonian South America.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Island Potrero, Changuinola Valley, *Dunlap 322* (F, GH, US). CANAL AREA: Barro Colorado Island, *Croat 4601* (F, NY, SCZ (2)), *8568, 8572* (DUKE, F, MO, NY, SCZ); *Foster 833* (DUKE); *Knight 69-20* (MO (2)); *Oppenheimer 837* (DUKE, MEXU, MO, TEX); *Shattuck 813* (F, MO (3)), *853* (F, MO (2), US). COCLÉ: El Valle de Antón, *Allen 2302* (MO); Cerro Pilón, 2,500–3,000 ft., *Dwyer 8315* (DUKE); along ridge of Cerro Gaital, N slope of mountains near La Mesa, N of El Valle, 800–900 m, *Knapp & Dressler 4879* (MO); La Mesa, 2 km W of Cerro Pilón, 860 m, *Sullivan 453, 498* (MO). DARIÉN: Río Pirre, *Duke & Bristan 8282, 8300* (MO); Puerto Indio, less than 50 m, *Hammel 1080* (MO); Trail from Canglon–Yaviza Road to Río Chucanaque, 7.7 mi. E of Canglon, 50 m, *Knapp & Mallet 3956* (MO); forests around Pinogana, *Pittier 6560* (US). PANAMÁ: Río Maje, along river from waterfalls near Bayano Lake to finca of Choco Indian Eduardo Maycha, ca. 2 mi. upstream, 30–60 m, *Croat 34581* (MO); vicinity of El Llano, *Duke 5837* (MO); del G.M.I. Isla Bayano, *Garibaldi 97* (F, MEXU, MO); Cerro Campana, 900 m, *Knapp & Sytsma 2308* (MO); Cerro Campana, above Su Lin Motel, *Porter et al. 4218* (MO).

Cordia leslieae James S. Miller, sp. nov. TYPE: Panama. Panamá: Cerro Jefe 5.8 mi. above Lago Cerro Azul, 840 m, 30 July 1983, *James S. Miller & Leslie A. Miller 886* (holotype, MO 3386970). Figure 4.

Arbor ad 7 m alta, ramunculis glabris, subalatis. Folia persistentia, petiolis 0.8–2 cm longis, applanatis, basibus continuis secus ramos; lamina coriacea, obovata, 9.2–16.2 cm longa, 5.3–8.4 cm lata, apicibus retusis ad acuminatis, basibus cuneatis, marginibus integris, revolutis. Inflorescentia terminalis, cymo-paniculata. Flores bisexualis; calyx tubulo-campanulatus, 5.5–6 mm longus; corolla alba, 8–10 mm longa, 5-lobata, lobis ovatis, incrassatis ad apices, stamina 5. Fructus drupaceus, aurantiacus, putamine inaequilateraliter ovoideo, 1.4 cm longo.

Tree to 7 m tall, the twigs glabrous, subalate. Leaves persistent; petioles 0.8–2 cm long, flattened in cross section and canaliculate adaxially, the bases continuous along the stem for a short distance; blades coriaceous, obovate, 9.2–16.2 cm long, 5.3–8.4 cm wide, the apex variable, retuse or acuminate, the base cuneate, the margin entire, revolute, the adaxial surface glabrous, slightly papillose, the abaxial surface glabrous. Inflorescence terminal, cymose-paniculate, 5.5–7.5 cm long, 5–9.5 cm broad, with 50–120 or more flowers, the branches sparsely strigillose. Flowers sessile or nearly so, bisexual; calyx tubular-campanulate, 5.5–6 mm long, 3–3.4 mm wide at the mouth, ribs absent, sparsely strigillose, the 5 lobes deltate, 1–1.4 mm long; corolla white, tubular with reflexed lobes, 8–10 mm long, 5-merous, the lobes ovate to oblong with a triangular thickening at the apex, 4 mm long, 2–3 mm wide, the tube 4–6 mm long; stamens 5, the filaments 9.3 mm long, the upper 4.3 mm free, pubescent at insertion, the anthers oblong, 2 mm long; ovary obloid, 1.8 mm long, 0.7 mm broad; style 5.5 mm long, the stylar branches 2 mm long, the stigma lobes clavate to discoid. Fruits seated in the cupulate, slightly accrescent calyx, orange, drupaceous, the stone inequilaterally ovoid, 1.4 cm long, mesocarp mucilaginous, endocarp bony, 1-locular.

Distribution. *Cordia leslieae* occurs in cloud forests at 800–1,000 m in elevation and is known only from Cerro Jefe, in the province of Panamá.

Cordia leslieae is apparently not closely related to any other species of *Cordia* in Central America. This species is distinct in having sub-alate stems and petioles and in having thickened areas at the ends of the corolla lobes. It is named in honor of my wife, Leslie Miller, who assisted me with field studies in Panama and discovered the tree from which the type collection was made.

Additional specimens examined. PANAMA. PANAMÁ: Cerro Jefe, *Dressler 3489* (MO, PMA); Cerro Jefe region roadside and forest, 200–800 m, *Hammel 4850* (MO); Cerro Jefe, NE of Panama City, forested slopes below summit, 850–900 m, *McPherson 9735* (MO); Cerro Jefe, near summit, along road to east about a quarter mile below tower, 750–850 m, *McPherson 11191* (MO); Cerro Jefe, 850–900 m, *Sytsma 2009* (MO).

Cordia linnaei Stearn, J. Arnold Arbor. 52: 627. 1971. TYPE: Jamaica. St. Andrews: pastures behind Hope Gardens, 600–700 ft., 22 Oct. 1956, *Proctor 15789* (holotype, BM, not seen; isotype, IJ).

Shrub to 4 m tall, the twigs coarsely pubescent, the hairs erect, brown. Leaves deciduous, on short spurs 1–1.5 mm long; petioles (1–)1.5–3(–7) mm long, pubescent, the hairs erect, brown; blades ovate to lanceolate, (2–)3.4–9(–10.6) cm long, (0.9–)1.2–2.9(–5.3) cm wide, the apex acute to acuminate, the base cuneate, the margin sharply serrate, the adaxial surface coarsely puberulent, the hairs short, slightly swollen at the base, appressed, the abaxial surface softly pubescent, the hairs wavy, erect. Inflorescences numerous, axillary, capitate, 7–11 mm broad, the peduncle (0.5–)0.8–2.8(–6.4) cm long, pubescent, the hairs erect, brown. Flowers sessile, distylous; calyx cup-shaped, 2–2.5(–2.7) mm long, ribs absent, strigillose, the 5(–6) lobes deltate to shallowly triangular, sometimes with a short apiculate tip; corolla white, tubular, 3–3.8(–4.2) mm long, truncate at the apex; stamens 5, the filaments (2.5–)3–3.5(–3.8) mm long, the upper 0.3–1(–1.2) mm free, glabrous to canescent at insertion, the anthers ellipsoid, 0.4–0.6 mm

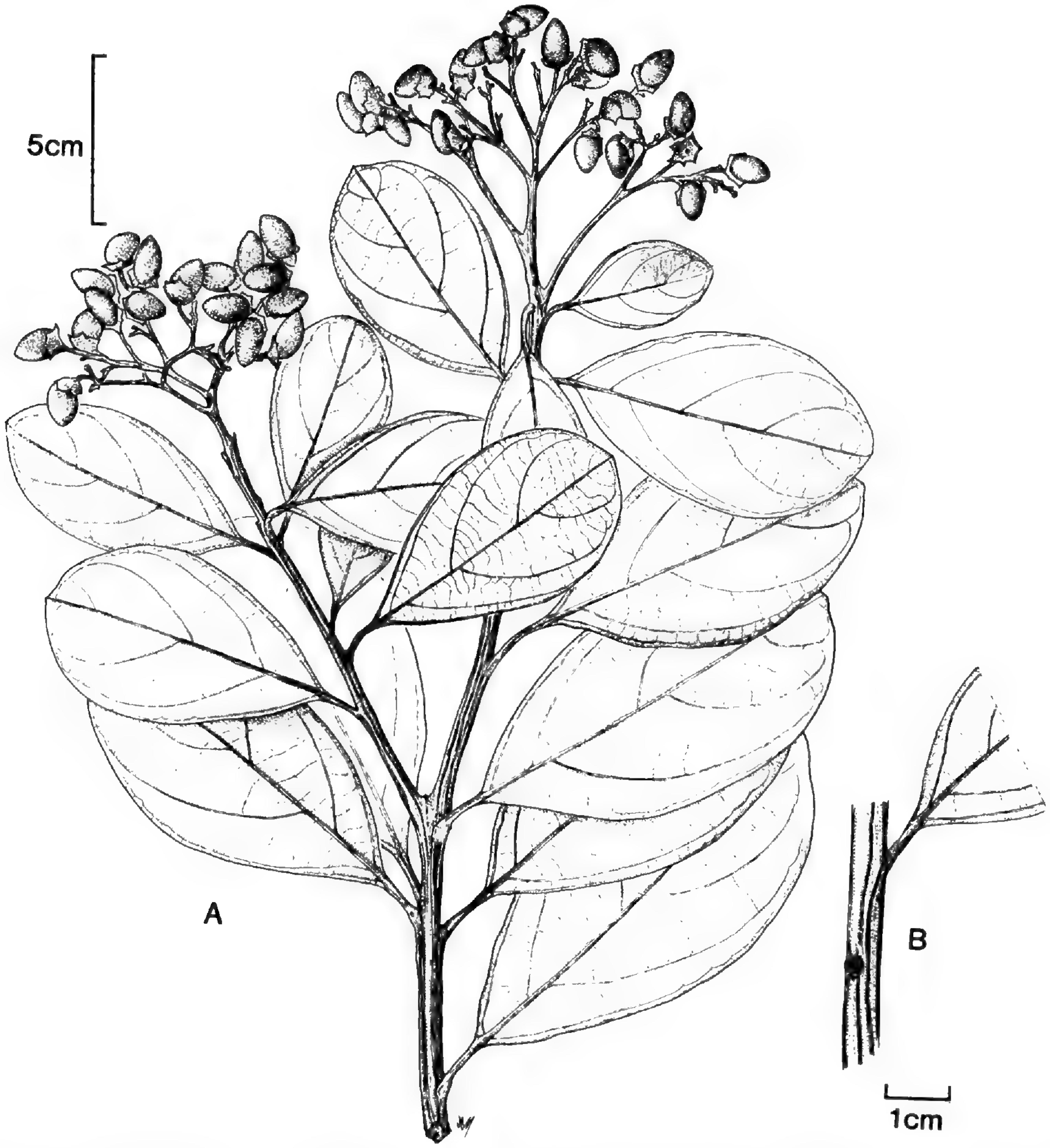

FIGURE 4. Cordia leslieae.—*A. Fruiting branch.—B. Sub-alate twig with petiolar attachment. From* Miller & Miller 886 *(MO), Panamá, Panama.*

long; ovary ellipsoid, 0.6–1 mm long; disc crateriform to nearly flat, thin, ca. 0.2 mm tall; style (2.1–) 2.5–3(–3.5) mm long, the stigma lobes filiform or nearly so. Fruits drupaceous, 3.5–4(–5) mm long, (2.6–)3–3.5(–5) mm broad, ⅔ to nearly totally enclosed in the calyx, red, the stone ovoid to broadly ovoid, the endocarp bony.

Distribution. *Cordia linnaei* occurs in moist to wet forests from sea level to 900 m in elevation from Mexico to Colombia and in the West Indies. In Panama, *C. linnaei* is known from the Canal Area, Colón, Darién, Panamá, San Blas, and Veraguas.

This species was treated as *Cordia lineata* (L.) Roem. & Schultes in the *Flora of Panama* (Nowicke, 1969), as it has been in most recent works, but Stearn (1971) showed that this name is based on a long string of illegitimate names. It is easily recognized by its numerous, small, axillary inflorescences, which never branch cymosely as they do in *C. bifurcata.* The most likely Panamanian species with which *C. linnaei* could be confused is *C. inermis,* which has terminal and internodal, rather than axillary, inflorescences.

Additional specimens examined. PANAMA. CANAL AREA: near beach, at Ft. Kobbe, *Duke 4195* (MEXU, MO); along abandoned road C29 just N of Las Cruces

Trail, 6 km E of Gamboa, 150 m, *Nee 9042* (MEXU, MO, US); Balboa, *Standley 25474, 26068, 29245* (US). COLÓN: 20 km from Transisthmian Highway on Santa Rita Ridge, SE facing slope, 400 m, *Knapp & Schmalzel 1765* (MO); Santa Rita Ridge, ca. 4–5.5 mi. E of Transisthmian Highway, *Lewis et al. 5267* (MO); lumber road at about 8 km NE of Santa Rita Ridge along ridge, 650 ft., *Wilbur & Weaver 10830* (DUKE); wooded slopes on Santa Rita Ridge about 5 mi. from highway at Sabanita, 650 ft., *Wilbur & Weaver 11827* (DUKE). DARIÉN: Chepigana, *Duke & Briston 264* (DUKE, MO); Isla Boca Grande, *Duke 8846* (MO). PANAMÁ: vicinity of Cerro Jefe, Altas de Pacora, 2,400 ft., *Antonio 3218* (MO); vicinity of Río Pacora, E of Panama City on Panama National Highway, *Bartlett & Lasser 16954* (MO); 3 mi. from Interamerican Highway on road to Cerro Campana, *Croat 12057* (F, MO, NY); Cerro Jefe, *D'Arcy 9748* (MO); Panamerican Highway at Río Mamonica, 4 mi. beyond Chepo, *Duke 5580* (GH, MO); grasslands on Cerro Campana, 2,400–2,700 ft., *Duke 8677* (DUKE, MO); end of road near Río Boquerón, road is 2 km N of cement plant on Colón Highway, ca. 26 km E of turnoff to end of road, 500 ft., *Hammel 915* (MO); summit of Cerro Jefe and forests along road beyond summit, *Hayden 1025* (MO); in woods near Panama, *Hayes 559* (K); Punta Paitilla, just E of Panama City, *Heriberto 212* (GH, US); Cerro Jefe, 4.8 mi. above Lago Cerro Azul, 600–800 m, *Miller & Miller 883* (MO); El Llano–Carti Road, 3 mi. from Panamerican Highway, 400 m, *Miller et al. 1016* (MO); El Llano–Carti Road, 5 km N of Panamerican Highway at El Llano, 300 m, *Nee 7902* (MO); Río Tapic, *Standley 28153* (US); Cerro Jefe, 850–900 m, *Sytsma 1959* (MO); slopes of Cerro Jefe beyond Cerro Azul between 4–8 mi. in mostly heavily wooded slopes, *Wilbur & Weaver 11348* (DUKE); between Pacora and Chepo, ca. 25 m, *Woodson et al. 1671* (MO). SAN BLAS: Permé, *Cooper 276* (F, GH, NY, US); hills SE of Puerto Obaldía, *Croat 16737* (MO (2), SCZ); through cultivation on mainland in front of Ustupo, *D'Arcy 9481* (MO); Malatuppi, Río Ibedi, *Duke 8487* (MO); along headwaters of Río Mulatupo, *Elias 1742* (MO); mainland opposite Playón Chico, 0–3 mi. from Caribbean, 0–200 m, *Gentry 6399* (MO); mainland opposite Playón Chico, 0–3 mi. from Caribbean, 0–200 m, *Gentry 6415* (MO); mainland opposite Ailigandi, from mouth of Ailigandi River to 2.5 mi. inland, *Lewis et al. 204* (MO, NY, UC, US). VERAGUAS: Isla de Coiba, *Dwyer 2323* (MO (2), US); 1–2 mi. above Santa Fe, Gentry 3049 (F, MO, NY).

Cordia lucidula I. M. Johnston, J. Arnold Arbor. 21: 352. 1940. TYPE: Panama. Bocas del Toro: Potrero, Changuinola Valley, 20 Oct. 1923, *V. C. Dunlap 284* (holotype, US; isotypes, F, NY).

Tree to 5(–10) m tall, the twigs glabrous to sparsely strigillose. Leaves persistent; petioles (4–)7–12(–16) mm long, glabrous to strigillose; blades ovate to narrowly ovate, (9–) 11–22(–28) cm long, 5–9(–12) cm wide, the apex acuminate, the base obtuse and slightly decurrent or rarely rounded or acute, the margin entire, the adaxial surface glabrous or rarely strigillose, the abaxial surface minutely strigillose rarely approaching glabrous. Inflorescence terminal or rarely internodal or axillary, cymose, 4.5–8.7 cm broad, the peduncle 1.8–3.7(–7.8) cm long, strigillose. Flowers sessile, monomorphic; calyx cupulate to campanulate, 3–4 mm long, ribs absent, glabrous to strigillose, the 3 lobes ± deltate, 0.8–1 mm long; corolla white, tubular with reflexed lobes, 5–7 mm long, 5-merous, the lobes oblong, 2.3–3 mm long, the tube 2.8–4.2 mm long; stamens 5, exserted, the filaments 4.5–7.5 mm long, the upper 2.4–3 mm free, pubescent at the point of insertion, the anthers ellipsoid to oblong, ca. 1.2 mm long; ovary ovoid, 1–1.3 mm long, glabrous; disc crateriform, ca. 0.7 mm tall; style 1.9–4.1 mm long, the stigma lobes clavate. Fruits 10–13 mm long, 9.5–12 mm broad, borne in the slightly expanded, cup-shaped calyx, drupaceous, red, the stone broadly inequilaterally ovoid, the surface ruminate and slightly ridged, the endocarp bony.

Distribution. *Cordia lucidula* occurs in wet forests from sea level to 1,500 m in elevation and ranges from Nicaragua to Panama. In Panama *C. lucidula* is known from the provinces of Bocas del Toro, Chiriquí, Darién, and Panamá.

Cordia lucidula is extremely variable and is the most commonly collected member of a difficult group of closely related species, including *C. lasiocalyx* and *C. porcata,* found in Panama and Costa Rica. *Cordia lucidula* can be distinguished by its three-lobed calyx, more or less ovate leaves, and bright red fruits without apical prolongation. Leaf shape and texture often vary on a single plant and with time of year and locality. *Cordia lucidula* differs from *C. lasiocalyx* by having an acuminate, rather than caudate leaf apex. *Cordia lucidula* is most likely to be confused with *C. porcata,* which differs in having white fruits and anthers more than 1.9 mm long.

Additional specimens examined. PANAMA. BOCAS DEL TORO: region of Almirante, *Cooper 372* (C, CFMR, F, GH, US); Changuinola Valley, *Dunlap 356* (CFMR, F, US); Río Terebe just below Puerto Palenque, 350 ft., *Kirkbride & Duke 549* (F, MO, NY, SCZ); cloud forest of Cerro Bonyic, above Quebrada Hurón, 500–1,200 ft., *Kirkbride & Duke 596* (F, MO, NY, SCZ); Chiriquicito to 5 mi. S along Río Guarumo, *Lewis et al. 2089* (MO, UC); Chiriquí Lagoon, Fish Creek Hills, *Wedel 2394* (GH (2), MO), *2425* (GH, MO, US). CHIRIQUÍ: San Bartolo Limite near Costa Rican border, 12 mi. W of Puerto Armuelles, 400–500 m, *Croat 22150* (BR, C, CAS, F, LL, MEXU, MO, NY, RSA); Burica Peninsula, 8 mi. W of Puerto Armuelles, 200 m, *Liesner 353* (MO, WIS). COCLÉ: 7 km N of El Copé, *Folsom & Collins 6470* (NY). DARIÉN: primary forest along headwater of Río Tuqueza, ca. 2 km air distance from continental divide, in the vicinity of upper gold mining camp of Tyler Kittredge, *Croat 27126* (MO); trail from Pucuro to Cerro Mali, vicinity of mouth of Tapaliza River, ca. 100 m, *Gentry & Mori 13546* (MO, SCZ, US); 0–2 mi. E of Tres Bocas along the shortest headwater of the Río Cuasi, *Kirkbride & Duke 1184* (MO, NY). PANAMÁ: El Llano–Carti Road, 10.6 mi. from the Pan-American Highway, 400 m, *Miller et al. 871* (MO); El Llano–Carti Road, just south of San Blas border, 400 m, *Miller et al. 1014* (MO); El Llano–Carti Road, 10–12 km from junction with Inter-American Highway, 410 m, *Mori & Kallunki 2881* (AAU, MO, NY, U); El Llano–Carti Road, 8–11 km from Inter-American Highway, 300–400 m, *Mori 7709* (MO, U).

Cordia megalantha S. F. Blake, Proc. Biol. Soc. Wash. 36: 200. 1923; nom. nov. for *Cordia macrantha* S. F. Blake, Contr. U.S. Natl. Herb. 24: 19. 1922, non Chodat, 1921. TYPE: Guatemala. Izabal: Quebrada, 18 May 1919, *S. F. Blake 7498* (holotype, US 989592).

Tree to 30(–60) m tall, the twigs glabrous. Leaves deciduous; petioles (8–)11–33(–55) mm long, glabrous; blades elliptic to obovate, (4.6–)6–19(–21) cm long, 2.9–8(–12.6) cm wide, the apex acute to acuminate or rarely obtuse, the base acute or rarely obtuse to rounded, the margin entire, the adaxial and abaxial surfaces glabrous. Inflorescence terminal, paniculate, to 30 cm broad, the branches glabrous except for puberulent tips. Flowers on short spurs 2–5 mm long, distylous; calyx tubular, (8.5–)9–10(–11) mm long, striate to 10–20 ribbed, glabrous to puberulent, the hairs dark brown, unevenly lobed, tearing upon dehiscence or dehiscing circumscissilly; corolla marcescent, white, funnelform, 28–43(–50) mm long, the 5(–6) lobes deltate to ovate, 11–13 mm long; stamens 5(–6), the filaments 14.5–19 mm long, the upper 5–10(–13) mm free, pubescent at insertion and frequently over the entire free portion, the anthers oblong, 2–4 mm long; ovary ovoid to conical, 1.3–2.5(–4) mm long; disc depressed ovoid, 0.5–1 mm tall; style 16–19 mm long, the stigma lobes clavate. Fruits enclosed by the persistent calyx and corolla, ellipsoid to narrowly ellipsoid, 8–12 mm long, 4–6 mm broad, the wall thin, fibrous.

Distribution. *Cordia megalantha* ranges along the Atlantic coast of Central America in wet forests from sea level to 400 m in elevation. Disjunct populations occur on the Pacific side of Central America on the Osa Peninsula of Costa Rica and the Burica Peninsula in Chiriquí where the only known collection from Panama was made.

Often exceeding 30 m in height, *Cordia megalantha* is the tallest Central American species of *Cordia*. Although there are no reports of *C. megalantha* being cultivated as a timber tree, as is *C. alliodora*, it may have potential in wet regions. It apparently does not flower each year (T. Wendt, pers. comm.) and this, combined with its height, may be responsible for the paucity of collections. *Cordia megalantha* is very distinctive among the Panamanian members of the genus in its large size, marcescent corolla, and deltate corolla lobes.

Additional specimens examined. PANAMA. CHIRIQUÍ: west of San Bartolo Limite near Costa Rican border, *Croat 22175* (MO).

Cordia panamensis Riley, Kew Bull. 1927: 135. 1927. TYPE: Panama. Panamá: secondary growth at sea level near Old Panama, *L. A. M. Riley 143* (holotype, K; isotypes, MO, US).

Tree to 10(–15) m tall, the young twigs hirsute. Leaves persistent; petioles (5–)7–12 (–17) mm long, villous to hirsute or occasionally strigillose and with scattered, erect, longer hairs; blades dimorphic, the larger ones ovate to ovate-elliptic, (12–)17–28(–35) cm long, (5–)6.5–13.5(–15) cm wide, the apex acuminate, the base obtuse to rounded or occasionally somewhat cordate, often somewhat asymmetrical, the smaller ones orbicular, (5–) 6.5–9(–10) cm long, (3.8–)5–8.4(–10) cm wide, the margin entire, the adaxial surface scabrous, the abaxial surface ± pubescent, the hairs stiff but not rough to the touch, nearly erect to spreading. Inflorescence terminal or in the axils of the branches, cymose, (5–)7–13.5(–16) cm broad, the lower portion of the branches villous to hirsute, the tips of the branches densely strigillose. Flowers sessile, unisexual by abortion, the plants dioecious, the male flowers with reduced styles, the female flowers with small, nonfunctional anthers. Female flowers with a tubular calyx 2–3.6 mm long, ribs absent, strigillose, the 3–5 lobes unevenly deltate to triangular, 0.4–0.6(–1) mm long; corolla white, tubular with reflexed lobes, 3.8–4.5(–5.5) mm long, (4–) 5(–6)-merous, the lobes oblong-ovoid, 1–1.8 mm long, the tube (2–)2.5–3(–3.7) mm long; stamens (4–)5(–6), the filaments 3–3.6(–4.3) mm long, the upper 0.4–1.1 mm free, glabrous, the anthers ellipsoid, shriveled and containing only aborted pollen, ca. 0.3 mm long; ovary ellipsoid, 1–1.3(–1.8) mm long, glabrous; disc scarcely distinct from the base of the ovary; style 2–3.4(–4) mm long, the stigma lobes discoid. Male flowers with a campanulate calyx (2.5–)3–4 mm long, ribs absent, strigillose, the 3–5 lobes uneven, deltate to triangular, 0.7–1.1 mm long; corolla white, tubular-campanulate with reflexed lobes, 4.5–6(–6.5) mm long, 5(–6)-merous, the lobes oblong-ovoid, (1.5–)2–2.3(–2.7) mm long, the tube (1.5–)2.5–3.9 mm long; stamens 5(–6), the filaments 4.8–7.2 mm long, the upper 2–3.5(–4.3) mm free, villous at the point of insertion, the anthers ellipsoid, 0.8–1.3 mm long; ovary ovoid, 0.6–1.2 mm long, glabrous; disc crateriform, 0.5–0.7 mm long; style abortive, 1–2(–3.3) mm long, the stigma lobes filiform. Fruits seated in the cupulate calyx, white, drupaceous, glabrous, the stone inequilaterally ovoid, 6–7.5 mm long, (4.3–) 5.5–6 mm broad, the endocarp bony.

Distribution. *Cordia panamensis* occurs in dry to wet forests and ranges from southern Mexico to northern South America from sea level to 1,000 m in elevation. In Panama it is known from all regions except Bocas del Toro.

The *Cordia panamensis* complex is one of the most taxonomically difficult groups in the genus. Its Central American members, which include *C. anisophylla* and *C. cymosa*, are similar in appearance and are sometimes sympatric. The group reaches its greatest diversity in Panama and northern South America. *Cordia panamensis* differs from *C. cymosa* by being smaller in all aspects and by having only simple (vs. echinate) hairs. It differs from *C. anisophylla* in having a shorter corolla and fruits that are nearly as broad as long. *Cordia panamensis* is extremely variable in Panama with individual populations differing considerably in leaf size, shape, and indument. North of Costa Rica, it is more constant morphologically. *Cordia panamensis* is most closely related to *Cordia hebeclada* I. M. Johnston of Colombia, Ecuador, and Peru, which differs only in its evenly velutinous twigs and lower leaf surfaces.

Additional specimens examined. PANAMA. CANAL AREA: Juan Mina, *Bartlett & Lasser 16523* (DUKE, MO); beside railroad tracks along road to Tropic Test Center Miraflores Annex, *Correa 261* (DUKE, MO); Guillard Highway near Paraiso, *Croat 10141* (MO, SCZ); Barro Colorado Island, *Croat 10250* (MO, UC), *10390* (DUKE, F, MO, NY, SCZ, UC); Ancon Hill near gates to Quarry Heights Military Preserve rear gate, *Croat 11950* (F, MO, SCZ); Barro Colorado Island, *Croat 11967* (DUKE, F, MO, NY, SCZ); road S-11, NW of Escobal, *Croat 12460* (MEXU, MO (2)); Road K-2G, *Croat 15142* (MO); roadside in forest between Gatún and Fort Sherman, *Croat 15400* (MO); Pipeline Road 2 mi. from Gamboa gate, *Croat 16612* (MO); vicinity of Madden Lake along Boy Scout Road, less than 100 m, *Croat 38322* (MO); near Pedro Miguel railway station, *D'Arcy & D'Arcy 6021* (CHAPA, MO (2), RSA, US (2)); near beach at Ft. Kobbe, towards Vera Cruz, *Duke & Mussell 6559* (F, MO); Farfan Beach, *Dwyer 6766* (MO); Barro Colorado Island, *Foster 972* (DUKE, F), *1916* (DUKE, F, MO); Curundu Air Force Survival School, *Gentry 1464* (MO); Cerro de Ancon, *Gervais 133* (F, US); without definite locality, *Johansen 3* (US); Fort San Lorenzo, area W of Limón Bay, Gatún Locks and Gatún Lake, *Johnston 1515* (A (2)); Barro Colorado Island, *Kenoyer 632* (MO); Ancon Hill, 100–200 m, *Killip 12113* (US); 1 mi. W of the junction of the Cocosolo Hospital and the lookout to Gatún Lake, *Lazor & Blum 5377* (MO); Fort Kobbe Military Reservation, *Luteyn 1087* (DUKE, F, MICH, MO); Balboa, *Maxon 6926* (US); Pipeline Road, 10–15 mi. from Gamboa, 100 m, *Miller 1028b* (MO); Summit Gardens, 0–100 m, *Mori & Kallunki 1777* (MO); along road to golf course along Chagres River, Gamboa, 30 m, *Nee 7378* (ENCB, L, MEXU, MO, NY, RSA, US); along road to Radar Station on Semaphor Hill, 1 km N of Summit Garden, 100–150 m, *Nee 7493* (DUKE, MO, POM, US); Gamboa, *Pittier 3708* (NY, US); vicinity of Río Cocoli, Road K9, *Stern et al. 328* (G, MO, UC, US); observatory at Miraflores Locks, 75 m, *Sullivan 608* (MO); Albrook Air Force Base, *Tyson 1114* (MO, SCZ); Fort Clayton, Farfan Beach area, *Tyson 1823* (MO, SCZ); Curundu near Survival School, *Tyson 4174* (MO, SCZ); Miraflores on road to water plant, *Tyson 6596* (DUKE, MO); along Pipeline Road, 3 mi. NW of Gamboa, 100–200 ft., *Webster 16768* (MO); Balboa, *Wheeler s.n.* (GH); vicinity of Miraflores, *White 134* (F, MO); near lake opposite the island, *White 125* (F, MO). CHIRIQUÍ: pastures and forested river banks east of Gualaca, 500 ft., *Allen 5032* (MO); Progresso, *Cooper & Slater 317* (CFMR, F, US); Burica Peninsula, Dist. Guanabano, disturbed areas along Quebrada Quanabaro, *Croat 22530A* (MO); 2 mi. SW of Guabala, *Tyson et al. 4247* (MO); vicinity of Puerto Armuelles, *Woodson & Schery 814* (MO, US). COCLÉ: Río Hato Airstrip, *Blum & Dwyer 2471* (MO, SCZ); between Las Margaritas and El Valle, *Woodson et al. 1296* (F, MO, NY). COLÓN: entre Colón y Portobelo, 5 m, *Holderidge 6440B* (DUKE, MO); Tres Brazos sawmill, Icacal, which is in between Salud y Boca de Río Indio, *Howell 48* (MO); Salud, *Lao & Holderidge 222* (MO); Nuevo Chagres, beach and adjacent roadside, *Lewis et al. 1858* (ENCB, MO); along the beach between Fato and Playa de Damas, *Pittier 3932* (US), *3982* (NY). DARIÉN: about 10 mi. S of El Real on Río Pirre (House no. 22), *Duke 5482* (MO, NY); Río Pirre, *Duke 8248* (MO); Río Pucro, below village of Pucro, *Duke 13125* (F, MO, NY); 4.5 km S of El Real, along dry stream bed of Río Uruseco, *Mori & Kallunki 5372* (AAU, MO, NY); 3 mi. E of Santa Fe, *Tyson et al. 4676* (DUKE, MO, SCZ). HERRERA: entre Tres Puntas y Chepo (Las Minas), *Carrasquilla & Lao 340* (MO); Llano de las Minas, 350 m, *Lao 47* (MO). LOS SANTOS: Las Tablas, *Dwyer 1159* (MO). PANAMÁ: hills south of El Valle de Antón, 700 m, *Allen 2481* (MO, US); Trapiche, Perlas Islands, *Allen 2613* (MO); San José Island, *Anderson s.n.* (NY); out C-15 road, just outside the zone, *Blum & Dwyer 2677* (MO, SCZ); roadside on way to Cerro Campana, ¼ mi. from highway, *Croat 12030* (MEXU, MO, NY); Cerro Campana, along road above FSU cabin, *Croat 14207* (MO (2), SCZ); between Cerro Azul and Cerro Jefe, *Dressler 3865* (DUKE, F, MO); El Llano–Carti Road, 12–14 km N of El Llano, *Dressler 4359* (DUKE, ENCB, F, MO); vicinity of El Llano, *Duke 5813* (MO); Río San Tomas, *Duke & Mussell 6650* (AAU, MO); grassland on Cerro Campana, 2,400–2,700 ft., *Duke 8667* (MO, US); Isla de Pedro Gonzales, *Dwyer 1705* (MO); Tocumen, thicket near airport, *Dwyer 4044* (US); San José Island, *Erlanson 226* (MICH, US), *276* (G (2), NY, US), *446* (US); Cerro Campana, near tower, *Folsom et al. 2312* (MO); adjacent to Ft. Clayton, 50 m, *Haines 564* (DUKE (2), MO); San José Island, near Punta del Cabo, *Harlow 17* (GH, US); in woods about Panama, *Hayes 89* (BR); San José Island, *Johnston 51* (GH (2), MO, US), *79* (GH); Bella Vista, sea level, *Killip 12014* (GH, NY, US); low woods E of Bella Vista, a suburb of Panama City, *Maxon & Valentino 6962* (US); S of Farfan beach along shore and adjoining road, sea level, *Miller & Hamilton 730* (MO); along the road to Cerro Campana, 600 m, *Miller et al. 738* (MO); along the road to Cerro Campana, 1–3 mi. from the Pan-American Highway, *Miller & Miller 959, 961* (MO); along the road to Cerro Campana, ca. 5 mi. from the Pan-American Highway, *Miller & Miller 1000* (MO); Morro Island, just off N shore of Taboga Island, *Mori et al. 4074* (AAU, MO, NY, WIS); Bella Vista, *Standley 25347* (MO, US); near the big swamp E of Río Tocumen, *Standley 26647* (US); near Matias Hernández, *Standley 28877* (US); Punta Paitilla, *Standley 30816* (US); between Matias Hernández and Juan Diaz, *Standley 32039* (US); Archipielago de Las Perlas, San José Island, coast beside La Bodega, *Stimson 5323* (DUKE, SCZ (2)); Taboga Island near village, Perlas Islands, *Tyson 5593* (DUKE, SCZ); wet savanna E of Pacora, 25 m, *Woodson et al. 757* (F, MO, NY); Isla Taboga, *Woodson 1544* (MO, NY), *Woodson et al. 1547* (F, NY). SAN BLAS: Mulatuppu, *Duke 8540* (MO); Ailigandi, *Dwyer 6827* (MO). VERAGUAS: Isla de Coiba, *Dwyer 1574* (F, MO), *2343* (BR, MO (2), SCZ); Cerro Tute, 1,000 ft., *Dwyer 4293* (US), *4335* (MO); Santiago, 4 mi. from Transisthmian Highway toward Atalaya, *Dwyer & Kirkbride 7412* (MO (2), NY, UC); southern shore of Ensenada Santa Cruz, northern tip of Coiba Island, *Foster 1626* (DUKE (2), F).

Cordia porcata Nowicke, Phytologia 18: 397. 1969. TYPE: Panama. Colón: Santa Rita Ridge lumber road, 3 Oct. 1968, *M. Correa A. & R. Dressler 1076* (holotype, MO 2062961; isotype, MO).

Shrub or small tree 2–6 m tall, the twigs glabrous. Leaves persistent; petioles 5–11 mm long, broadly canaliculate adaxially, glabrous; blades narrowly elliptic to lance-elliptic, (5–)8.3–21(–24) cm long, 3–7.5(–10) cm wide, the apex acuminate, the base acute or rarely obtuse, slightly decurrent, the margin entire, sometimes slightly revolute, the adaxial surface glabrous, often drying with a silvery sheen, the abaxial surface glabrous to sparsely and minutely strigillose. Inflorescence terminal or internodal, cymose, 2.5–5.5(–10) cm broad, usually with 50–100 flowers, the peduncle 1.8–4.4 cm long, the branches canescent to strigillose, the hairs brown. Flowers monomorphic, sessile; calyx campanulate, 5.2–6.5 mm long, 2.6–5 mm wide at the mouth, ribs absent, nearly glabrous to minutely strigillose, the (2–)3(–4) lobes ± deltate, 1.3–1.8 mm long; corolla white, tubular with reflexed lobes, 6.5–10 mm long, (4–)5-merous, the lobes oblong, 3.1–4.5 mm long, 1.5–2 mm wide, the tube 3.7–6.4 mm long; stamens (4–)5, the filaments (4.5–)7–8.4 mm long, the upper (1.3–) 2.5–4 mm free, the lower free portion pubescent, the anthers narrowly oblong, 1.9–2.3 mm long; ovary ovoid to broadly ovoid, 0.8–1 mm broad, glabrous; style (4–)5.2–5.8 mm long, the stylar branches 2–2.5 mm long, the stigma lobes clavate. Fruits borne in the slightly expanded, saucer-shaped calyx, white at maturity, drupaceous, glabrous, the stone inequilaterally ovoid and sharply apiculate at the apex, 8.7–11 mm long, 4.8–6.5 mm broad, essentially smooth, the endocarp bony.

Distribution. *Cordia porcata* occurs in wet forests and ranges from southern Nicaragua to Panama from sea level to 1,500 m in elevation. In Panama it is known from the provinces of Coclé, Colón, Los Santos, and Panamá.

Cordia porcata differs from *C. lucidula*, the species with which it is most likely to be confused, in having lance-elliptic leaves, anthers more than 1.9 mm long, and smooth, rostrate fruits. Although *C. porcata* is quite common in some areas of Panama, it is known from only a small number of collections in northern Costa Rica and a single collection from Nicaragua.

Additional specimens examined. PANAMA. COCLÉ: region N of El Valle de Antón, 1,000 m, *Allen 3710* (BR, F, G, MO, U); Cerro Pilón, above El Valle de Antón, *Croat 14323* (MO, NY); La Mesa above El Valle, along road which ends in pasture, 810 m, *Croat 25310* (MO, NY); Cerro Pilón, El Valle, 3,000 ft., *Duke & Lallathin 15015* (MO); vicinity of La Mesa, N of El Valle, 1,000 m, *Gentry 6813* (AAU, MO, NY). COLÓN: Cerro Santa Rita, ca. 6 mi. from the Transisthmian Highway, 800–900 ft., *Antonio 1805* (MO); Santa Rita Ridge Road, ca. 1 hour walk from end of road, *Antonio 4490* (MO); East Santa Rita Ridge, *Correa & Dressler 635* (MO, SCZ); Santa Rita Ridge, *Correa & Dressler 1076* (MO), *Croat 13837* (MO), *D'Arcy & D'Arcy 6169* (C, F, MO); Santa Rita lumber road, ca. 15 km E of Colón, *Dressler & Lewis 3702* (F, MO, US); Santa Rita Ridge, *Dwyer 8581* (F, MO); Santa Rita Ridge, highway to 8 mi. east, 800 ft., *Dwyer et al. 9027* (MO (2), NY); Santa Rita Ridge, *Dwyer & Gentry 9366* (MO, NY), *9373* (MO); near Agua Clara rainfall station, Santa Rita Ridge, *Foster 1730* (DUKE); Santa Rita Ridge, 2–3 mi. from Transisthmian Highway, *Gentry 1865* (MO); Santa Rita Ridge, E ridge, *Gentry & Dwyer 4816* (DUKE, F, MO, RSA); Santa Rita Ridge east of Transisthmian Highway, 300–500 m, *Gentry 6546* (F, MO); Santa Rita Ridge, 400–500 m, *Knapp et al. 1680* (MO); end of Santa Rita Ridge Road, 21 km from Transisthmian Highway, 400–500 m, *Knapp & Schmalzel 5243* (MO); Santa Rita Ridge Road, 21–26 km from Transisthmian Highway, 500–550 m, *Knapp 5867* (MO); Santa Rita Ridge, 2 mi. from Transisthmian Highway, 100 m, *Lao et al. 7* (F, MO (2)); Santa Rita Ridge, ca. 5.5–6 mi. E of Transisthmian Highway, *Lewis et al. 5391* (MO, UC); *Lewis 5397* (F, MO, NY); Santa Rita Ridge trail, beyond end of Santa Rita Ridge Road (Panamanian Highway R 20 D), 17–35 km from Boyd-Roosevelt Highway, 400–800 m, *Mori & Crosby 6308* (MO, US); Santa Rita Ridge Road, 7.8 km from the Boyd-Roosevelt Highway, ca. 25 km W of Colón, *Mori & Dressler 7906* (AAU, MO, NY); 2.7 mi. by gravel road, NE of carretera Transisthmica, on the Santa Rita Ridge, *Nee & Mori 3676* (MO, WIS (2)); Santa Rita Ridge, end of road from Transisthmian Highway, ca. 10 mi. from highway, *Porter et al. 4762* (MO); Santa Rita, *Suere & Dressler 4818* (MO); Santa Rita Ridge road, 20 km from Transisthmian Highway, 100–1,200 ft., *Sytsma 1094* (MO); Santa Rita Ridge, 20 km from Transisthmian Highway, *Sytsma 1108* (MO); Santa Rita Ridge Road, 20–22 km from Transismithian Highway, 1,000–1,200 ft., *Sytsma 1311, 1312* (MO); Santa Rita Ridge, *Sytsma 1548* (MO); upper Río Piedras headwaters, along trail from end of Santa Rita Ridge Road, ca. 11 km SW of Cerro Bruja, 600–700 m, *Sytsma et al. 4184* (MO). LOS SANTOS: Cerro Pilón, 2,700 ft., *Dwyer & Lallathin 8586* (MO). PANAMÁ: El Llano–Carti Road, 13.7 km N of Pan-American Highway, *Folsom 3589* (MO).

Cordia protracta I. M. Johnston, J. Arnold Arbor. 21: 349. 1948. TYPE: Panama. San Blas: Permé, *G. P. Cooper 244* (holotype, GH; isotypes, F, MICH, NY, US (2)).

Tall shrub, the twigs sparsely strigillose. Leaves persistent; petioles 4–9 mm long, canaliculate adaxially, sparsely strigillose; blades anisophyllous, falcate, the larger oblong-ovate, 15.6–24.6 cm long, 5.4–10.3 cm wide, the apex long acuminate, the acumen to 3 cm long, the base asymmetrical, rounded to obtuse, the margin entire to slightly undulate, the adaxial surface glabrous, the abaxial surface glabrous but sparsely strigillose along the veins. Inflorescences terminal or borne in the branch axils, few per stem, cymose, to 6.5 cm long, 4.5 cm broad, with 20 or more flowers, the branches strigillose. Flowers sessile or nearly so, bisexual, monomorphic; calyx tubular, 7–7.5 mm long, ca. 4 mm wide at mouth, ribs absent, sparsely strigillose, the 5 lobes deltate, ca. 1 mm long; corolla white, tubular with reflexed or spreading lobes, ca. 12 mm long, 5-merous, the lobes oblong to ovate, 4–4.5 mm long, ca. 2.5 mm wide, the tube 7–7.5 mm long; stamens 5, exserted, the filaments ca. 11 mm long, the upper 4–4.5 mm free, slightly puberulent at insertion, the anthers oblong, ca. 2.2 mm long; ovary narrowly ovoid, ca. 2.0 mm long, ca. 1.1 mm broad, glabrous; style ca. 7.5 mm long, the stylar branches ca. 2.5 mm long, the stigma lobes clavate. Fruits borne in the slightly accrescent saucer-shaped calyx, white, drupaceous, glabrous, the stone inequilaterally ovoid, 10–11 mm long, 6–7 mm broad, ruminate, the endocarp bony, 1-locular.

Distribution. *Cordia protracta* is known only from wet forests at low elevations along the coast of San Blas and Chocó provinces in Colombia.

Cordia protracta is known from only a few localities in Panama. A distinctive species, it is perhaps most closely related to *C. correae* but differs by having falcate, shiny leaves, and white fruits. Further, *C. correae* occurs at high elevations in cloud forests in contrast with the lowland wet forests inhabited by *C. protracta.*

Additional specimens examined. PANAMA. SAN BLAS: vicinity of Puerto Obaldía, *Croat 16873* (MO (2)); Mulatuppu, Río Ibedi, *Duke 8483* (MO); 3–4 hours up Río Mulatupo by foot, *Kirkbride 233, 234* (MO).

Cordia sebestena L., Sp. Pl. 190. 1753. TYPE: without locality or collector's name (holotype, LINN (Savage Catalog number 253.2), not seen; microfiche, MO).

Cordia speciosa Salisb., Prodr. Stirp. Chap. Allerton 111. 1796. TYPE: not seen.

Small tree or shrub to 8 m tall, the twigs glabrescent. Leaves persistent; petioles (1.0–)1.5–3.8(–4.5) cm long, pubescent, the hairs simple, appressed; blades ovate, (7–)9–20(–22) cm long, (4.5–)6–12(–14) cm wide, the apex acute, the base rounded to obtuse, rarely somewhat cordate, often slightly uneven, the margin entire or occasionally slightly undulate, the adaxial surface scabrous, the hairs from a basal cystolith, the abaxial surface nearly glabrous with hairs sparse and restricted to the veins. Inflorescence subterminal, cymose, 6.5–12 cm broad, with 12–45 flowers, the branches strigillose. Flowers on pedicels 4–6 mm long, distylous; calyx tubular-campanulate, 11–24 mm long, ribs absent, glabrous or with an indument of 2 types of hairs, the first type simple and straight, 0.4–0.6 mm long, appressed, white to translucent, the second type simple, curly, 0.2 mm long or shorter, brown, usually 2-lobed but sometimes with up to 5 irregular and uneven lobes; corolla bright reddish orange, funnelform, 30–58 mm long, 5–7-merous, the lobes ovate to very widely ovate, 8–10 mm long; stamens 5–7, the filaments 22–33 mm long, the upper 2–6 mm free, glabrous, the anthers oblong, 2.8–3.8 mm long; ovary conical, 1.5–3 mm long; style 13–35 mm long, the stigma lobes clavate. Fruits completely enclosed in the accrescent calyx and often extending in a thin tip up to 12 mm beyond the fruit, drupaceous, white, the stone ovoid, 2–4 mm long, 1.5–2.3 cm wide, the endocarp bony.

Distribution. *Cordia sebestena* is basically pan-Caribbean in distribution, occurring from southern Florida through the West Indies, and to the Atlantic coast of southern Mexico, Central America, and northern South America. It grows along coastal strands and is particularly common on the offshore islands of Central America. In Panama it appears to be native only in the Comarca de San Blas.

Cordia sebestena is grown ornamentally throughout warm areas of the world for its bright orange-red flowers. It is the only Panamanian species of sect. *Cordia* and is distinctive in its large, funnelform corolla and large, drupaceous fruits completely enclosed by the accrescent calyx. The fruits are edible and are very sweet, although quite mucilaginous.

Additional specimens examined. PANAMA. PANAMÁ: San Francisco de la Caleta (atras del S.A.S.), *Carrasquilla 178* (F, MO) (probably cultivated). SAN BLAS: Isla Soskatupu, *Duke 8963* (MO, US), *15476* (MO); Guadia Tupo, *Dwyer 6864* (MO (3)); 50 mi. W of Ailigandi, on SW shore, *Edwards 1* (F, MO); Soskatupu Island, 0–150 m, *Elias 1698* (MO); small coral island NW of Ailigandi, *Hammel & D'Arcy 5051* (MO); Playón Chico and vicinity, Pinkanti hillside near bay, *Stier 186* (MO); Playón Chico and vicinity, Yantuppu, *Stier 192* (MO).

Cordia spinescens L., Mant. Pl. 2: 206. 1771; I. M. Johnston, J. Arnold Arbor. 30: 103. 1949. TYPE: based on a collection from "*India orientali*" (cf. Johnston, 1949a) (holotype, LINN (Savage Catalog number 253.2), not seen; microfiche, MO).

Varronia ferruginea Lam., Tab. Encyc. 1: 418. 1791; Poir., Encyc. 4: 263. 1797; Desv., J. Bot. (Desvaux) 1: 266, t. 9. 1809; *Cordia ferruginea* (Lam.) Roemer & Schultes, Syst. Veg. 4: 458. 1819. TYPE: based on plants cultivated in Paris (holotype, P-JU, number 6525a, not seen; microfiche, MO).

Cordia riparia Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 71, t. 207. 1818; I. M. Johnston, J. Arnold Arbor. 30: 103. 1949. TYPE: Colombia: Mompox, Magdalena Valley, no collector named on specimen (holotype, P in herb. Humboldt, not seen; microfiche, MO).

Cordia laxiflora Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 72. 1818; I. M. Johnston, J. Arnold Arbor. 30: 103. 1949. TYPE: Colombia: between Mompox and Morales, Magdalena Valley, no collector named on specimen (holotype, P in herb. Humboldt, not seen; microfiche, MO).

Cordia schomburgkii DC., Prodr. 9: 490. 1845. TYPE: Guyana. Without definite locality: 1838, *Schomburgk 406* (holotype, G-DC, not seen; microfiche, MO).

Cordia thibaudiana DC., Prodr. 9: 489. 1845. TYPE: without locality or collector (holotype, G-DC, not seen; microfiche, MO).

Cordia pauciflora Rusby, Mem. Torrey Bot. Club 6: 83. 1896. TYPE: Bolivia: near Cochabamba, *Bang 1291* (not seen).

Cordia costaricensis I. M. Johnston, J. Arnold Arbor. 30: 103. 1949. TYPE: Costa Rica. San José: vicinity of El Generál, 1,190 m, Aug. 1936, *A. F. Skutch 2828* (holotype, GH; isotypes, K, MICH, MO, NY, US).

Shrub 1–3(–6) m tall, the branches arching to sprawling, the twigs puberulent to hirsute. Leaves deciduous, on slightly recurved spurs 1.5–3(–4) mm long; petioles (1–)3–11(–15) mm long, puberulent to hirsute; blade ovate to elliptic-ovate, (3–)4–11.5(–14) cm long, (1.4–)2–6.5(–7.8) cm wide, the apex acute to attenuate or slightly acuminate, the base obtuse to rounded, the margin coarsely serrate to minutely denticulate, the adaxial surface scabrous to scabrid, rarely merely papillose, the abaxial surface puberulent to tomentulose, sometimes with most of the hairs restricted to the veins. Inflorescences axillary, spicate, (1.3–)2.5–8.5(–11.5) cm long, 4–7(–9) mm broad, the peduncle adnate to the petiole at the base, (1–)2–4.5(–6.5) cm long, puberulent to hirsute. Flowers sessile, distylous; calyx campanulate, (1.8–)2.3–3.5(–4.2) mm long, ribs absent, strigillose to puberulent and usually with small, globose wax particles, the 5 lobes deltate to shallowly triangular; corolla white, tubular, (3–)3.8–5.4(–6.2) mm long, truncate to frilled at the apex, the tube (1.7–)2–2.7(–3.1) mm long; stamens 5(–6), the filaments (2.7–)3.3–5(–6.2) mm long, the upper (0.5–)1–2(–2.4) mm free, puberulent just beneath the point of insertion, the free portion glabrous, the anthers ellipsoid, 0.6–0.8(–1) mm long; ovary ovoid to broadly ovoid, 0.7–1.3 mm long; disc crateriform to annular (0.2–)0.4–0.6(–1.1) mm tall or enclosing the entire surface of the ovary; style (1.5–)2–4(–4.8) mm long, the stigma lobes clavate. Fruits drupaceous, ½ to nearly completely enclosed in the slightly accrescent calyx, red, 3.7–4.1 mm long, (2–)2.7–3.3 mm broad, the stone ovoid to broadly ovoid, the endocarp bony.

Distribution. *Cordia spinescens* is a very widespread, weedy species that occurs from Central Mexico into South America, although it is apparently absent in the West Indies. It grows from sea level to 2,000 m in elevation in a wide variety of habitats. In Panama it is known from all regions except Los Santos.

Cordia spinescens is extremely variable but is easily recognized by its axillary spicate inflorescences with the base of the peduncle adnate to the petiole of the subtending leaf. This is the most commonly collected species of *Cordia* in Mexico and Central America. *Cordia spinescens* is often found in open disturbed areas and is very common in moist ditches along roadsides. Unlike the other shrubby species of sect. *Varronia* that usually have a rather erect form of growth, *C. spinescens* often has long arching branches.

The species of sect. *Varronia* characterized by spicate inflorescences, three of which occur in Central America, make up the most complex group in the entire genus (discussion under *C. curassavica*). This assemblage is centered in the Andes, and numerous species have been described from this region, although some should certainly be placed in synonymy. As a group, they are phenotypically plastic, and apparently all of the species involved are interfertile. Since most species of sect. *Varronia* with spicate inflorescences are widespread, natural hybridization is common, which has contributed to the confusion surrounding this group. As defined here, *Cordia spinescens* has its closest relatives in South America in *Cordia multispicata* Cham., and perhaps in the West Indies in *Cordia brownei* (Friesen) I. M. Johnston.

There is extreme morphological variability between populations of *Cordia spinescens.* Plants from low to middle elevations have ovate leaves with acute to slightly acuminate apices and elongate spikes in the axils of fully expanded leaves with the peduncle adnate to the petiole. At higher elevations in Panama and Costa Rica, the plants have more attenuate leaves, and the spikes appear well before the leaves are expanded, often giving the appearance of a paniculate rather than spicate inflorescence. These are not true panicles, however, since as flowering proceeds, the leaves expand and the inflorescence structure thus becomes the same as in plants from lower elevations. This variant from the uplands of Panama and Costa Rica was originally described by Johnston (1949a) as *Cordia costaricensis*, and the type (*Skutch 2828*) as well as several collections made at a similar stage of development differ from the more typical lowland plants in having shorter, broader spikes with more crowded flowers, more acuminate calyx lobes, more attenuate leaf apices, more prominently serrate leaf margins, and evenly hirsute or velutinous stems. However, intergradation between these upland populations and typical *C. spinescens* is so extensive that more intermediates are observed throughout their combined range than are individuals exhibiting characters of the extremes. These intermediates do not exhibit any reduction in pollen stainability and there is no evidence of habitat differentiation between them and either of the extremes.

With a species as variable as *Cordia spinescens*, it is not surprising that there has been considerable nomenclatural confusion. The name *Cordia ferruginea* (Lam.) Roemer & Schultes was widely applied by earlier authors, although Johnston (1949a) correctly pointed out that the Linnaean name *C. spinescens* has priority and must be accepted. The types of these two names are clearly conspecific, despite the fact that Linnaeus mistakenly described *C. spinescens* as East Indian; no species of sect. *Varronia* are native in the Old World. This confusion probably resulted from the fact that *C. spinescens* had been cultivated in Europe at least as early as the late eighteenth century, as indicated by Johnston (1949a), suggesting that Linnaeus probably based his description on a cultivated specimen. Lamarck clearly based his description of *Varronia ferruginea* on plants that were cultivated in Paris in 1791.

Additional specimens examined. PANAMA. BOCAS DEL TORO: along railroad track near station at Milla 5, *Croat 16485* (F, MO); Changuinola Valley, *Dunlap 280* (US), *281* (GH); Changuinola Valley, Isla Potrero, *Dunlap 460* (CFMR, F); upper Río Changuinola, few miles upstream from Changuinola, *Dwyer 4385A* (MO); trail leading to ridge above Almirante, *Gentry 2758* (F, MO, NY); Río San Pedro, *Gordon 48* (MO); Chiriquí border along continental divide on carretera del Oleoducto ca. 1 km N of Quebrada Arena, IRHE Fortuna Hydro Electric Project, 1,150 m, *Knapp 5085* (MO); Changuinola to 5 mi. S at junction of ríos Changuinola and Terebe, 100–200 ft., *Lewis et al. 845* (K, MO, UC, US); Almirante, near road to Chiriquí, ca. 200 ft., *McDaniel 5075* (MO); Chiriquí Lagoon, Water Valley, *Wedel 1633* (MO, US), *1672* (MO), *1801* (GH, MO); Chiriquí Lagoon, Old Bank Island, *Wedel 2169* (MO, US); Quebra Nigua, *Wedel 2741* (MO, US); Chiriquí Lagoon, Isla Colón, *Wedel 2839* (MICH, MO, NY, US). CANAL AREA: Barro Colorado Island, *Aviles 103* (MO); *Bangham 495* (F, GH); Escandente, alrededores de la repressa Miraflores, *Correa 1181* (MO); Barro Colorado Island, *Croat 4400* (F, MO, SCZ); Pipeline Road at Río Agua Salud, *Croat 4731* (MO, SCZ (2)); Frijoles, near railroad station, *Croat 6265A* (MO); Barro Colorado Island, *Croat 7470* (F, MO, NY, SCZ); near Frijoles station, *Croat 8922* (MO, NY, SCZ), *8922* (MO, SCZ); Barro Colorado Island, *Croat 11763* (F (2), MO), *12811* (F, MO); Pipeline Road N of Gamboa ca. 24 km beyond gate, less than 300 ft., *Croat 38264* (MO); Barro Colorado Island, *D'Arcy 3983* (MO); Pan-American Highway near La Chorrera, *D'Arcy 9429* (MO); road C-21, *Duke 5791* (MO (2), NY); Albrook, *Dwyer 6714* (MO); Frijoles, *Ebinger 307* (F, MEXU, MO, US); near Farfan beach, *Gentry 1399* (F, MO, NY, SCZ); Pipeline Road, 2–4 mi. N of Gamboa, ca. 100 m, *Gentry 6541* (C, CAS, F, L, MEXU, MO, NY, RSA); Corozal, *Greenman & Greenman 5207* (GH, MO (2)); Gatún Station, *Hayes s.n.* (G, MO), *s.n.* (GH (2), MO, US), *608* (MO, NY (2), US); *Heriberto 49* (NY, US); Barro Colorado Island, *Hladik 65* (MO); Pipeline Road near Río Agua Salud, *Kennedy & Redemsky-Young 1809* (C, F, MO, NY, US); Barro Colorado Island, *Kenoyer 410, 641* (US); Gamboa, *McDaniel 5045* (MO); Curundu, 30–40 m, *Miller 1046* (MO); Gatún, *Ostenfeld 81* (C); near old Fort Lorenzo, mouth of Río Chagres, *Piper 5938, 5967, 5988* (US); vicinity of Ancon, *Piper 6030* (US); between Corozal and Ancon, 10–30 m, *Pittier 2171* (NY, US); grounds of Fort San Lorenzo, *Porter et al. 5006* (MO, SCZ, UC); W slope of Ancon Hill, vicinity of Balboa, 20–75 m, *Seibert 403* (MO, NY, US); Barro Colorado Island, *Shattuck 42* (F, GH, MO), *480* (F, MO (2)), *1073* (F, MO (2)); Balboa, *Standley 25570, 25591* (US); Summit, *Standley 26954* (US); Balboa, *Standley 27008* (US); Hills W of the Canal, near Gatún, *Standley 27183* (US); Gamboa, *Standley 28534* (US); along the old Las Cruces Trail, between Fort Clayton and Corozal, *Standley 29114* (US); vicinity of Summit, *Standley 29998* (US); vicinity of Fort Sherman, *Standley 31060* (US); Obispo, *Standley 31785* (US); Miraflores Locks area, *Tyson 1134* (MO, SCZ); 1 mi. N of summit on road to FAA radar tower, *Tyson et al. 2773* (MO, SCZ); Fort San Lorenzo, *Tyson & Blum 3792* (MO); vicinity of Miraflores Lake, *White 166* (MO, NY); north side of canal beyond bridge, *White 91* (F, MO); vicinity of Miraflores Lake, *White 245* (MO, NY); 1 mi. SW of Cocoli in the Rodman Naval Ammunition Depot, *Wilbur et al. 12914* (F, LL, MEXU, MICH, NY); Barro Colorado Island, *Woodworth & Vestal 441* (F, GH), *444* (MO), *519* (F, MO). CHIRIQUÍ: Bajo Mono–Robalo Trail, western slopes of Cerro Horqueta, 500–1,000 ft., *Allen 4781* (MO); Cerro Colorado, 1,400 m, *Antonio 1417* (MO); Boquete–Palo Alto–Arco Iris, *Beliz 169* (MO); Finca Collins, vicinity of Boquete, *Blum & Dwyer 2525A* (MO, SCZ (2)); Dist. San Felix, corregimiento of Hato Culantro, Hamlet of Cerro Otoe, 3,000 ft., *Bort 2* (MO); Burica Peninsula, San Bartolo Limite, 19 km W of Puerto Armuelles, 500 m, *Busey 612* (MO); Chorcha, *Castillo 3* (F, MO); camino hacia La Finca Landian, NE del campamento de Fortuna (Hornito), 1,100 m, *Correa et al. 2355* (F, MO); Nor-oeste del campamento Fortuna, 1,000–1,200 m, *Correa et al. 2590* (MO), *2619* (F, MO); NE del campamento de Fortuna (Hornito), 1,000–1,200 m, *Correa et al. 2882* (MO); trail north of Cerro Punta, *Croat 10499* (MO); between Bambito and Cerro Punta, *Croat 10672* (MO); along the Río Chiriquí Viejo just above Guadelupe, *Croat 16045* (F, LL, MO, NY); Burica Peninsula, 10–11 mi. W of Puerto Armuelles in vicinity of San Bartolo Limite, 300 500 m, *Croat 22018* (F, L, LL, MO, NY, US); Burica Peninsula, Distrito Barú, along ridge above Brazo Seco near Costa Rican border, 100–200 m, *Croat 22566* (MO); Methodist youth camp between Nueva Swissa and Cerro Punta, *Croat 26256* (MO, NY, US); in and along wooded slopes on Cerro Horqueta, 1,650 m, *Croat 26999* (MO); along continental divide on Cerro Colorado, on upper mining road 20–28 mi. from San Felix, 1,200–1,500 m, *Croat 33379* (MO); Cerro Colorado, along road to copper mine, 34.1 km beyond bridge over Río San Felix near town of San Felix, 13.1 km beyond turnoff to Escopeta, 1,390 m, *Croat 37312* (MO); Boquete, *D'Arcy & D'Arcy 6354* (MO (2), US); Boquete District, Chiquero, *Davidson 557* (F, MO, US); Cerro Horqueta, 1,500 m, *Duke et al. 13628* (MO, SCZ); NW of Boquete, Cerro Horqueta, 5,000–5,800 ft., *Dwyer et al. 537* (MO, UC, US); Tole vicinity of Santa Ana Well, ca. 1,000 ft., *Dwyer & Kirkbride 7453* (MO, UC); Boquete, Cerro Horqueta, 5,000–6,000 ft., *Dwyer & Hayden 7692* (MO, UC); Boquete, 7,000 ft., *Ebinger 705* (F, MO); road from Volcán to Río Serano, road that turns eastward 7.2 km from Río Serano, 3.2 km along the side of the road, *Folsom 4032* (MO); Boquete region, Cerro Horqueta, *Hagen & Hagen 2072* (NY); 3.5 mi. NE of Boquete, end of road along Río Palo Alto, *Hammel 5753* (MO); Palo Alto, 4.5 mi. NE of Boquete, 6,000 ft., *Hammel 7478* (MO); NW of Boquete, 1,350–1,680 m, *Huft 1812* (MO); Burica Peninsula, forest along quebradas and adjacent pastures, Quebrada Merida, 4 mi. S of Puerto Armuelles, 0–100 m, *Liesner 397* (F, MO); upland forest 5.2 mi. NW of El Hato del Volcán on the road to Costa Rica, 5,500 ft., *Luteyn 832* (MO); Guadelupe, 1.5 km N of Cerro Punta, *Mori & Kallunki 5718* (MO); Dos Lagunas, 4 km W of El Hato del Volcán, 1,300 m, *Mori & Bolten 7395* (MO); Cerro Vaca, 900–1,136 m, *Pittier 5311* (NY, US); along the Quiel road 12.2 km above Boquete, 5,500 ft., *Proctor 31842* (LL); Boquete, Palo Alto, just E of Boquete, 5,000 ft., *Stern et al. 1088* (GH, MO, US); SE slopes of Cerro Pate Macho, trail from Río Palo Alto, 4 km NE of Boquete, 1,500–1,700 m, *Sytsma et al. 4811* (MO); 6 mi. W of David, *Tyson 924* (MO, RSA); Bambito, 1 mi. SW of Cerro Punta, 5,600 ft., *Tyson 5661* (MO, SCZ); Dist. Boquete, above Jarimillo Arriba, along N slopes of Cerro Palo Alto, *Webster 16687* (MO); wooded slopes and thicketed trailside along the trail between Cerro Punta and the Quebrada Bajo Grande, 2,000–2,100 m, *Wilbur et al. 11908* (DS, F, LL, MICH, MO, NY, US); valley of the Río Chiriquí Viejo E of Guadalupe, *Wilbur et al. 13026* (F, LL, MICH, MO, NY); Finca Lerida to Pena Blanca, 1,750–2,000 m, *Woodson & Schery 314* (MO); vicinity of Bajo Chorro, 1,900 m, *Woodson & Schery 613* (MO); vicinity of Casita Alta, Volcán de Chiriquí, 1,500–2,000 m, *Woodson et al. 912* (MO, NY (2)). COCLÉ: El Valle de Antón, trails near Finca Tomas Arias, 600 m, *Allen 4232* (F, MO); El Valle, back of Club Campestre, *Dwyer 10511* (MO (2)); W of Río Guias, *Gentry 5844* (MO); 46 km N of Penonome on road to Coclesito, 100 ft., *Hammel 1702* (MO); El Valle de Antón, 1,000–2,000 ft., *Lewis et al. 2575* (MO, UC); Boca del Toabre at confluence of Río Toabre and Río Coclé del Norte, *Lewis et al. 5498* (MO, SCZ, UC); foot of Cerro Pilón, above El Valle de Antón, 2,000 ft., *Porter et al. 4364* (MO); foot of Cerro Pilón, above El Valle de Antón, 2,000 ft., *Porter et al. 4620* (MO, SCZ), *4656* (MO, UC); El Valle de Antón, narrow valley behind hotel Pan Americana, *Wilbur & Luteyn 11714* (F, LL, MICH, MO, NY, RSA, US). COLÓN: vicinity of Portobelo, *Croat 33573* (MO); along Río Iguanita near bridge along Portobelo road, *Croat 49776* (MO); Monkey Hill near Colón, *Lehmann 996* (US); between France Field and Catival, *Standley 30320* (US); between France Field, Canal Zone, and Catival, province of Colón, *Standley 30376* (US); along roadside between 5–7 mi. SW of Portobelo towards María Chiquita, *Wilbur & Weaver 11175* (F, GH (2), MICH, MO). DARIÉN: on hills above west end of airstrip at Caña near Río Caña, *Croat 38073* (MO); along Río Pirre, *Duke 4974* (MO, NY); wooded ridge just S of El Real, *Duke 5051* (MO); Río Balsa between N. Q. Chusomocatre and Río Areti, *Duke 8706* (MO); Isla Casaya, *Duke 10385* (MO); 0.5–1.5 mi. E of Manene, *Hartman 12102* (MO); El Real, trail to Río Pirre, *Kennedy 2817* (MO); Manene to mouth of Río Cuasi, *Kirkbride & Bristan 1417* (MO, NY). HERRERA: 11 mi. S of Ocú on Las Minas Road, *Graham 240* (GH, MICH). PANAMÁ: vicinity of Pacora, 35 m, *Allen 1010* (F, MO, US); San José Island, *Anderson s.n.* (GH); weedy area S of Tocumen Airport, *D'Arcy 9643* (MO); Río Pacora just below confluence with Río Corso, *Duke 12009* (MO); Tocumen, *Dwyer s.n.* (MO), *4225* (MO); San José Island, *Erlanson 47* (US), *59* (G, NY), *191* (US); *Harlow 96* (US); *Johnston 120* (GH, US), *592, 907, 980* (GH), *1325* (GH (2)); Perlas Islands, S tip of Isla Del Rey, Punta de Cocos, 0–20 m, *Knapp & Mallet 2911* (MO); upper slopes of Cerro Campana, *LeDoux 2631* (MO); Chiman, *Lewis et al. 3364* (MO); Altos de Campana, unos 35 m del Motel Sulin, 3,045 ft., *Mendez 83* (F, MO); near Bejuca, *G. S. Miller 1809* (US); San José Island, *G. S. Miller 1914* (US); Sabanas, N of Panama City, *Paul 563* (MICH, US); Punta Paitilla, *Piper 5403, 5432* (US); Las Sabanas, *Riley 117* (MO, US); *Standley 25869* (US); near the big swamp E of Río Tocumen, *Standley 26602* (US); vicinity of Juan Franco Race Track, *Standley 27721* (US); Río Tocumen, *Standley 29483* (US); between Las Sabanas and Matias Hernández, *Standley 31812* (US); between Matias Hernández and Juan Diaz, *Standley 32037* (US); road from Cerro Azul to Cerro Jefe, 2,300 ft., *Tyson 6173* (F); La Chorrera, Las Mendozas, quebrada cerca del campo de Juegos, *Vergara & Torres 81* (MEXU); Cerro Azul, *Viquezol 34* (MO); thickets and forests near Arraijan, 15 m, *Woodson et al. 1357* (F, MO, NY). SAN BLAS: hills SE of Puerto Obaldía, *Croat 16703* (MO, NY); Mulatupu, Río Ibedi, *Duke 8479* (MO); Sasardi, 20 m, *Duke 10144* (MO); along canal just N of Mandinga Airport, *Duke 14846* (MO); along headwaters of Río Mulatupu, *Elias 1739* (MO); mountains above Puerto Obaldía, *Gentry 1479* (MO); mainland opposite Playón Chico, 0–3 mi. from Caribbean, 0–200 m, *Gentry 6400* (MO); mainland opposite Ailigandi, from mouth of Ailigandi River to 2.5 mi. inland, *Lewis et al. 165* (MO, US); along Río Ailigandi, 0–100 ft., *Warner 182* (MO). VERAGUAS: hills W of Sona, 500 m, *Allen 1044* (MO, NY, US); Isla de Coiba, near María River, across bay from Colonia Penal, *Antonio 2327* (MO); S of Santa Fe, *Nee 8014* (MEXU, MO, RSA, US); 2 km NW of Atalaya, 100 m, *Nee 8200* (MO); La Mesa, *Tyson 6070* (MO, SCZ).

Cordia tacarcunensis James S. Miller, sp. nov. TYPE: Panama. Darién: trail from Pucuro to Cerro Mali, vicinity of Tapaliza River, 100 m, tropical moist forest, 13 Jan. 1975, *Alwyn H. Gentry & Scott Mori 13546* (holotype, MO 2288082). Figure 5.

Arbor vel frutex ad 3 m alta, ramunculo glabro. Folia persistentia, petiolis 6–10 mm longis; laminae anguste ovato-ellipticae, 8.1–14.5 cm longae, 4.5–6.5 cm latae, apice acuminatis, base acutis, superficie papillosa. Inflorescentiae axillares, parvae dichotome cymosae, 4–6 cm latae. Flores unisexuales, plantis dioeciis; calyx campanulatus, 2.7–3 mm longus, 5-lobatus, strigillosus; corolla alba, tubuliformis, 4.8 mm longa, 5-lobata, lobo reflexa, oblonga, 2.2 mm longa; stamina 5, filis villosis, antheris ellipticis. Fructus drupaceus, putamine inaequilateraliter ovoideo, 5 mm longo.

Small tree or shrub 3 m tall, the twigs glabrous. Leaves persistent; petioles 6–10 mm long, canaliculate adaxially, minutely strigillose; blades narrowly elliptic-ovate, 8.1–14.5 cm long, 4.5–6.5 cm wide, the apex acuminate, the base acute and sometimes slightly decurrent, the margin entire, the adaxial surface lacking hairs but densely covered with small scaly papillae, the abaxial surface nearly glabrous, with small scaly papillae and a few widely scattered appressed hairs. Inflorescences axillary, numerous per stem, dichotomous cymes, 4–6 cm broad, the axes densely brown strigillose. Flowers unisexual, the plants dioecious. Female flowers with small, nonfunctional anthers, sessile; calyx campanulate, 2.7–3 mm long, 3–3.5 mm wide at mouth, ribs absent, dark-brown strigillose, the 5 lobes shallowly triangular, 0.5 mm long; corolla white, tubular with reflexed lobes, 4.8 mm long, 5-merous, the lobes oblong, 2.2 mm long, 1 mm wide, the tube 2 mm long; stamens 5, nonfunctional, the filaments 2.8 mm long, the upper 2 mm free, villous toward the middle of the free portion, the anthers ellipsoid, 0.5 mm long; ovary ovoid, 2.3 mm long, 2 mm broad; disc crateriform, 0.4 mm tall, 1.2 mm broad, glabrous; style 2.5 mm long, the stylar branches 1.9 mm long, the stigma lobes fan-shaped. Male flowers unknown. Fruits seated in the slightly accrescent saucer-shaped calyx, drupaceous, glabrous, the stone inequilaterally broadly ovoid, 5 mm long, 5 mm broad, endocarp bony, 1-seeded.

Distribution. *Cordia tacarcunensis* is known only from the type collection made

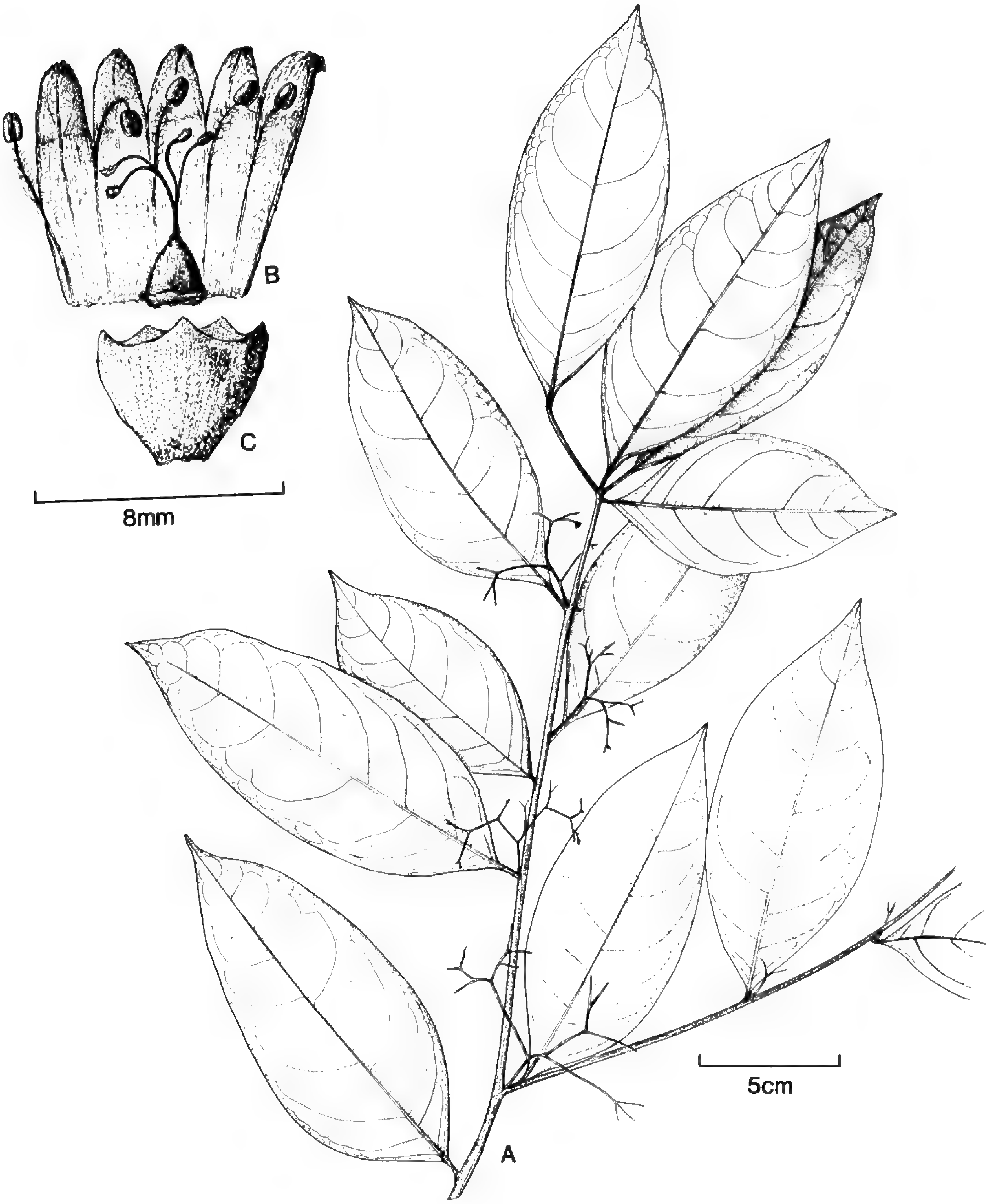

FIGURE 5. Cordia tacarcunensis.—*A. Flowering branch.—B. flower with corolla opened.—C. Calyx. From* Gentry & Mori 13546 *(MO), Darién, Panama.*

near the base of Cerro Tacarcuna on the Colombia–Darién border.

Cordia tacarcunensis is probably most closely related to *C. protracta* and *C. correae,* with which it shares a similar growth habit and a three-parted calyx. It is distinctive, however, in its small, axillary inflorescences and its fan-shaped stigma lobes. In addition to the *C. panamensis* and *C. diversifolia* species groups, *C. tacarcunensis* is the only member of sect. *Myxa* in Central

America known to be dioecious; the breeding systems of its two presumed closest relatives are not known.

Cynoglossum L., Sp. Pl. 134. 1753; Gen. Pl. ed. 5. 65. 1754. TYPE: *Cynoglossum officinale* L., vide Britton & A. Brown, Ill. Fl. N. U.S. ed. 2, 3: 75. 1913.

Perennial (rarely annual or biennial) herbs from a thickened rootstock, usually branched, pubescent or rarely glabrous. Leaves alternate, simple, entire, the basal leaves on distinct petioles, the cauline leaves usually sessile. Inflorescences racemes or panicles, the branches scorpioid, usually ebracteate. Flowers bisexual, usually pedicellate; sepals 5, nearly distinct to the base, accrescent in fruit; corolla blue, purple, or rarely white, salverform to campanulate, 5-lobed, with 5 apparent protuberances in the mouth; stamens 5, the anthers on short filaments or nearly sessile, oblong to ellipsoid; ovary 4-lobed, the style gynobasic, the stigma 1, capitate. Fruits of 4 spreading nutlets, attached apically to the gynobase, the scar restricted to the apical half of the ventral surface, the dorsal surface with short glochidiate spines.

Cynoglossum contains about 80 species found throughout much of the world although generally absent from lowland tropical forest. Many species are cultivated ornamentals and this, combined with the epizoochorously dispersed, glochidiate spiny fruits, has allowed many members of the genus to become naturalized far from their natural ranges.

Cynoglossum amabile Stapf & J. R. Drumm., Kew Bull. 1906: 202. 1906. SYNTYPES: China. Yunnan: Mengtze, *W. Hancock 133* (K, not seen); Szemao, 350 m, *A. Henry 9365* (MO). Sichuan: Tatsienlu, *Soulié 861* (K, not seen); without locality, 2,700–4,050 m, *A. E. Pratt 887* (K, not seen); without locality, *M. Leichtlin s.n.* (K, not seen).

Erect biennial or perennial herb from a thick rootstock, to 0.5(–1) m tall, the stems densely strigose. Basal leaves on petioles to 4.5(–11) cm long, the blade narrowly elliptic, 6–11(–17) cm long, (1–)1.5–2.5(–3) cm wide, the apex acute, the base attenuate to cuneate, the margin entire, the adaxial surface strigillose to strigose, the abaxial surface pilose to pubescent; cauline leaves sessile, lanceolate to narrowly elliptic, 3–6(–8) cm long, 0.7–2 cm wide, the apex acute, the base clasping and usually somewhat lobed, the margin entire, the adaxial surface strigillose to strigose, the abaxial surface pubescent to hirtellous. Inflorescence terminal, a panicle of small cymes, to 16(–30) cm long, the branches cymose, densely strigillose. Flowers bisexual, on pedicels to 5 mm long; sepals 5(–7), lanceolate to lance-ovate, 2–3(–4) mm long, strigose; corolla blue, rotate, 5(–7)-merous, the lobes widely obovate, 2–3(–4) mm long, the tube 1.3–2.5 mm long, with 5 hooded protuberances in the mouth, these alternate with the stamens and often puberulent; stamens 5(–7), the anthers ellipsoid, (0.5–) 0.8–1.3 mm long, nearly sessile or on short filaments to 0.5 mm long, inserted just below the mouth of the corolla tube; ovary 4-lobed, the surface smooth, the disc basal, the style gynobasic, 0.8–2 mm long, the stigma capitate. Fruits of 4 spreading nutlets, 4–6 mm broad, the nutlets ovate, flat to convex on the dorsal surface, with glochidiate spines to 0.5 mm long.

Distribution. *Cynoglossum amabile* is native to China but has become commonly naturalized in the Neotropics, being found in open areas at elevations above 1,500 m in elevation. In Panama, it is known only from Chiriquí; it is undoubtedly also in adjacent parts of Bocas del Toro.

Cynoglossum amabile can be easily distinguished from *Hackelia mexicana* (Schldl. & Cham.) I. M. Johnston, the other common small blue-flowered species of Boraginaceae in Chiriquí, by the shorter spines on its fruits and the cauline leaves usually clasping at the base, rather than cuneate as in *H. mexicana.* The only one of the syntypes that I have seen is the collection made by A. Henry, which is labeled as having pink flowers. As blue flowers are characteristic of the species and pink-flowered forms are unusual, the selection of a lectotype will have to be from one of the remaining specimens.

Additional specimens examined. PANAMA. CHIRIQUÍ: Dist. of Boquete, E of Cerro Punta, area called Bajo Chorro, 2,600 m, *Antonio 1032* (MO); Monte Azul, 1.4 mi. N of Entre Ríos on E slopes of Cerro Punta, 3 mi. by road from town of Cerro Punta, 2,250 m, *Antonio 2723* (MO); Cerro Punta–David, 1,000–2,500 m, *Beliz 218* (MO); Volcán Barú, 3,474 m, *Beliz 355* (MO); Finca Collins, vicinity of Boquete, *Blum & Dwyer 2580* (MO); 5.4 km del Hato de Volcán en el camino a Las Lagunas, *Correa & Lazor 1472* (MO); 2 mi. N of El Hato del Volcán, *Croat 10466* (MO (2)); roadside between Bambito and Cerro Punta, *Croat 10592* (MO); roadsides between Cerro Punta and Bajo Grande, *Croat & Porter 16003* (MO); along the Río Chiriquí Viejo just above Guadelupe, *Croat & Porter 16053* (MO); E of Boquete along forested slopes and pastures on Cerro Azul near Quebrada Jaramillo, 1,500–1,620 m, *Croat 26779* (MO); 10 mi. above Boquete on road to Volcán Barú, 2,600 m, *Croat 34828, 34829* (MO); across river from town of Cerro Punta, *D'Arcy & D'Arcy 6528* (MO); Alto Respinga, 2,750 m, *D'Arcy 12158* (MO); E slope of Volcán de Chiriquí (Barú) WNW of Boquete, 2,200–2,300 m, *Davidse & D'Arcy 10173* (MO); Cerro Horqueta, 1,500 m, *Duke et al. 13608* (MO); NW of Boquete, Cerro Horqueta, 5,000–5,800 ft., *Dwyer et al. 443* (GH, MO); Boquete, Finca Collins, 5,000 ft., *Dwyer & Hayden 7650* (MO); Cerro Horqueta, 4,500–5,000 ft., *Dwyer & Tallallum 8748* (MO); above Cerro Punta, 6,500 ft., *Folsom et al. 2039* (MO); along Boquete trail, Cerro Respinga, E of town of Cerro Punta, 2,000–2,500 m, *Gentry 5931* (GH, MO); path above Cerro Punta to Boquete, 2,500 m, *Hamilton & Stockwell 3345, 3420* (MO); *Hamilton & Krager 3739* (MO); hill E of Audobon Cabin, S of Cerro Punta, 1,400–1,800 m, *Hamilton & Krager 3870* (MO); Bajo Chorro, *Hladik 183* (MO); Finca Collins, 6,000 ft., *Kirkbride 128* (MO (2)); vicinity of Las Nubes, 2.7 mi. NW of Río Chiriquí Viejo W of Cerro Punta, 2,200 m, *Liesner 290* (MO); N end of town of Cerro Punta, *Mori & Kallunki 5626* (MO); Bajo Grande, ca. 3 km E of town of Cerro Punta, 2,200 m, *Nee 9952* (MO); vicinity of Cerro Punta, 6,800 ft., *Ridgway & Solis 2396* (MO); Volcán Barú, E slope along road to Boquete, 8 km W of Boquete, 2,200 m, *Stein 1282* (MO); vicinity of Boquete, Finca Collins, 5,500 ft., *Stern et al. 1097* (GH, MO); vicinity of Boquete, Finca Collins, "El Velo," 6,150 ft., *Stern et al. 1962* (MO); 3.7 km E of bridge NE of Cerro Punta on road through Bajo Grande, 2,250–2,400 m, *Stevens 18150* (MO); 3.7 km along road through Bajo Grande from bridge NE of Cerro Punta, 2,250–2,400 m, *Sytsma & Stevens 2155* (MO); Bambito, 1 mi. SW of Cerro Punta, 5,600 ft., *Tyson 5623* (MO); above Cerro Punta toward Bajo Grande in Quebrada Bajo Grande, 6,500 ft., *Wilbur et al. 10909* (MO); vicinity of Bajo Mono and Quebrada Chiquero, 1,500 m, *Woodson & Schery 523* (GH (2), MO).

Ehretia P. Browne, Civ. Nat. Hist. Jamaica 168. 1756. TYPE: *Ehretia tinifolia* L., Syst. Nat., ed. 10. 936. 1759.

Trees or shrubs, pubescent or glabrous. Leaves alternate, petiolate, entire or serrate. Inflorescences terminal, cymose to paniculate. Flowers bisexual; sepals 5, imbricate or open in bud; corolla white, tubular with 5 spreading lobes; stamens 5, usually exserted, the lower portion of the filaments adnate to the corolla tube, the anthers oblong to ellipsoid; ovary ovoid, 2- or 4-locular, the style terminal, bifid, the stigmas 2, clavate or capitate. Fruits drupaceous, ovoid to nearly spherical, the stone separating into 2, 2-seeded or 4, 1-seeded pyrenes.

The pantropical genus *Ehretia* comprises about 50 species with most occurring in Africa and tropical Asia. Only three species are known from the New World, one of which is found in Panama.

Ehretia latifolia DC., Prodr. 9: 503. 1845. TYPE: Herb. Amat. (holotype, G-DC, not seen; microfiche, MO).

Ehretia mexicana S. Watson, Proc. Amer. Acad. Arts 26: 144. 1891. TYPE: Mexico. Jalisco: base of mountains near Lake Chapala, *C. G. Pringle 3085* (lectotype, here designated, GH; isolectotypes, BH, BM, F, GH, MO, NY (2), UC, US (2)).

Ehretia luxiana J. D. Smith, Bot. Gaz. (Crawfordsville) 18: 5. 1893 (corrected reprint). TYPE: Guatemala. Quiche: San Miguel Uspantán, 6,100 ft., Apr. 1892, *Heyde & Lux 3065* (holotype, F 575900; isotypes, MO, NY, US).

Ehretia cordifolia Robinson, Proc. Amer. Acad. Arts 29: 319. 1894. TYPE: Mexico. Jalisco: valley, Zapotlán, 19 May 1893, *C. G. Pringle 4382* (holotype, F 106011; isotypes, A, BM, GH, MO, NY, UC, US (2)).

Ehretia viscosa Fern. in Sarg., Trees & Shrubs 1: 25, pl. 13. 1902. TYPE: Mexico: Morelos, near Cuernavaca, 29 May 1899, *C. G. Pringle 7777* (holotype, F 120287; isotypes, BH, GH, MEXU (2), MO, NY, UC).

Ehretia tehuacana Greenman, Publ. Field Columbian Mus., Bot. Ser. 2: 339. 1912. TYPE: Mexico. Puebla: Las Mohoneras, Tehuacán, 2,200 m, *C. Conzatti 2220* (holotype, F 235156; isotype, GH).

Ehretia austin-smithii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 984. 1938. TYPE: Costa Rica. Alajuela: Zarcero, in pasture, 1,850 m, Mar. 1938, *Austin Smith H528* (holotype, F 919653; isotype, MO).

Tree to 10 m tall, the twigs glabrous or nearly so. Leaves persistent; petioles 7–18 mm long, glabrous or nearly so; blades ovate, 4–13 mm long, 2–6.6 cm wide, the apex acute to slightly acuminate, the base obtuse to rounded, the margin serrate, the adaxial surface glabrous to sparsely strigillose, the abaxial surface glabrous. Inflorescence terminal, paniculate, to 8 cm long and 7 cm broad, the peduncle glabrous to sparsely puberulent. Flowers sessile, bisexual; sepals 5, ovate to narrowly triangular, 1.5–2 mm long, ciliate along the margin but otherwise glabrous; corolla white, 5-merous, the lobes ovate, 1.5–2.8 mm long; stamens 5, the filaments 4.5–5 mm long, the upper 3.4–4.4 mm free, glabrous, the anthers ellipsoid, 1–1.5 mm long; ovary broadly ovoid, 1–1.5 mm long, the style bifid, 1.4–3.3 mm long, the stigma lobes truncate. Fruits drupaceous, white, ellipsoid to ovoid, 10–15 mm long.

Distribution. *Ehretia latifolia* is known from Mexico south to Chiriquí Province in Panama, where it is found at 1,000–2,500 m in elevation.

Ehretia latifolia, as here defined, is a widespread, variable species. The numerous synonyms are based on minor variations in leaf shape and indument, characters that vary considerably on an individual tree as well as between individuals of a single population (Miller, unpubl.). As in most species of *Ehretia,* the plants are quite attractive while in flower, but flowering occurs only for a short period.

Additional specimens examined. PANAMA. CHIRIQUÍ: a lo largo del camino que va de Bambito a los llanos de lava, 6,000 ft., *Correa & Lazor 1410* (F, MO); at opening to canyon to Bambito, 5,000 ft., *Tyson 5870* (MO (2)); Río Chiriquí Viejo Valley, near Bambito, *White 220* (F, GH, MO).

Hackelia Opiz in Bercht., Oekon.-techn. Fl. Böhm. 2(2): 146. 1838. TYPE: *Hackelia deflexa* (Wahlenb.) Opiz in Bercht., Oekon-techn. Fl. Böhm. 2, pt. 2, 147. 1839; I. M. Johnston, Contr. Gray Herb. 68: 45. 1923.

Erect, perennial or biennial herbs, pubescent or less commonly glabrous. Leaves alternate, entire, the basal leaves usually long-petiolate, the cauline leaves short-petiolate to sessile. Inflorescence a raceme or panicle, the branches scorpioid, ebracteate or with inconspicuous bracts. Flowers bisexual; sepals 5, free to the base or nearly so, slightly accrescent in fruit; corolla blue, often with a yellow center, or rarely white to pale yellow, salverform, 5-lobed, with 5 well-developed protuberances in the mouth; stamens 5, included in the corolla tube, the anthers elliptic to oblong, on short filaments; ovary 4-lobed, the style gynobasic, the stigma capitate. Fruits of 4 nutlets, the attachment to the pyramidal gynobase medial, the scar conspicuous, the dorsal surface with elongate glochidiate spines, these longer along the margins.

Hackelia is a genus of about 40 species of the New World, Europe, and Asia; it is clearly centered in western North America. Only a single species occurs in Panama.

Hackelia mexicana (Schldl. & Cham.) I. M. Johnston, Contr. Gray Herb. 68: 46. 1923. *Cynoglossum mexicanum* Schldl. & Cham., Linnaea 5: 114. 1830. *Echinospermum mexicanum* (Schldl. & Cham.) Hemsley, Biol. Cent.-Amer., Bot. 2: 377. 1882. *Lappula mexicanum* (Schldl. & Cham.) E. Greene, Pittonia 2: 1882. 1891. TYPE: Mexico. Veracruz: in Monte Macuiltepetl, near Jalapa, *Schiede 208* (not seen).

Lappula costaricensis Brand in Fedde, Repert. Spec. Nov. Regni Veg. 18: 310. 1922. *Hackelia costaricensis* (Brand) I. M. Johnston, Contr. Gray Herb. 68: 46. 1923. TYPE: Costa Rica: San José, *Hoffman 152* (not seen).

Lappula guatemalensis Brand in Fedde, Repert. Spec. Nov. Regni Veg. 18: 311. 1922. *Hackelia guatemalensis* Brand in Engl., Pflanzenr. 4, 252: 120. 1931. SYNTYPES: Guatemala: Quiche, *Heyde & Lux 3043* (not seen). Guatemala: Huehuetenango, *Seler & Seler 3144* (not seen).

Erect perennial herb from a thick rootstock, to 1.5 m tall, the stems pubescent. Basal leaves on petioles 9–17 cm long, lanceolate, 6–15 cm long, 2.5–4.5 cm wide, the apex acuminate to attenuate, the base cuneate to decurrent, the margin entire, cauline leaves lanceolate to elliptic, 8–23 cm long, 2–7.5 cm wide, the apex acuminate, the base cuneate to decurrent, the margin entire, the uppermost usually sessile, those below on petioles to 16 cm long, the adaxial surface strigose, the abaxial surface strigose to sparsely pilose, densely strigose along the main veins. Inflorescences terminal or from the upper leaf axils, a simple or once-branched raceme, 12–25 cm long, the rachis strigose to hirsute. Flowers bisexual, on pedicels to 5 mm long, these elongating to 15 mm in fruit; sepals 5, lanceolate, 1.5–2 mm long, strigose; corolla blue, yellow in the mouth, rotate, 5-merous, the lobes very widely ovate or obovate to widely oblong, 1.5–2.5 mm long, the tube 1.4–2 mm long, with 5 protuberances in the mouth; stamens 5, the anthers ellipsoid, 0.5–0.7 mm long, nearly sessile, inserted in the middle of the corolla tube; ovary 4-lobed, the lobes tuberculate, enclosed at the base by the disc, the style gynobasic, 0.5–0.7 mm long, the stigma capitate. Fruits of 4 nutlets, 2.5–3.2 mm long, densely glochidiate, the spines 1–4 mm long.

Distribution. Hackelia mexicana occurs from Mexico, south through Central America, to Venezuela, Colombia, Ecuador, and Peru, where it can be found in open disturbed areas at 1,200–3,500 m in elevation. In Panama, it is known only from upland Chiriquí, but it is certainly expected in adjacent areas of Bocas del Toro.

Hackelia mexicana is a common weed of upland Chiriquí, where it is highly visible and distinct with its bright blue flowers. In this region *H. mexicana* is most easily confused with *Cynoglossum amabile*, although, as indicated under the latter species, *H. mexicana* differs in having cauline leaves that are not clasping at the base, nutlets with a medial attachment to the gynobase, and much longer glochidiate spines on the nutlets.

Additional specimens examined. PANAMA. CHIRIQUÍ: E of Cerro Punta, area called Bajo Chorro, 2,600 m, *Antonio 1023* (MO); Cerro Punta, 7,000 ft., *Blum et al. 2422* (MO); slopes of Las Cumbres near Cerro Punta, *Croat 13679* (MO); Las Cumbres, hogback ridge N of Quebrada Iglesia, near town of Cerro Punta, *Croat & Porter 16096* (MO); 12 mi. above Boquete on road to Volcán Barú, 2,900–2,950 m, *Croat 34900* (MO); E slope of Volcán de Chiriquí (Barú), above Boquete, *Davidse & D'Arcy 10284* (MO); Potrero Muleto, Volcán de Chiriquí, 10,400 ft., *Davidson 1018* (GH, MO); just below last climb in Alto Respinga, 2,700 m, *D'Arcy 12135* (MO); Alto Respinga and above, 2,800 m, *D'Arcy s.n.* (MO); along Boquete Trail, Cerro Respinga, 2,000–2,500 m, E of town of Cerro Punta, *Gentry 5949* (GH, MO); along Boquete trail, Cerro Respinga, 2,000–2,500 m, E of town of Cerro Punta, *Gentry 6014* (MO); path above Cerro Punta to Boquete, 2,500 m, *Hamilton & Stockwell 3421* (MO); path above Cerro Punta to Boquete, 2,500 m, *Hamilton & Krager 3738* (MO); Bajo Chorro, *Hladik 195* (MO); near Paso de Respingo, in pasture and disturbed oak forest, ca. 2,300 m, *Mori & Kallunki 5737* (MO); around El Potrero camp, 2,800–3,000 m, *Pittier 3106* (GH); vicinity of Cerro Punta, 6,800 ft., *Ridgway & Solis 2394* (MO); ca. 3.7 km E of bridge NE of Cerro Punta on road through Bajo Grande, 2,250–2,400 m, *Stevens 18217* (MO); 3.7 km along road through Bajo Grande from bridge NE of Cerro Punta, 2,250–2,400 m, *Sytsma & Stevens 2117* (MO); along the trail between Cerro Punta and the Quebrada Bajo Grande, 2,000–2,100 m, *Wilbur et al. 11897* (GH); Finca Lerida to Peña Blanca, 1,750–2,000 m, *Woodson & Schery 333* (GH (2), MO); vicinity of Casita Alta, Volcán de Chiriquí, 1,500–2,000 m, *Woodson et al. 890* (GH (2), MO).

Heliotropium L., Sp. Pl. 130. 1753; Gen. Pl. ed. 5, 130. 1754. TYPE: *Heliotropium europeaum* L., Sp. Pl. 130. 1753.

Annual or perennial herbs or rarely low shrubs. Leaves alternate, rarely opposite or whorled. Inflorescences bracteate or ebracteate, helicoid cymes borne singly or in groups of 2–4, or the flowers borne individually along leafy stems. Flowers bisexual; sepals 5, imbricate, free or nearly so to the base, often unequal in size, occasionally accrescent; corolla salverform, funnelform, or tubular, white, or white with a yellow center, or occasionally blue to purple, 5-lobed; stamens 5, inserted in the throat of the corolla tube, the anthers free or apically connate; ovary 4-locular, often 4-lobed, the style terminal or absent, the stigma 1, conical. Fruits dry, breaking into 2 or 4 nutlets at maturity.

Heliotropium comprises about 200 species and is essentially cosmopolitan, with the greatest number of species occurring in dry, tropical regions. Despite the relative abundance of species in most neotropical countries, only four species are known from Panama. These are all widespread, weedy species found throughout the Neotropics, and two have become widespread in the Old World. *Heliotropium arborescens* L., a South American species, is often cultivated for its attractive purple flowers and might be found in gardens in Panama, although no collections exist.

The pantropical genera *Heliotropium* and *Tournefortia* L., and the monotypic Argentine genus *Ixorhea* Fenzl make up the subfamily Heliotropioideae. *Heliotropium* is a morphologically diverse genus, and Johnston (1928) recognized 11 sections in South America, three of which are known from Panama. *Heliotropium* is a genus of herbs with dry fruits, in contrast with the woody habit and fleshy fruits that characterize *Tournefortia*.

KEY TO THE SPECIES OF *HELIOTROPIUM* IN PANAMA

1a. Plants glabrous .... *Heliotropium curassavicum*
1b. Plants with pubescent stems and leaves.
  2a. Inflorescence terminal or internodal, spicate or a helicoid cyme, with numerous flowers.
    3a. Corolla lavender; plants erect; leaves wider than 2 cm .. *Heliotropium indicum*
    3b. Corolla white; plants procumbent; leaves narrower than 2 cm .... *Heliotropium procumbens*
  2b. Inflorescence axillary, 1-flowered .... *Heliotropium lagoense*

Heliotropium curassavicum L., Sp. Pl. 130. 1753. TYPE: Curaçao: *P. Browne s.n.* (holotype, LINN (Savage Catalog number 179.11), not seen; microfiche, MO).

Low herb, often somewhat succulent, glabrous, often glaucous, the stems procumbent to ascending. Leaves lacking a distinct petiole; blades oblanceolate, 10–35 mm long, 1–5(–10) mm wide, the apex acute to rounded, the base cuneate, the margin entire, glabrous and often glaucous on both surfaces. Inflorescence internodal, a once- or twice-branched helicoid cyme, rarely simple, the peduncle 11–20(–32) mm long, the branches (1.8–)3–6(–8) cm long. Flowers bisexual; sepals 5, lanceolate to ovate or oblong, ca. 1.5 mm long, glabrous; corolla white, 2–2.5 mm long, the 5 lobes 1 mm long, the tube 1 mm long, glabrous; stamens 5, the anthers nearly sessile, inserted near the middle of the corolla tube, ellipsoid, 0.5–0.8 mm long; ovary ovoid, the disc well developed, the stigma sessile, broadly conical. Fruits ovoid, 1–2 mm long, glabrous, 4-lobed, separating into 4 nutlets at maturity.

Distribution. Heliotropium curassavicum is usually found growing along the edges of lakes, streams, or tidal flats from sea level to 600 m in elevation. It occurs from the United States through Central America and the West Indies and South America; it has also apparently become introduced and widespread in the Old World (Nowicke & Miller, in press). This species is known in Panama only from the province of Los Santos.

Heliotropium curassavicum is one of the most distinctive species of the genus and is the only member of sect. *Halmyrophila* I. M. Johnston. It is easily recognized by its glabrous, succulent nature. Several varieties of this species have been recognized (Johnston, 1928; Frohlich, 1981); the populations in Panama are all of the typical variety.

Additional specimens examined. PANAMA. LOS SANTOS: Salinas de Chitré, *D'Arcy & Croat 4199* (MO); Monagre Beach, *Dwyer 4177* (MO (2)); Monagre Beach, 5 mi. SE of Chitré, *Tyson et al. 3023* (MO).

Heliotropium indicum L., Sp. Pl. 130. 1753. TYPE: *P. Browne s.n.* (holotype, LINN (Savage Catalog number 179.2), not seen; microfiche, MO).

Annual herb to 50 cm tall, the stems pubescent to pilose, the hairs simple. Leaves on petioles (7–)10–25(–40) mm long, pubescent, often pilose at the base; leaf blade ovate, (2.7–)5–10(–12) cm long, (2–)3–5(–7) cm wide, the apex acute to obtuse, the base obtuse to truncate and usually decurrent along the petiole, the margin unevenly serrate to undulate, the adaxial surface with widely scattered appressed hairs, the abaxial surface nearly glabrous with only a few hairs scattered along the veins, to nearly villous. Inflorescence internodal, an unbranched or very rarely dichotomous helicoid cyme, the peduncle (1–)2–3(–6) cm long, pubescent, the fertile portion (6–)9–16(–20) cm long. Flowers bisexual; sepals 5, lanceolate, 2–3 mm long, pubescent; corolla purple to occasionally white, salverform, 5-merous, the lobes ovate, 1–1.5 mm long, the tube 3–4 mm long, pubescent outside; stamens 5, the anthers sessile or nearly so, inserted just below the middle of the corolla tube, ellipsoid, 0.6–0.8 mm long; ovary globose, 0.5–1 mm long, the disc well-developed, the style 0.5–1 mm long, the stigma capitate. Fruits angular ovoid, with an apical beak, 2–3 mm long, glabrous, the 2 lobes spread apart and ultimately separating into 2 nutlets at maturity.

Distribution. *Heliotropium indicum* is a weed of disturbed habitats from sea level to 1,000 m in elevation nearly throughout the world with the exception of cold regions. In Panama, it is known from all regions except the Comarca de San Blas, but is probably there as well.

Heliotropium indicum is a coarse, annual weed and one of the most commonly encountered species of the genus. Although it is essentially worldwide in distribution, Johnston (1928) suggested that it was probably South American, possibly Brazilian, in origin. Its closest relative is *H. elongatum* Hoffm. ex Roemer & Schultes, a species of southeastern South America, and the two make up sect. *Tiaridium* (Lehm.) Griseb., which is characterized by a weedy, annual habit, salverform corollas, and ribbed, glabrous fruits. *Heliotropium indicum* is easily recognized by its purple (rarely white) corollas and strongly angular fruits with prolonged apices.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Bocas del Toro, *Carleton 195* (GH); Old Bank Island, *Wedel 1986* (GH, MO). CANAL AREA: Pipeline Road to 18 km N of Gamboa, *D'Arcy 10618* (MO); flooded pasture bordering Chagres River, about 2 mi. N of Gamboa, *Lazor 3498* (MO); Barro Colorado Island, *Starry 249* (MO). CHIRIQUÍ: Burica Peninsula, 1 mi. W of Puerto Armuelles, 50 m, *Croat 22029* (MO); Burica Peninsula, dist. Guanabano, disturbed areas along Quebrada Quanabano, 0–100 m, *Croat 22532* (MO); vicinity of San Bartolome, Peninsula de Burica, 0–50 m, *Woodson & Schery 925* (GH). COCLÉ: El Valle, *Aguilar 48* (MO); Río Coclé, W of Penonomé, *Folsom 2917* (MO); 12 mi. NE of Penonomé, 1,200 ft., *Lewis et al. 1524* (GH, MO); Boca del Toabre at confluence of Río Toabre and Río Coclé del Norte, *Lewis et al. 5512* (MO). COLÓN: Portobelo, 5–100 m, *Pittier 2470* (GH). DARIÉN: El Real, *Correa & Lazor 1534* (MO); El Real, Río Tuira, *Stern et al. 452* (GH, MO). HERRERA: Roadside between El Potrero and Las Minas, *Croat 9650* (MO); just S of Ocú, *D'Arcy 4127* (MO (2)); 5 km W of turnoff from highway 105 to Potuga, *Hammel 5254* (MO); 3 km from Pesé on road to Ocú, *Huft 1734* (MO). LOS SANTOS: along road between Tonosi and Jobero, 50–80 m, *Croat 34446* (MO); 5 mi. S of Pocri, *D'Arcy & Croat 4209B* (MO); Río Tonosi, vicinity of Tonosi, *Lewis et al. 1558* (GH, MO). PANAMÁ: Isla Taboga, 0–350 m, *Allen 1297* (GH, MO); beneath bridge on Interamerican Highway near end of Tocumen Airport runway, *Croat 9771* (MO); between Chepo and wharf, *Dodge 10721* (MO); Isla San Miguel, *Duke 10937* (MO); Bayano Guipo forest, disturbed area round lake near Bayano Bridge, *Folsom 3551* (MO); Taboga Island, *Macbride 2792* (MO); between Chepo and Río Bayano, *Porter et al. 5173* (MO); Taboga Island near village, Perlas Islands, *Tyson 5591* (MO); Río Tatare, *Woodson & Schery 995* (GH). VERAGUAS: 1.3 km E of the intersection of the Panamerican Highway and road P38 to Atlaya, *Folsom 2932* (MO); 2 mi. S of Canazas, *Tyson 3725* (MO).

Heliotropium lagoense (Warm.) Gürke in Engl. & Prantl, Nat. Pflanzenfam. 4 Abt. 3a, 97. 1893. *Schleidenia lagoensis* Warm., Vidensk. Meddel. Dansk Naturhist. Forren. Kjobenhavn 1867: 15. 1868. TYPE: Brazil. Minas Gerais: Lagoa Santa, 1863–1866, *Warming 21971* (C, holotype, not seen; photo, MO).

Procumbent herb, the stems with a few scattered, appressed hairs. Leaves on short petioles to 1.5 mm long; blade narrowly elliptic to oblanceolate, 3–6 mm long, 1.2 mm wide, the apex acute, the base acute, the margin entire, the adaxial surface glabrous, the abaxial surface glabrous or with a few scattered, appressed hairs. Flowers borne individually in the leaf axils, on pedicels 2–4(–6) mm long; sepals 5, ovoid, ca. 2 mm long, glabrous; corolla pale blue to white and yellow in the throat, the 5 lobes widely ovate, ca. 1 mm long, the tube ca. 2 mm long, glabrous; stamens 5, the anthers ovoid, ca. 0.4 mm long, sessile, inserted near the middle of the corolla tube; ovary ovoid, ca. 0.5 mm long, the disc scarcely evident, the stigma sessile, capitate. Fruits ovoid, 1.2 mm long, glabrous, 4-lobed, separating into 4 nutlets at maturity.

Distribution. *Heliotropium lagoense* occurs from Mexico through South America and the West Indies, and is found at elevations below 200 m (rarely to above 1,000 m) usually in open savannas. In Panama, it is known from a single collection from the province of Coclé.

Heliotropium sect. *Orthostachys* R. Br. is the largest section of the genus and certainly the most complex taxonomically. It is found throughout tropical regions of the world and is particularly well represented in the Neotropics, where Johnston (1928) suggested that approximately 50 species occur. *Heliotropium lagoense* and *H. procumbens* are the only members of the section known to occur in Panama. *Heliotropium lagoense* is a member of subsect. *Axillaria* and is easily recognized by its diminutive habit of growth and axillary flowers that are not aggregated into the helicoid cymes that characterize all of the other Panamanian species.

Additional specimens examined. PANAMA. COCLÉ: mountains beyond Pintada, 400–600 m, *Hunter & Allen 525* (MO).

Heliotropium procumbens Miller, Gard. Dict. ed. 8, no. 10. 1768; I. M. Johnston, Contr. Gray Herb. 81: 52. 1928. TYPE: Colombia. Bolívar: Cartagena, *Houston s.n.* (holotype, BM, not seen).

Heliotropium americanum Miller, Gard. Dict. ed. 8, no. 10. 1768. TYPE: Mexico. Veracruz: *Houston s.n.* (holotype, BM, not seen).

Heliotropium inundatum Sw., Prodr. 40. 1788. TYPE: Jamaica (not seen).

Heliotropium decumbens Lehm., Nov. Actorum Acad. Caes. Leop. Carol. German. Nat. Cur. 9: 128. 1818. TYPE: Venezuela. Sucre: Cumaná, *Humboldt 57* (holotype, P, not seen; microfiche, MO).

Heliotropium simplex Meyen, Reise 1: 436. 1834. TYPE: Chile. Tacna: Arica, *Meyen s.n.* (holotype, B, not seen).

Heliotropium inundatum var. *cubense* DC., Prodr. 9: 540. 1845. TYPE: Cuba. La Habana: near Havana, 1829, *Ramón de la Sagre 239* (holotype, G-DC, not seen; microfiche, MO).

Heliotropium bridgesii Rusby, Mem. Torrey Bot. Club 4: 224. 1895. TYPE: Bolivia. Cochabamba: Cochabamba, *M. Bang 950* (holotype, NY; microfiche, MO; isotype, US).

Heliotropium inundatum var. *chacoense* R. E. Fries, Ark. Bot. 6(11): 22. 1906. TYPE: Bolivia. Tarija: along Río Pilcomayo near Ft. Crevaux, *Fries 1614* (isotype, US).

Herb to 30 cm tall, the stems procumbent to ascending, strigose to pubescent. Leaves on petioles (3–)5–10(–15) mm long, strigose to pubescent; leaf blade elliptic to narrowly elliptic, 11–20(–35) mm long, 6–11(–17) mm wide, the apex acute to rounded, the base acute to cuneate, the margin entire, the adaxial surface strigose, the abaxial surface strigose to sericeous. Inflorescence internodal or terminal, a once- or twice-branched helicoid cyme, the peduncle (3–)8–20(–26) mm long, strigose to sericeous, the fertile portion 20–45(–75) mm long. Flowers bisexual; sepals 5, lanceolate, 1–1.2 mm long, one often exceeding the others in length, strigose; corolla white, the 5 lobes lanceolate to lance-ovate, 0.5–0.6 mm long, the tube 0.9–1.2 mm long, villous in mouth, strigose to strigillose outside; stamens 5, the anthers ellipsoid but acuminate at the apex, 0.2–0.3 mm long, sessile or nearly so, inserted from near the base to just beneath the middle of the corolla tube; ovary globose, 0.2–0.3 mm long, the disc scarcely evident, the stigma sessile, capitate. Fruits globose, ca. 1 mm long, strigillose, faintly 4-lobed, separating into 4 nutlets at maturity.

Distribution. *Heliotropium procumbens* is widespread from the southern United States south throughout all of the Neotropics, at elevations of 0–1,500 m in a wide variety of habitats. In Panama, it is known from the provinces of Coclé, Herrera, Los Santos, and Panamá.

A common weed, *Heliotropium procumbens* is extremely variable in shape, size, and indument of its leaves. Its wide geographic distribution and morphological variability have spawned considerable taxonomic problems, and numerous segregates have been proposed. Despite this, the species has been interpreted broadly by most recent authors.

Additional specimens examined. PANAMA. COCLÉ: 20 mi. S of Nata, *D'Arcy & Croat 4120* (MO); Río Coclé, W of Penonomé, *Folsom 2920* (MO). HERRERA: alrededores de Ocú, *Diaz 13A* (GH, MO). LOS SANTOS: Río Tonosí, vicinity of Tonosí, *Lewis et al. 1575* (MO). PANAMÁ: area around Madden Dam, 50–80 m, *Huft 1775* (MO); near Tapia River, Juan Diaz region, *Maxon & Harvey 6750* (GH); roadside between Chepo and Río Bayano, *Porter 5170* (MO); Macapale Island in Madden Lake, *Tyson 5501* (MO); weedy roadsides within 1 mi. of Chepo, *Wilbur & Luteyn 11799* (GH, MO).

Moritzia DC. in Meisner, Pl. Vasc. Gen. 1: 280; 2: 188. 1840. TYPE: *Moritzia ciliata* (Cham.) DC. in Meisner, Pl. Vasc. Gen. 2: 188. 1840.

Erect perennial herbs. Basal leaves often forming a spreading, open rosette, the cauline leaves alternate and usually considerably smaller than the basal ones. Inflorescence terminal, ebracteate, a sparsely branched cyme of spikes or racemes. Flowers bisexual; calyx tubular to narrowly campanulate; corolla tubular with spreading lobes, 5-merous, the lobes ovate to deltate, the tube with protuberances or tufts of hairs in the mouth; stamens 5, on short filaments, the anthers oblong; inserted above the middle of the corolla tube; ovary 4-lobed, the style gynobasic, the stigma obscurely bilobed. Nutlets solitary by abortion, erect, smooth to muricate but lacking spines.

Moritzia is an essentially South American genus of five species, only one of which, *M. lindenii*, extends into Central America. It is closely related to *Thaumatocaryon* (Johnston, 1924, 1927), from which it differs in having all of the leaves alternate and in lacking protuberances in the mouth of the corolla tube.

Moritzia lindenii (A. DC.) Gürke ex Benth. in Engl. & Prantl, Nat. Pflanzenfam. 4(3): 121. 1894. *Meratia lindenii* A. DC. in DC., Prodr. 10: 104. 1846. TYPE: Venezuela. Distrito Federal: Caracas, *Linden 944* (not seen).

Erect perennial herb to 50 cm tall, the stems strigose. Basal leaves sessile or on broad petioles to 5 cm long, narrowly elliptic to lanceolate or oblanceolate, 8–16 cm long, 1–3.5 cm wide, the apex acute, the base attenuate, the margin entire, the adaxial surface strigose, the abaxial surface strigose, the cauline leaves sessile, lanceolate to lance-ovate, 2.5–7 cm long, 0.4–1.4 cm wide, the apex attenuate to acuminate, the base acute, the margin entire, strigose on both surfaces. Inflorescences terminal, cymose, 3–10 cm long, the branches strigose. Flowers bisexual; calyx cylindrical, the 5 lobes lanceolate, 1.5–2.2 mm long, strigose; corolla blue, tubular with spreading lobes, 5-merous, the lobes widely ovate to depressed ovate, 0.9–1.3 mm long, the tube 2–2.4 mm long, pubescent in the mouth, strigillose outside; stamens 5, the anthers ellipsoid, 0.6–1 mm long, sessile, inserted just below the mouth of the corolla tube; ovary 4-lobed, the style gynobasic, 0.9–1.1 mm long, the stigma capitate. Nutlet ovoid, 2–2.5 mm long, muricate.

Distribution. *Moritzia lindenii* ranges from Venezuela, Colombia, and Ecuador north to Panama and adjacent Costa Rica. It occurs above 3,000 m in elevation. In Panama, it is known only from the province of Bocas del Toro but may be in upland Chiriquí as well.

Moritzia lindenii has been collected only once in Panama, although several collections are known from adjacent areas of Costa Rica. It is expected at high elevations in the same general region as *Cynoglossum* and *Hackelia*, the other two blue-flowered, herbaceous Boraginaceae known from Panama. It differs from members of these genera by lacking spines on its nutlets, only one of which develops to maturity, in contrast with the glochidiate spines on the four nutlets of *Cynoglossum* and *Hackelia*.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Cerro Fabrega and vicinity near Costa Rican frontier, south of summit, 3,150–3,335 m, *Weston 10162* (MO).

Tournefortia L., Sp. Pl. 140. 1753. TYPE: *Tournefortia hirsutissima* L., Sp. Pl. 140. 1753; I. M. Johnston, Contr. Gray Herb. 92: 66. 1930.

Small trees, shrubs, or woody vines. Leaves alternate or rarely opposite, petiolate or rarely sessile, entire. Inflorescence terminal or internodal, dense to lax, a sparsely to profusely branched cyme. Flowers bisexual; sepals 5, one often exceeding the others in length, persistent; corolla white to green or yellow-green, tubular, with 5 spreading lobes; stamens 5, the anthers usually sessile or nearly so, borne within the corolla tube; ovary ovoid to globose, 4-locular, the style terminal or absent, the stigma conical. Fruit drupaceous, often white at maturity, later drying and separating into 2 or 4 bony nutlets containing 1 or 2 seeds.

Tournefortia includes about 150 species and has representatives in most warm areas of the world, although most species occur in the Neotropics. *Mallatonia* (Griseb.) Britton, *Argusia* Amman, and *Messerschmidia* L. ex Hebenstreit have been treated as distinct by several authors, but Nowicke & Skvarla (1974) showed that pollen morphology does not support their continued separation. The three species that have been placed in these segregate genera differ from other members of *Tournefortia* in being strand plants with a pronounced corky exocarp and a similar sericeous indument.

Species of *Tournefortia* vary in habit. Most Panamanian species are lianas, sprawling shrubs, or sparsely branched erect shrubs, only a few becoming small trees. There often appears to be considerable variation in habit within a single species.

KEY TO THE SPECIES OF *TOURNEFORTIA* IN PANAMA

1a. Plants vining; fruits distinctly 4-lobed; the anthers apically connate (sect. *Cyphocyema* I. M. Johnston).
2a. Leaves densely white puberulent to tomentose below; corolla tube 2–2.3 mm long .... *T. volubilis*
2b. Leaves evenly short-strigillose below; corolla tube 3.3–5 mm long .... *T. maculata*
1b. Plants various in habit; fruit not deeply 4-lobed; the anthers free (sect. *Tournefortia*).
3a. Leaves opposite.
4a. Stems densely puberulent .... *T. ramonensis*
4b. Stems densely and unevenly pubescent to hirsute .... *T. johnstonii*
3b. Leaves alternate.
5a. Corolla tube 10–13 mm long .... *T. angustiflora*
5b. Corolla tube up to 10 mm long.
6a. Stems shaggy-villose, the hairs 3–4 mm long; sepals 5.5–7.5 mm long .... *T. cuspidata*
6b. Stems glabrous or with hairs less than 1.5 mm long; sepals less than 5 mm long.
7a. Corolla lobes 3–4.5 mm long.
8a. Corolla tube white with green stripes, 3.5–5 mm long; sepals 1.7–3.2 mm long; anthers bilobed, pendent in the mouth of the corolla tube .... *T. multiflora*
8b. Corolla green to yellow-green, the tube 7–10 mm long; sepals 3.5–5 mm long; anthers lanceolate, sessile and inserted below the mouth of the corolla tube .... *T. urceolata*
7b. Corolla lobes 1–3 mm long.
9a. Sepals up to 2 mm long.
10a. Corolla tube 5.5–6.5 mm long, the lobes 2.3–3 mm long; tertiary veins obscure .... *T. bicolor*
10b. Corolla 3.5–4 mm long, the lobes 1.5–2 mm long; tertiary veins evident .... *T. glabra*
9b. Sepals longer than 2 mm.
11a. Corolla tube 9–9.5 mm long; tertiary veins obscure .... *T. tacarcunensis*
11b. Corolla tube 3–6 mm long; tertiary veins evident.
12a. Sepals 4.3–4.5 mm long .... *T. brenesii*
12b. Sepals 2.5–4 mm long.
13a. Stems strigose to hirsute; leaves strigose; corolla lobes 1–1.6 mm long .... *T. hirsutissima*
13b. Stems glabrous or sparsely strigillose; leaves essentially glabrous; corolla lobes 2–2.5 mm long .... *T. longispica*

Tournefortia angustiflora Ruíz Lopez & Pavón, Fl. Peruv. 2: 25, pl. 151. 1799. TYPE: Peru. Huánuco: Chicoplaya and Pueblo Nuevo, *Hipólito Ruíz & José Pavón s.n.* (not seen).

Scandent shrub to 1 m tall, occasionally a liana or tree to 5 m tall, the twigs glabrous to puberulent. Leaves alternate; petioles 5–12(–16) mm long, sparsely strigillose to puberulent; blade lance-ovate to lanceolate, 6–

15(–17) cm long, 2–6(–8) cm wide, the apex acuminate to attenuate, the base acute to cuneate, the margin entire, the adaxial surface sparsely strigillose to nearly glabrous, the abaxial surface with short, appressed hairs along the veins. Inflorescence terminal or internodal, a sparsely branched cyme, the peduncle (1–)2–4(–8) cm long, strigillose or puberulent to nearly glabrous, the fertile branches recurved, 2–9(–14) cm long. Flowers sessile, borne 2–4 mm apart; sepals 5, triangular, 1.2–1.6 mm long, sparsely strigillose; corolla white, 5-merous, the lobes ovate, 2–2.6 mm long, the tube 10–13 mm long, strigillose outside, puberulent on the inner surface of the lobes; stamens 5, the anthers lanceoloid, 2.5–3 mm long, sessile, inserted in the lower half of the corolla tube; ovary globose, ca. 1 mm long, the style to 0.8 mm long or lacking, the stigma conical. Fruits white, ovoid, often slightly inequilateral, 3–5 mm long, glabrous.

Distribution. Tournefortia angustiflora is wide-ranging and common in wet forests from Mexico south through northwestern South America to Peru, from sea level to 600 m in elevation. It is known from most provinces in Panama and is probably in all of them.

Tournefortia angustiflora is distinctive within the genus in having narrow, tubular corollas more than 1 cm long and somewhat asymmetrical fruits. It is vegetatively similar to *T. bicolor*, but the two are quite different when fertile.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Daytonia Farm, region of Almirante, *Cooper 166* (GH); 10–15 mi. inland from mouth of Changuinola River, *Lewis et al. 876* (GH, MO); Chiriquí Lagoon, Water Valley, *Wedel 1600, 1785* (GH, MO), *1802* (MO), *1832* (GH, MO); Chiriquí Lagoon, Old Bank Island, *Wedel 1880, 2004* (GH, MO); Chiriquí Lagoon, Isla Colón, *Wedel 2867, 2960* (GH, MO). CANAL AREA: W end of Gatún Lake Dam, *Blum & Tyson 2000* (MO); Barro Colorado Island, *Croat 7018, 8677, 9100* (MO); *Foster 1681* (GH); alluvial bottom near Bohio, 10–20 m, *Maxon 4777* (GH); between Gorgona and Mamei, 10–30 m, *Pittier 2259* (GH); valley of Masambi on the road to Las Cascadas Plantation, 20–100 m, *Pittier 2592* (GH); Fort San Lorenzo, *Porter et al. 5009* (MO); Barro Colorado Island, *Shattuck 495* (MO); *Woodworth & Vestal 378* (A, MO). COCLÉ: El Valle de Antón, 600 m, *Allen 2059* (GH, MO); summit of Cerro Pilón, above El Valle de Antón, 2,700 ft., *Dwyer et al. 4501* (MO); 46 km N from Penonomé on road to Coclesito, 100 ft., *Hammel 1695* (MO); hills NE of El Valle de Antón, 2,000 ft., *Lewis et al. 1799* (MO); Boca del Toabre at confluence of Río Toabre and Río Coclé del Norte, *Lewis et al. 5508* (MO). COLÓN: near Nuevo Tonosí 2 mi. from Portobelo on road to Nombre de Dios, 100 m, *Croat 33523* (MO); along Río Guanche about 1–2 km from Portobelo Highway toward Cerro Bruja, 0–50 m, *Huft & Knapp 1783* (MO); along dirt trail, 4 km NW of Salamanca, 13 km NE of Buenos Aires, 340–410 m, *Nee 9063* (MO). DARIÉN: Río Tuqueza below Quebrada Venado, *Bristan 1076* (GH); El Real, Quebrada Trapiche, *Duke & Bristan 315* (MO); vicinity of Santa Fe, *Duke 9496* (MO); Cocalito, *Dwyer 4465* (MO (2)). HERRERA: roadside between El Potrero and Las Minas, *Croat 9655* (MO); 12 mi. S of Ocú on Las Minas road, *Graham 235* (GH); Punta Mala, *Tyson 2714* (MO); 10 mi. S of Ocú, *Tyson et al. 2863* (MO). PANAMÁ: Panamerican Highway 22 km E of Bayano Bridge, near bridge over stream, less than 200 m, *Folsom 1396* (MO); Sabanas near Chepo, *Hunter & Allen 94* (MO); Alahajuela Chagres Valley, 30–100 m, *Pittier 2371* (GH). SAN BLAS: mainland opposite Ailigandi, from mouth of Ailigandi River to 2.5 mi. inland, *Lewis et al. 167* (MO).

Tournefortia bicolor Sw., Prodr. 40. 1788. TYPE: Jamaica (not seen).

Tournefortia laevigata Lam., Encycl. 1: 416. 1791. TYPE: Guadeloupe, *Badier s.n.* (not seen).

Tournefortia nitida Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 84. 1819. TYPE: Colombia. Bolívar: near Cartagena (not seen).

Tournefortia bicolor Sw. var. *calycosa* J. D. Smith, Bot. Gaz. (Crawfordsville) 14: 27. 1889. TYPE: Guatemala. Alta Verapaz: Pansamalá, 3,800 ft., *H. von Tuerckheim 980* (holotype, US 944708).

Woody vine, shrub, or small tree to 3(–7) m tall, the twigs glabrous or sparsely short-strigillose. Leaves alternate; petioles (0.8–)1–2 cm long, glabrous or very sparsely short-strigillose; leaf blade elliptic or ovate to narrowly elliptic or lance-ovate, (8–)11–14(–19) cm long, (3.5–)5–8 cm wide, the apex acuminate to acute, the base obtuse to rounded or less commonly acute, the margin entire, the adaxial and abaxial surfaces glabrous or with a few widely scattered, appressed hairs, the tertiary veins obscure. Inflorescence terminal, a dense cyme, the peduncle to 3 mm long, the branches glabrous to sparsely strigillose, the fertile branches 2–5 cm long. Flowers sessile, crowded, usually borne less than 2 mm apart; sepals 5, lanceolate, 1.5–2 mm long, sparsely to evenly strigillose; corolla white, sometimes with a greenish tint, 5-merous, the lobes ovate and often apiculate, 2.3–3 mm long, the tube 5.5–6.5 mm long, strigillose outside; stamens 5, the anthers lanceoloid, 1.3–2 mm long, sessile, inserted below the middle of the corolla tube; ovary globose, 0.4–0.6 mm long, the stigma sessile, conical. Fruits ovoid, white, 3–5 mm long, glabrous.

Distribution. *Tournefortia bicolor* is common in wet forest from sea level to 1,800 m throughout the Neotropics, ranging from Mexico through Central America and the West Indies to northern and western South America. In Panama, it is known from all provinces except Herrera.

Tournefortia bicolor is closely related to *T. hirsutissima* (Johnston, 1935) but has generally been considered to be distinct (Nowicke, 1969; Gibson, 1970). Nash & Moreno (1981), however, treated *T. bicolor* as a form of *T. hirsutissima.* Both species are widespread in the Neotropics, and although *T. bicolor* generally occurs in wetter habitats, the two can be found together at numerous localities such as along the shore of Barro Colorado Island (Croat, 1978). *Tournefortia bicolor* differs from *T. hirsutissima* in being essentially glabrous and in having sepals 1.5–2 mm long, a corolla 5.5–6.4 mm long, and corolla lobes 2.3–3 mm long; *T. hirsutissima* is generally pubescent, the sepals are 2.5–4 mm long, and the corollas are 3.5–5.3 mm long with lobes 1–1.6 mm long. Morphological and ecological data strongly support recognition of *T. bicolor.*

Additional specimens examined. PANAMA. BOCAS DEL TORO: Río San Pedro, *Gordon 78C* (MO); along runway at Bocas, *Lazor et al. 2347* (MO); Chiriquí Lagoon, Water Valley, *Wedel 986, 1838* (GH, MO); Chiriquí Lagoon, Old Bank Island, *Wedel 1952, 1992, 2090* (GH, MO); Chiriquí Lagoon, Fish Creek Hills, *Wedel 2427* (GH, MO); Chiriquí Lagoon, Cocoa Cay, *Wedel 2877* (GH, MO). CANAL AREA: Victoria Fill, near Miraflores Locks, *Allen 1713* (GH, MO); east slope of Cerro Jefe, 2,700 ft., *Blum & Duke 2190* (MO); Barro Colorado Island, *Croat 7686, 7822, 8373* (MO); hills S of Pedro Locks, *Croat 9176* (MO); Barro Colorado Island, *Croat 9560* (MO); road from Gatún Locks to old French Canal and vicinity, *Duke & Mussell 6654* (GH, MO); near Gatún Station, Panama railroad, *Hayes s.n.* (GH); Chagres, *Fendler 232* (MO); 1 mi. from Gaillard Highway on small dirt track off Chiva Chiva, 0–25 m, *Knapp & Schmalzel 4850* (MO); 2 mi. W of Canal Zone–Ferry Thatcher bridge, *Lazor 2189* (MO); Bella Vista, *Piper 5380* (GH); Barro Colorado Island, *Shattuck 807* (MO (2)), *1064, s.n.* (MO); Fort Clayton near old hospital building #519, *Tyson & Blum 3932* (MO); near Gorgas Memorial Lab, *White 83* (GH, MO); Barro Colorado Island, *Woodworth & Vestal 345* (GH, MO), *482* (GH), *514, 615* (GH, MO). CHIRIQUÍ: disturbed cloud forest at Monte Rey about Boquete, *Croat 15770* (GH, MO); windswept ridge 8 km N of Los Planes de Hornito, I.R.H.E. Fortuna Hydroelectric Project, *Knapp 4982* (MO); Quebrada Melliza, 6 mi. S of Puerto Armuelles, 0–150 m, *Liesner 507* (GH, MO). COCLÉ: El Valle, *Aguilar 47* (MO); N rim of El Valle de Antón, 600–1,000 m, *Allen 1738* (GH, MO); roadside S of El Valle, *D'Arcy et al. 13321* (MO); forest behind Club Campestre, *Duke 13259* (MO (2)); hills NE of El Valle de Antón, 2,000 ft., *Lewis et al. 1707* (GH, MO); David, 1,000–1,300 m, *Pittier 2839* (GH); 4 mi. past Llano Grande on road to Cascajal, 200 yards past continental divide, 450–500 m, *Sytsma 3929* (MO); 4 mi. past Llano Grande on road to Cascajal, rocky faced hill ca. 2 km W along continental divide, 600 m, *Sytsma 3961* (MO); 4 mi. past Llano Grande on road to Cascajal, rocky faced hill ca. 2 km W along continental divide, 600 m, *Sytsma 3980* (MO). COLÓN: Portobelo, *Billberg 270* (GH); Santa Rita Ridge lumber road, *Correa & Dressler 737* (MO); Santa Rita, camino a la zona maderera a 15 km NE de la Transisthmica, *Correa & Dressler 1137* (MO); Miguel de la Borda, *Croat 9853* (MO); Santa Rita Ridge, *Croat 13864* (MO); vicinity of Río Indio on road from Portobelo to Nombre de Dios, *Croat 33585* (MO); along Río Iguanita near bridge along Portobelo road, less than 50 m, *Croat 49777* (MO); Santa Rita lumber road, near Agua Clara weather station, *Dressler 3851* (MO); Santa Rita East Ridge, *Dwyer & Correa 8401* (MO (2)); along Río Guanche, 1–4 km S of the Portobelo highway, 0–50 m, *Knapp et al. 4610* (MO); Santa Rita Ridge, ca. 4–5.5 mi. E of Transisthmian Highway, *Lewis et al. 5252* (MO); Santa Rita Ridge, ca. 4–5.5 mi. E of Transisthmian Highway, *Lewis et al. 5285* (GH, MO); 10 mi. SW of Portobelo, 2–4 mi. from coast, 10–200 m, *Liesner 1079* (GH, MO); thickets and weedy roadside along Portobelo road at bridge over Río Viejo, 9 m, *Nee & Tyson 10896* (MO (2)). DARIÉN: Punta Guayabo Grande, 0–50 m, *Antonio & Hahn 4225* (MO); Cerca de El Real al lado de quebrada, *Correa & Lazor 1527* (MO); a lo largo de la unión del Río Tuira con El Chucanaque, a lo largo del ultimo hasta Río Tupisa, *Correa & Lazor 1543* (MO); Río Sambu, 0–5 mi. above Río Venado, *Duke 9270* (MO); Isla Casaya, *Duke 10379* (MO); Isla Pedro Gonzalez, *Duke 10405* (MO); Río Pinas, *Duke 10558* (MO); coastal thicket near Jaqué, *Duke 10665* (MO); Hydro Camp Pico Pendejo in Monsoon forest on Río Sabana, 50 ft., *Duke 15450* (MO); Mannene to the mouth of the Río Cuasi, *Kirkbride & Bristan 1500* (MO); trail between Caña and Boca de Cupe, vicinity of El Real, along road to Pirre River, *Stern et al. 619* (GH, MO); vicinity of Caña, 1,750 ft., *Stern et al. 692* (GH, MO); Tucute, *Terry & Terry 1397* (GH, MO). LOS SANTOS: Punta Mala, *Croat 9759* (MO); *D'Arcy & Croat 4218* (MO); Loma Prieta, 800–900 m, *Duke 11848* (MO); road between Tonosí and Guanica, *Stern et al. 33684*

(MO); Guayabo, several miles W of Tonosí, *Stern 33704* (MO). PANAMÁ: Santa Lucía, Río San Pablo, near Pueblo Nuevo, *Barclay 1799* (MO); San José Island, Canyon road, *Campbell 3* (GH); along dirt road to Cerro Campana, *Correa & Dressler 853* (A, MO); along road to Cerro Campana, *Croat 14676* (MO); El Llano–Carti Road 8.2 mi. N of Interamerican Highway, 300–350 m, *Croat 33701* (MO); middle slopes of Cerro Campana, ca. 1 mi. from Interamerican Highway, 150 m, *Croat 35946* (MO); Cerro Campana, 800 m, *D'Arcy 11143* (MO); alrededores de Chagres, *Diaz 37* (MO); Cerro Jefe, *Duke 9391, 9430* (MO); Río Pacora, just below confluence with Río Corso, *Duke 12029* (MO); San José Island, along road between Bodega Bay and Río Mata Puerco, *Duke 12056* (MO (2)); Tocumen, *Dwyer 7238* (MO); Cerro Jefe, 2,900 ft., *Dwyer et al. 7254* (GH, MO); San José Island, *Erlanson 3, 87, 140* (GH); Chagres, *Fendler 232* (GH); Taboga Island, behind rocky beach, near hotel, sea level, *Gentry 5745* (MO); Llano–Carti Road, 200 m, *Hahn 345* (MO); forest and roadside between 6–12 km north of El Llano on Carti road, 1,200 ft., *Hammel 854* (MO); 10 mi. from Pan-American Highway on the road from El Llano to Carti, 350 m, *Huft et al. 1875* (MO); San José Island, *Johnston 629, 758, 1355* (GH); 12–16 km above Pan-Am Highway on road from El Llano to Carti-Tupile, 150–400 m, *Kennedy et al. 3109* (GH, MO); along road up to Cerro Campana, along edge of montane forest, *Lazor 2219* (MO); Panama City, *Macbride 2730* (MO); El Llano–Carti Road, 8.5 km from highway, 1,200 ft., *Mori 4556* (MO); El Llano–Carti Road, 8.5 km from Inter-American Highway, 350 m, *Mori et al. 4556* (MO); El Llano–Carti Road, 8.5 km from Inter-American Highway, 350 m, *Mori & Kallunki 5173* (MO); 6.5 km by road N of Lago Cerro Azul, 650–730 m, *Nee 9311* (MO); Cerro Jefe, 4.7 mi. above Goofy Lake, 800 m, *Sytsma et al. 2812* (MO); El Llano–Carti Road, 9 km above Pan-American Highway, 900–1,000 ft., *Sytsma 3096* (MO); 6 km S of El Valle on highway 71, 2,400 ft., *Sytsma & D'Arcy 3558* (MO); El Llano–Carti Road, 6 mi. from Pan-American Highway, 300–400 m, *Sytsma 4001* (MO); Isla Taboga, 0–186 m, *Woodson et al. 1538* (MO). SAN BLAS: Permé, *Cooper 218* (GH); Río Ailigandi, *Duke 10834* (MO); mainland opposite Ailigandi, from mouth of Ailigandi river to 2.5 mi. inland, *Lewis et al. 65* (MO); near Puerto Obaldía, W of village, on foot-trail to La Bonga, 50–140 m, *McPherson 6963* (MO). VERAGUAS: along last major stream between Santa Fe and Escuela Agricola Alto Piedras, 420 m, *Croat & Folsom 33832* (MO); Río Santa María near bridge below Santa Fe, 300–400 m, *Knapp & Kress 4326* (MO); 2 mi. W of Santa Fe, 400–800 m, *Liesner 838* (GH, MO (2)).

Tournefortia brenesii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 989. 1938. TYPE: Costa Rica. Alajuela: El Silencio (Los Angeles) de San Ramón, Feb. 1933, *Brenes 17103* (holotype, F 859855).

Shrub to 3 m tall, the branches brown-strigose to pubescent, later glabrous. Leaves alternate but often densely clustered near the ends of branches; petioles 3–10(–27) mm long, glabrous to brown pubescent; leaf blades lanceolate, 9.5–17(–19) cm long, (2–)2.5–5.5(–6.3) cm wide, the apex acuminate to attenuate, the base acute, the margin entire to unevenly undulate or dentate, the adaxial surface glabrous, the abaxial surface glabrous except for scattered short appressed hairs along the secondary veins, the tertiary and quarternary veins clearly visible. Inflorescence terminal or subterminal, cymose, branching dichotomously 2–4 times, the peduncle to 11 cm long, brown puberulent to strigillose. Flowers on short pedicels to 5 mm long, borne (2–)4–10 mm apart; sepals 5, ovate to lanceolate, 4.3–4.5 mm long, ca. 1.7 mm wide, glabrous to sparsely strigillose; corolla white, tubular with spreading ovate to lanceolate lobes, these acute at the apex, 2.6–2.7 mm long, the tube 4.8–5 mm long, strigillose outside; stamens 5, the anthers oblong to lanceoloid, sessile or nearly so, inserted in the middle of the corolla tube; ovary globose, ca. 1 mm long, the disc crateriform, the style ca. 1 mm long, the stigma pyramidal. Fruit ovoid, 6–8 mm long, 5–6 mm wide, white at maturity, often capped by the persistent stigma.

Distribution. *Tournefortia brenesii* is restricted to cloud forests from 800–1,350 m in elevation in Panama and Costa Rica. In Panama it is known only from the province of Veraguas.

Tournefortia brenesii is distinct in its compact habit of growth, with the leaves clustered densely near the branch tips, and broad, accrescent sepals.

Additional specimens examined. PANAMA. VERAGUAS: vicinity of Escuela Agricultura Alto Piedra near Santa Fe, along trail to top of Cerro Tute, 3,500 ft., *Antonio 4957* (MO); Cerro Tute, ridge up from former Escuela Agricola, Santa Fe, 1,000–1,300 m, *Hamilton & Dressler 3080* (MO); ridge of Cordillera de Tute, trail to Cerro Tute, above Escuela Agricola Alto de Piedra, just W of Santa Fe, 800–1,350 m, *Knapp & Dressler 5403* (MO); Cerro Tute, ca. 10 mi. NW of Santa Fe, on ridgetop in cloud forest, above 1,000 m, *Mori 6760* (MO).

Tournefortia cuspidata Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 83.

1818. TYPE: Ecuador. Guayas: Guayaquil, *Humboldt & Bonpland s.n.* (holotype, P, not seen).

Tournefortia obscura A. DC. in DC., Prodr. 9: 517. 1845. TYPE: Guyana: *Schomburgk 571* (holotype, G-DC, not seen; microfiche, MO).

Scandent woody vine or sprawling shrub to 2 m tall, the twigs villose with hairs to 4 mm long. Leaves alternate; petioles 3–8 mm long, stout, shaggy-villose; blade lance-ovate, elliptic, ovate, or rarely obovate, 8–13(–19) cm long, 3–6(–9) cm wide, the apex acuminate, the base acute to obtuse, the margin entire, the adaxial surface strigose, the abaxial surface strigose to nearly villous, especially along the veins. Inflorescence terminal, a few- to much-branched, dense cyme, the sterile portions of branches shaggy villous. Flowers sessile, very closely spaced; sepals lanceolate, 5.5–7.5 mm long, strigose to hirsute; corolla white to green, 5-merous, the lobes ovate, 1–1.8 mm long, the tube 6.5–8 mm long, strigose to sericeous on the outside; stamens 5, the anthers lanceoloid, 1.3–1.5 mm long, sessile, inserted beneath the middle of the corolla tube; ovary globose to ovoid, ca. 1 mm long, the style 0.4–0.5 mm long, the stigma conical. Fruits ovoid, 3–4.5 mm long, white at maturity, breaking into (2–)4 nutlets at maturity, glabrous.

Distribution. *Tournefortia cuspidata* is common in disturbed areas of moist to wet forests at elevations below 400 m from Mexico to South America, and it occurs on Trinidad and Tobago. In Panama it is known from Bocas del Toro, Canal Area, Coclé, Colón, Darién, Panamá, and San Blas.

Tournefortia cuspidata is a distinctive species readily recognized by its shaggy, villous twigs with the hairs up to 4 mm long and sepals greater than 5 mm long. This is one of the most commonly collected species in southern Central America and northern South America. It is perhaps most closely related to *T. hirsutissima* but differs in its much longer hairs and sepals. Although the long hairs on the stems are usually diagnostic, these are greatly reduced in plants from adjacent Chocó, Colombia.

Additional specimens examined. PANAMA. BOCAS DEL TORO: along railroad tracks near station at Milla 5, *Croat & Porter 16493* (MO); Changuinola to 5 mi. S at junction of ríos Changuinola and Terebe, 100–200 ft., *Lewis et al. 951* (GH, MO); Almirante, near Dos Milla, *McDaniel 5138* (MO); Chiriquí Lagoon, Water Valley, *Wedel 770* (GH, MO), *1282* (MO), *1674* (GH, MO); Chiriquí Lagoon, Old Bank Island, *Wedel 1959* (GH, MO); Chiriquí Lagoon, Little Bocas, *Wedel 2510* (MO), *2559* (GH, MO); Chiriquí Lagoon, Isla Colón, *Wedel 2961* (GH). CANAL AREA: France Field, *Blum & Dwyer 2125a* (MO); Gamboa Navy Pipe Line along main dirt road, *Correa & Haines 544* (MO); Barro Colorado Island, *Croat 4207, 4683, 7194, 7415, 7684, 7748* (MO); road S-10, N of Escobal, *Croat 12445, 13114* (MO); Gaillard Highway between Paraiso and the Continental Divide, *Croat 14833* (MO); Pipeline Road to 18 km N of Gamboa, *D'Arcy s.n.* (MO); Barro Colorado Island, *Dwyer et al. 8447* (MO); Gamboa, Naval Reservation, *Ebinger 892* (GH, MO); Pipeline Road, 5–6 mi. N of Gamboa, 100–200 m, *Gentry 6671* (MO); Barro Colorado Island, *Hayden 41* (MO); NW shore of Gatún Lake, ca. 4 mi. S of Río Chagres, *Lewis 1823* (MO); Pipeline Road between mile markers 0 and 11.1, ca. 16 mi. N of Gamboa, *Lewis et al. 5452* (MO); on Pipeline Road, 14.4 km from Chagres Airport Road, 0–100 m, *Mori & Kallunki 2062* (MO); Barro Colorado Island, *Shattuck 100* (GH, MO (2)), *676* (GH, MO (3)), *957* (MO); *Starry 228* (MO); *Whetmore & Abbe 201* (GH (2), MO); *Whetmore & Woodworth 854* (GH); along the margin of Pipeline Road N of Gamboa, *Wilbur & Weaver 11267* (MO); Barro Colorado Island, *Woodworth & Vestal 328* (GH, MO), *523* (GH). COCLÉ: forest on hills above road 18 km past Sardinilla on way to Nombre de Dios, 150–300 m, *Croat 26105* (MO); around Rivera Sawmill, 7 km N of El Copé, 700–850 m, *Folsom et al. 5696* (MO); along Río San Juan below its junction with Río Tife, 1,200 ft., *Hammel 3390* (MO). COLÓN: forested area near Guasimo along river, *Croat 9968* (MO); Peluca, ca. 2.7 km from Transisthmian Highway on road to Nombre de Dios, *Kennedy 2638* (MO); along Río Boquerón above Mina Boquerón #1 (manganese mine), main valley of the Río Boquerón, 100–200 m, *Knapp & Sytsma 2465* (MO); along Río Boquerón near No.1 (manganese mine), E of Salamanca, 50 m, *Knapp et al. 5821A* (MO); roadside and woods near bridge over Quebrada La Furnia on highway 5-8 (82), road to Pinas, 10 m, *Mori & Kallunki 1946* (GH, MO). DARIÉN: headwaters of Río Chico, 500–750 ft., *Allen 4638* (MO); 110 mi. from Bayano Dam Bridge, vicinity of Canglon, trail to south, 1 km W of bridge in Canglon, 50 ft., *Antonio 4584* (MO); camino de El Real a Pinogana, *Correa & Lazor 1555* (MO); vicinity of El Real along road to airport, *Croat & Porter 15445* (MO); El Real, *D'Arcy 5512* (MO); 2–3 mi. SE of El Real, *Duke 4853* (MO); road from El Real to Pinogana, *Duke 5001* (GH (2), MO); Isla Boca Grande, *Duke 8843* (MO); Río Sambu, 0–5 mi. above Río Venado, *Duke 9268* (MO); Enseñada del Guayabo, 16–19 km SE of Jaqué, *Garwood 921* (MO); Manene to mouth of Río Cuasi, *Kirkbride & Bristan 1415* (MO); Río Tuquesa, at lower Tuquesa Mining Company camp called Charco Chiva, 100 m, *Mori*

6995 (MO); vicinity of Yaviza, along Río Chucunaque, El Punteadero bridge, Inter-American Highway over Río Chucunaque, a short distance down river from Yaviza, *Stern et al. 170* (GH, MO); vicinity of Paya, Río Paya, trail between Paya and Payita, *Stern et al. 363* (GH, MO); Gold Mine at Caña, 480 m, *Sullivan 749* (MO); 3 mi. E of Santa Fe, *Tyson et al. 4652* (MO); 2 mi. E of Santa Fe, *Tyson 4818* (MO). PANAMÁ: Río Pita, 0–2 mi. above tidal limit, *Duke 4793* (MO (2)); forests along headwaters of Río Corso, off Río Pacora, 500 m, *Duke 11929* (MO); N of El Llano, 500–800 m, *Gentry 5560* (MO); Pipeline Road, 50 m, *Hamilton et al. 3266* (MO); 10 mi. from Pan-American Highway on the road from El Llano to Carti, 350 m, *Huft et al. 1874* (MO); Alcalde Diaz, *Jaen 23* (MO); forest edges along Río Pirati, about ½ hour walk from Pan-American Highway, foothills of the Serranía de Maje, 50–100 m, *Knapp & Mallet 5164* (MO); El Llano–Carti Road, 6–10 mi. from Pan-American Highway, 400 m, *Miller et al. 857* (MO); along the Pan-American Highway 6.5 mi. E of highway checkpoint at turnoff to Chepo, *Miller et al. 1019* (MO); Gorgas Memorial Labs yellow fever research camp, ca. 25 km NE of Cerro Azul on Río Piedras, 550 m, *Mori & Kallunki 3464* (MO); Arenoso, lower Río Trinidad, 26–50 m, *Seibert 625* (GH (2), MO); 2 mi. E of El Llano, *Tyson 1737* (MO); 5 mi. E of Canita or 23 mi. E of Chepo, *Tyson & Smith 4152* (MO); 1 mi. E of El Llano, *Tyson 6883* (MO); La Rana de Oro, Pedregal, *Villamil 33* (MO); wet savanna E of Pacora, 25 m, *Woodson et al. 721* (MO), *722* (GH (2), MO). SAN BLAS: El Llano–Carti Road, 350 m, *de Nevers & Herrera 4222* (MO); trail from Puerto Obaldía to La Bonga, tributary of the Río Armila, ca. 2 hours walk from Puerto Obaldía, 0–50 m, *Knapp & Mallet 4679* (MO); along newly cut road from El Llano to Carti-Tupile, continental divide to 1 mi. from divide, 300–500 m, *Liesner 1297* (GH, MO).

Tournefortia glabra L., Sp. Pl. 141. 1753. TYPE: without locality or collector (holotype, LINN (Savage Catalog number 193.5), not seen; microfiche, MO).

Small tree or shrub to 5(–10) m tall, the twigs glabrous to sparsely strigillose. Leaves alternate; petioles 1–4(–5) cm long, sparsely strigillose to nearly glabrous; leaf blade narrowly elliptic to lance-obovate, (8–)12–18 (–25) cm long, (2.5–)5–8(–12) cm wide, the apex acuminate, the base attenuate and usually strongly decurrent, the margin entire, the adaxial surface sparsely strigillose to nearly glabrous, the abaxial surface with a few hairs scattered along the veins, the tertiary veins evident. Inflorescence internodal or terminal, a loosely branched cyme, the peduncle 3–8 (–14) cm long, sparsely strigillose to nearly glabrous, the branches 3–8(–10) cm long. Flowers sessile, borne (1–)2–3(–4) mm apart; sepals lanceolate, 1–1.2 mm long, sparsely strigillose; corolla white or greenish white, 5-merous, the lobes lanceolate, 1.5–2 mm long, the tube 3.5–4 mm long, strigillose outside; stamens 5, the anthers ellipsoid, 0.6–1 mm long, sessile or nearly so, inserted above the middle of the corolla tube; ovary ovoid, 0.7–1.5 mm long, the disc crateriform to scarcely evident, the style 1–1.2 mm long, the stigma capitate. Fruits white at maturity, very broadly ovoid, 3–4 mm long, glabrous.

Distribution. Tournefortia glabra occurs in diverse moist to wet habitats from sea level to 2,700 m in elevation. It is found from Mexico through Central and South America and in the West Indies. In Panama, it is known from Bocas del Toro, Chiriquí, Coclé, Colón, Panamá, San Blas, and Veraguas.

Tournefortia glabra is one of the few small understory trees in the genus found in Central America. This species is vegetatively quite similar to *T. acutiflora* Martens & Galeotti of northern Central America and southern Mexico, but differs in having calyx lobes shorter than 1.5 mm long.

Additional specimens examined. PANAMA. BOCAS DEL TORO: region of Almirante, Daytonia farm, *Cooper 376* (GH, MO); along road to Chiriquí Grande, 450 m, *McPherson 7391* (MO); Chiriquí Lagoon, Water Valley, *Wedel 1573, 1746* (GH, MO). CHIRIQUÍ: 12 mi. from Gualaca on road to Cerro Hornito, 1,300 m, *Antonio 1751* (MO); Cerro Colorado Mine, 2 mi. from Lower Elevation Camp, 4,200 ft., *Antonio 4906* (MO); Palo Alto–Boquete, 1,300–1,772 m, *Beliz 215* (MO); 5.4 km del Hato del Volcán en el camino a Las Lagunas, *Correa & Lazor 1461* (MO); E of Boquete along forested slopes and pastures on Cerro Azul near Quebrada Jaramillo, 1,500–1,620 m, *Croat 26781* (GH, MO); Chiquero, Boquete, *Davidson 552* (GH, MO); TTC-BMI Cloud Forest Litter Study Cerro Horqueta, 1,500 m, *Duke et al. 13637* (MO); NW of Boquete, Cerro Horqueta, 5,000–5,800 ft., *Dwyer et al. 478* (MO); Boquete, Finca Collins, 5,000 ft., *Dwyer & Hayden 7644* (MO); Boquete, Fred Collins Finca, *Ebinger 667* (MO); road to Río Serano, *Folsom et al. 2107* (MO); path from Linares farm ca. 1,400 m to top of Cerro Hornito at 1,750 m, *Folsom et al. 7227* (MO); Las Lagunas area W of Hato del Volcán, 1,400 m, *Hamilton & Stockwell 3574* (MO); along Río Colorado, 1,200–1,400 m, *Hamilton & Krager 3806* (MO); road along Río Palo Alto ca. 3 km NE of Boquete to the end, *Huft 1858* (MO); Collins Finca, 2,000 m, *Kirkbride 119* (MO); N of San Felix, 36.2 km by road from the Interamerican Highway, *Mori & Kallunki 6017* (MO); Dos Lagunas, 4 km W of El Hato del Volcán, 1,300 m, *Mori & Bolten 7400* (MO); Las Lagunas, 2 mi. SW of El Volcán, 4,200 ft., *Tyson 850* (MO); Río Chiriquí Viejo valley, near Bambita, *White 46* (GH, MO); Finca Lerida to Peña Blanca, 1,750–2,000 m, *Woodson & Schery 285* (GH (2), MO); vicinity of Casita Alta, Volcán de Chiriquí, 1,500–2,000 m, *Woodson et al. 986* (GH, MO). COCLÉ: El Valle, 600–1,000 m, *Allen 1200* (GH), *1794* (GH, MO); La Mesa above El Valle, 810 m, *Croat 25298* (GH, MO); Cerro Pilon near El Valle, *Duke 12060* (MO); El Valle de Antón at the foot of Cerro Pilón, 2,000 ft., *Dwyer & Correa 7964* (MO); El Valle de Antón at the foot of Cerro Pilón, 2,000 ft., *Dwyer & Correa 7965* (MO); Cerro Pilón, 2,700 ft., *Dwyer & Lallathin 8610* (MO); vicinity of La Mesa above El Valle, 900 m, *Gentry 7408* (GH, MO); hills above El Valle, 1,000 m, *Gentry 6895* (MO); La Mesa region N of Cerro Gaital vicinity of El Valle, 2,400 ft., *Hammel 3899* (MO); El Valle de Antón, La Mesa, 1,000 m, *Kennedy et al. 3034* (MO); El Valle Wepcor site, on trail from end of road to the site, *Kirkbride 1088* (MO); foothills and summit of Cerro Caracoral, near La Mesa N of El Valle de Antón, 800–1,100 m, *Knapp 1111* (MO); Cerro Pilón, 900–1,173 m, *Liesner 768* (MO); along road above El Valle toward upper ridges above town, *Miller et al. 775* (MO); foot of Cerro Pilón, above El Valle de Antón, 2,000 ft., *Porter et al. 4640* (MO); NE slopes and summit of Cerro Caracoral, north rim of El Valle, 2,700–3,200 ft., *Sytsma 4051* (MO); trail to La Mesa about 4.5 mi. beyond El Valle de Antón, *Wilbur & Luteyn 11683* (MO). COLÓN: ridge top leading N from Río Escandaloso towards Cerro Bruja, 600 ft., *Hammel 2708* (MO). DARIÉN: between Quebrada Venado and Peje swamp on the headwaters of Río Tuquesa, *Bristan 1006* (MO); Río Ucurganti, *Bristan 1139* (MO); trail SE of Manene to Río Cuasi, *Hartman 12197* (MO); premontane rainforest 0–2 mi. E of Tres Bocas along the shortest headwater of Río Cuasi, *Kirkbride & Duke 1144* (MO (2)); Río Tuquesa, at middle Tuquesa Mining Company camp called Charco Peje, 250 m, *Mori 7002, 7093* (MO); Paya, Río Paya, *Stern et al. 396* (GH, MO). PANAMÁ: Cerro Campana, 600 m, *Antonio 1730* (MO); trail up to Campana Ridge, *Correa & Dressler 377* (MO (2)); forest near dam site south of Canita, *Croat 14531* (MO); cloud forest on Cerro Campana near FSU building, *Croat 14809* (MO); Cerro Campana, 800 m, *D'Arcy 11141* (MO); Cerro Campana, 2,500 ft., *D'Arcy & Hamilton 14931* (MO); Río Bayano, near crossing of Pan-Am Highway, above confluence with Río Chepo, *Duke 3974* (MO (2)), *3998* (MO); Piria–Canasas Trail near Piria, 100 m, *Duke 14330* (MO); area around Torti Arriba, *Folsom 5129* (MO); near top of Cerro Campana, above FSU cabin, *Gentry 5770* (MO); 3.8 mi. E of Río Ipeti, S along river and into lower slopes of Serranía de Maje, 50–200 m, *Huft & Jacobs 2002* (MO); near Cerro Campana, on trail radiating from end of road which passes Campana water tank, *Kirkbride & Hayden 312* (MO); forest edges along Río Pirati, about ½ hour walk from Pan-American Highway, foothills of the Serranía de Maje, 50–100 m, *Knapp & Mallet 5167* (MO); Cerro Campana, trails just inside entrance to Parque Nacional, 850 m, *Miller & Miller 995* (MO); Parque Nacional Cerro Campana, 2 km N of highway 707, 850 m, *Stein & Hamilton 1140* (MO); base of Serranía de Canazas, ca. 15 km SW of Canaza near Río Torti, 150 m, *Stein 1387* (MO); steep slopes S of Canita, 200 m, *Webster et al. 16885* (MO); lower slopes and trail to Cerro Campana, *Witherspoon 8400* (MO). SAN BLAS: El Llano–Carti Road, km 16.7, trail W to Río Carti Grande, 250–350 m, *de Nevers & Herrera 4177* (MO); along the headwaters of Río Mulatupo, *Elias 1751* (MO). VERAGUAS: El Cuchillo, near Cerro Tute, up from Santa Fe, 1,300 m, *Hamilton et al. 1240* (MO).

Tournefortia hirsutissima L., Sp. Pl. 140. 1753. *Messerschmidtia hirsutissima* (L.) Roemer & Schultes, Syst. Veg. 4: 451. 1819. TYPE: without locality or collector (holotype, LINN (Savage Catalog number 193.1), not seen; microfiche, MO).

Tournefortia schomburgkii DC., Prodr. 9: 517. 1845. TYPE: Guyana: 1837, *Schomburgk 70* (holotype, G-DC, not seen; microfiche, MO; isotype, K).

Woody vine, sprawling shrub, or small tree, the twigs strigose to hirsute. Leaves alternate; petioles (3–)8–15(–20) mm long, strigose to hirsute; leaf blade lance-ovate to narrowly elliptic, (7–)11–18(–20) cm long, (2.5–)3.5–6(–8) cm wide, the apex acuminate to acute, the base acute to obtuse, the margin entire, the adaxial surface strigose, the abaxial surface strigose to pubescent, the tertiary veins evident. Inflorescence terminal or rarely internodal or axillary, a much-branched, dense cyme, the peduncle (1–)2–4(–5) cm long, strigose to hirsute, the fertile branches 1.5–4(–6) cm long. Flowers sessile, borne 1–2 (–3) mm apart; sepals lanceolate, 2.5–4 mm long, strigillose; corolla white, 5-merous, the lobes ovate, 1–1.6 mm long, the tube 3.5–5.3 mm long, strigillose outside; stamens 5, the anthers lanceoloid, 1.1–1.3 mm long, sessile, inserted beneath the middle of the corolla tube; ovary globose, 0.8–1 mm long, the disc scarcely evident, the stigma nearly sessile, capitate. Fruits white, ovoid, 3–4 mm long, strigillose.

Distribution. *Tournefortia hirsutissima* is found in diverse habitats from sea level to 2,000 m in elevation, and is ubiquitous throughout the Neotropics. In Panama, it is known from the Canal Area, Chiriquí, Darién, Panamá, and San Blas.

Tournefortia hirsutissima is one of the most commonly collected members of the genus and appears to be most closely related to *T. bicolor* (discussion under that species). The two can be distinguished most easily by the usually strigose upper leaf surface in *T. hirsutissima,* while it is glabrous or nearly so in *T. bicolor.* One collection from Darién (*Stern 501*) is unique in having a white abaxial leaf surface, but it otherwise fits well within *T. hirsutissima,* agreeing in all other aspects.

Additional specimens examined. PANAMA. CANAL AREA: forest reserve, near crossing of Cruces trail and Madden Dam road, *Bartlett & Lasser 16348* (GH, MO); Juan Mina, *Bartlett & Lasser 16529* (GH, MO); Barro Colorado Island, *Croat 4797, 6246, 10750A, 11718* (MO); roadside W of Gatún Locks, *Croat 12432* (MO); vicinity of Fort San Lorenzo, *Croat 12521* (MO); Barro Colorado Island, *Croat 15054* (MO); along road between Gatún Locks and Ft. Sherman, *Croat 15380* (MO); hill above Thatcher-Ferry Bridge, *Croat 17014* (MO); Fort Sherman, *Dwyer & Robyns 172* (MO); *Dwyer 6685* (MO); Madden Dam, Boy Scout Camp Road, *Dwyer & Elias 7513* (MO); Gatún Station, *Hayes 61* (GH); vicinity of Río Chagres Bridge, road leading to abandoned weather post, ca. 2 km by road SE of Gamboa along highway to Balboa, *Lasseigne 4271* (MO); west side of Ferry Thatcher Bridge, along mangrove margin, *Lazor 2881* (MO); Pipeline Road, *Meijer 160* (MO); Pipeline Road, 10–15 mi. from Gamboa, 100 m, *Miller 1027* (MO); along road from Fort Sherman to Fort San Lorenzo, *Porter et al. 4984* (MO); vicinity of Madden Dam, near Río Chagres, 50–75 m, *Seibert 560* (MO); Barro Colorado Island, *Shattuck 970* (MO (3)); *Starry 238* (MO); Fort Sherman near mouth of Chagres River, *Tyson 1535* (MO); Old Fort San Lorenzo, *Tyson 1571, 1572* (MO); *Tyson & Blum 3698* (GH, MO); Barro Colorado Island, *Wilson 44* (MO). CHIRIQUÍ: Llanos on slopes of Volcán de Chiriquí Viejo and along Río Chiriquí Viejo, 1,200 m, *Allen 968* (MO); Boquete, lumber road into the hills east of the Río Caldera, 4,500–6,500 ft., *Allen 4654* (GH, MO); Burica Peninsula, Quebrada Manzanillo, 9 km SSW of Puerto Armuelles, *Busey 746* (MO); 1 mi. W of airport at Puerto Armuelles, *Croat 21905* (MO); Puerto Limónes, along coast near the beach, *Croat 22119* (MO); Burica Peninsula, Distrito Guanabano, disturbed areas along Quebrada Quanabano, 0–100 m, *Croat 22534* (MO); San Bartolo Arriba W of Puerto Armuelles, *Croat 26700* (MO); Las Lagunas area W of Hato del Volcán, 1,400 m, *Hamilton & Stockwell 3562* (MO); Burica Peninsula, 2.5 km W of Puerto Armuelles, 80 m, *Liesner 16* (MO); Burica Peninsula, Quebrada Merica, 4 mi. S of Puerto Armuelles, 0–100 m, *Liesner 384* (MO); along road 3–5 mi. NW of El Hato del Volcán towards Costa Rica across the Río Chiriquí Viejo, 3,000–4,000 ft., *Luteyn 859* (MO); valley of the upper Río Gariche, 1,050–1,100 m, *Seibert 357* (GH, MO). COLÓN: 4 mi. W of Portobelo, near sea level, *Antonio 1764* (MO); Portobelo, *Billberg 269* (GH); Isla Grande, *D'Arcy 4033B* (MO); Portobelo, *Dwyer 5146* (GH); La Guayra, E of Portobelo, *Knapp & Mallet 5725* (MO). DARIÉN: headwaters of Río Chico, 500–750 ft., *Allen 4638* (GH); vicinity of Caña, 1,750 ft., *Stern et al. 501* (GH). PANAMÁ: a orillas de la carretera hacia Pacora 1 km despues del Autodromo Panamá, *Carrasquilla 191* (MO); a 4 km del corregimiento de Pacora, *Carrera 19* (MO); vicinity of Macambo, *Croat 14906A* (MO); Cerro Azul, *Dwyer 1876* (MO); Tocumen, *Dwyer 4056* (MO (2)); Las Guacas, población a orillas del Río Chagres, *Kant 39* (MO); El Llano–Carti Road, 18 km from Interamerican Highway, 350 m, *Mori et al. 4582* (MO); El Llano–Carti Road 17.5 km from Interamerican Highway, 350 m, *Mori et al. 4623* (MO); road to Cerro Campana, 10 km from Interamerican Highway, 300 m, *Sullivan 438* (MO); between Chepo and La Capitana, *Tyson 6758* (MO (2)); wet savanna E of Pacora, *Woodson et al. 721* (GH (2)). SAN BLAS: through cultivation on mainland in front of Ustupo, *D'Arcy 9507* (MO).

Tournefortia johnstonii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 991. 1938. TYPE: Costa Rica. Heredia: Cerro de las Caricias, north of San Isidro, 2,000–2,400 m, *P. C. Standley & J. Valerio 52087* (holotype, US 1306982).

Shrub to 3 m tall, or rarely a small tree to 6 m tall, the twigs velutinous. Leaves opposite, the lateral buds usually with small expanding leaves with appearance of stipules; petioles 9–30(–40) mm long, velutinous; leaf blade lanceolate to ovate, (7.8–)10–18(–23) cm long, (3–)4–8(–10) cm wide, the apex acuminate, the base cuneate to acute, the margin entire to unevenly undulate, the adaxial surface velutinous, the abaxial surface velutinous, the secondary veins 10–12, the tertiary and quaternary veins clearly evident. Inflorescence terminal, a once- or rarely twice-branched cyme, the branches (2.5–)4–15 cm long, the peduncle (3–)5–12 cm long, velutinous. Flowers bisexual, sessile, borne 1–5 (–7) mm apart; sepals 5, lanceolate, 6–10.5 mm long, strigillose to strigose; corolla tubular with spreading lobes, white to green, 5-merous, the lobes lance-ovate to ovate, the apex acuminate, 2.6–5 mm long, the tube 8–10 mm long, strigillose, at least near the apex; stamens 5, the anthers lanceoloid, 1.5–2 mm long, sessile, inserted just below the mouth of the corolla tube; ovary ovoid, 0.8–1 mm long, the disc scarcely evident, the style 3–3.5 mm long, the stigma conical. Fruits white, ovoid, 4.5–7 mm long, separating into 2–4 nutlets at maturity.

Distribution. Tournefortia johnstonii occurs only in Panama and Costa Rica in cloud forests at elevations of 1,000–3,000 m. In Panama it is known only from the provinces of Chiriquí and Veraguas.

Tournefortia johnstonii is very similar in general aspect to *T. ramonensis* but differs in being a smaller plant with longer, coarser indument on the twigs. Also, the lower leaf surfaces of *T. johnstonii* are usually darker in color after drying.

Additional specimens examined. PANAMA. CHIRIQUÍ: Cerro Colorado, near continental divide, 1,500 m, *Antonio 1459* (MO); along road between Cerro Punta and Las Nubes, 1,800–2,100 m, *Croat 26391* (MO); Las Nubes, 2,000 m, *Croat 26456* (MO); E of Boquete along steep, forested slopes and in wooded pastures on Cerro Azul near Quebrada Jaramillo, 1,620–1,700 m, *Croat 26867* (MO); Alto Respinga and above, 2,800 m, *D'Arcy 9991* (MO); mountain directly S of Cerro Respinga, *D'Arcy 10811* (MO); E slope of Volcán de Chiriquí (Baru), above Boquete, along road in oak forest, 2,600 m, *Davidse & D'Arcy 10264* (MO); Volcán de Chiriquí, 9,000 ft., *Davidson 976* (GH, MO); along Boquete trail, Cerro Respinga, 2,000–2,500 m, *Gentry 5978, 6013* (MO); path above Cerro Punta to Boquete, 2,500 m, *Hamilton & Stockwell 3417* (MO); *Hamilton & Krager 3741* (MO); 7 km NW of Cerro Punta, 7,200 ft., *Hammel 1472* (MO); Cerro Hornito, 5,600 ft., *Hammel 3043* (MO); Quebrada Alemán, 8 mi. N of Los Planes de Hornito I.R.H.E. Fortuna Hydroelectric Project, 1,200 m, *Knapp et al. 4155* (MO); trail from Cerro Punta to Boquete, 2,160–2,260 m, *McDaniels 10255* (MO); N of San Felix at Chiriquí-Bocas del Toro border, on Cerro Colorado copper mine road along continental divide, 5,000–5,500 ft., *Mori & Kallunki 5939* (MO); 3.7 km E of bridge NE of Cerro Punta on road through Bajo Grande, 2,250–2,400 m, *Stevens 18199* (MO); 3.7 km along road through Bajo Grande from bridge NE of Cerro Punta, 2,250–2,400 m, *Sytsma & Stevens 2143* (MO); along the trail between Cerro Punta and the Quebrado Bajo Grande, 2,000–2,100 m, *Wilbur et al. 11903* (MO); thickets along trail between Las Mirandas and Las Nubes and a small valley running NW of the mountain of Cerro Punta about 3 mi. from village of Cerro Punta, *Wilbur & Teeri 13271* (GH, MO); vicinity of Casita Alta, Volcán de Chiriquí, 1,500–2,000 m, *Woodson et al. 888* (GH, MO). VERAGUAS: Cerro Tute, E slopes, 1 km beyond Escuela Agricola Alto Piedra above Santa Fe, 1,200–1,450 m, *Sytsma & Anderson 4593* (MO).

Tournefortia longispica James S. Miller, sp. nov. TYPE: Panama. Bocas del Toro: road from Fortuna Dam to Chiriquí Grande, 3.1 mi. N of continental divide, 700 m, disturbed primary forest, *G. McPherson 6778* (holotype, MO 3386969). Figure 6.

Suffrutex ad 2 m altus, ramulis glabris. Folia alterna; petioli (1.5–)2.5–4(–6.5) cm longi; lamina elliptica ad oblonga, (14–)17–25 cm longa, (5.5–)6.5–9(–10.5) cm lata, apice acuminata, basi acuta ad attenuata, glabra. Inflorescentia terminalis, cyma ramorum duorum, ad 30 cm longorum post anthesin composita, pedunculo 10–22 cm longo, glabro vel fere glabro. Flores sessiles, 1–5 mm distantibus; sepala lanceolata, 2.5–3 mm longa; corolla alba ad pallido-viridis, tubularis, lobis patulis, ovatis ad late ovatis, 2–2.5 mm longis, tubo extus strigilloso; antheris 1.5–2 mm longis, sessilibus, ad medium tubi insertis; stylus 0.6–1 mm longus, stigmate conoidi. Fructus globosi ad valde lato-ovoidei, 6–9 mm longi, 9–12 mm lati, glabri, laeves.

Shrub to 2 m tall, the twigs glabrous. Leaves alternate; the petioles (1.5–)2.5–4(–6.5) cm long, glabrous or nearly so; leaf blade elliptic to oblong, (14–)17–25 cm long, (5.5–)6.5–9(–10.5) cm wide, the apex acuminate, the base acute to attenuate, the margin entire, the adaxial surface glabrous, the abaxial surface glabrous but with very small appressed hairs along the major veins, the secondary veins 8–11, the tertiary veins evident, the quaternary veins often obscure. Inflorescence terminal or subterminal, usually a twice-branched cyme, the branches elongate, to 30 cm long at fruiting, the peduncle 10–22 cm long, glabrous to shortly brown puberulent or strigillose. Flowers sessile, bisexual, borne 1–5 mm apart; sepals 5, lanceolate, 2.5–3 mm long, sparsely to evenly strigillose; corolla tubular with spreading lobes, white to pale green, 5-merous, the lobes ovate to widely ovate, 2–2.5 mm long, the tube 4–5.5 mm long, strigillose outside; stamens 5, the anthers lanceoloid, 1.5–2 mm long, sessile, inserted in the middle of the corolla tube; ovary ovoid, 0.8–1 mm long, the disc crateriform or barely evident, the style 0.6–1 mm long, the stigma conical. Fruits white, globose to very broadly ovoid, 6–9 mm long, 9–12 mm broad, glabrous, smooth.

Distribution. Tournefortia longispica is known only from Panama from the provinces of Bocas del Toro, Chiriquí, Coclé, and Veraguas, where it occurs in cloud forests at elevations of 600–1,500 m.

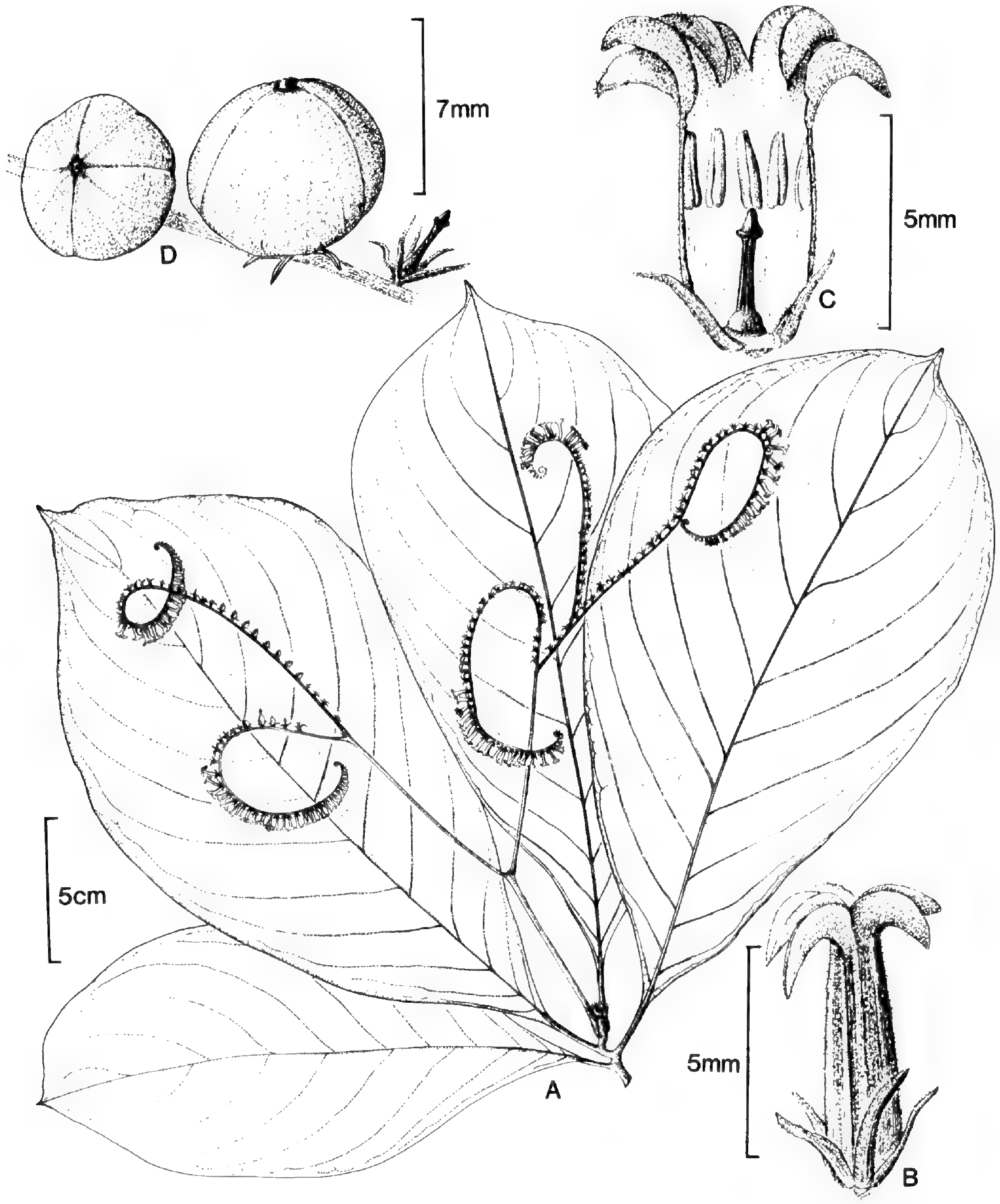

FIGURE 6. Tournefortia longispica.—*A. Flowering branch.—B. Flower.—C. Flower with corolla opened.—D. Fruits. A–C from* McPherson 6778 *(MO), Bocas del Toro, Panama; D from* McPherson 7247 *(MO), Bocas del Toro, Panama.*

Tournefortia longispica is distinct within the genus in having an elongate, dichotomously branched inflorescence and large, nearly glabrous leaves. It has no known close relatives in Panama but could be confused with *T. glabra*, which differs in having a much-branched inflorescence. Several of the collections have large, swollen fruits apparently parasitized by insects, a common condition in the genus.

Additional specimens examined. PANAMA. BOCAS DEL TORO: E slope of La Zorra to divide, *Kirkbride & Duke 824* (MO); in forest along trail down hill from Finca Serrano, 4,600 ft., *Hammel 6166* (MO); along trail on divide separating Chiriquí and Bocas del Toro, 1,150 m, *McPherson 7247* (MO). CHIRIQUÍ: Fortuna Dam area to N of reservoir near Quebrada Bonito, 1,100 m, *Churchill 5811* (MO); W side of Río Hornito, 1,100–1,300 m, *D'Arcy 16009* (MO). COCLÉ: El Copé on Pacific side ½ hour walk from sawmill, *Antonio 2109* (MO); Cerro Pilón, El Valle, 3,000 ft., *Duke & Lallathin 14962* (MO); Cerro Pilón, 2,900 ft., *Dwyer & Lallathin 8687* (MO); El Valle, *Folsom 2658* (MO); New Works at Rivera sawmill, Alto Calvario, 600–800 m, *Folsom 3164* (MO); Cerro Pilón, 900–1,173 m, *Liesner 786* (MO). VERAGUAS: Ridge of Cordillera de Tute, trail to Cerro Tute, above Escuela Agricola Alto de Piedra, just W of Santa Fe, 800–1,350 m, *Knapp & Dressler 5425* (MO).

Tournefortia maculata Jacq., Enum. Syst. Pl. 14. 1760; Select. Stirp. Amer. Hist. 47. 1763. TYPE: Colombia, Bolívar: Cartagena (not seen).

Woody climbing vine, the twigs sparsely strigillose, later glabrous. Leaves alternate; petioles (3–)5–12 mm long, sparsely short-strigillose; leaf blade (3–)5–9 cm long, (1.5–) 2.5–4 cm wide, the apex acuminate to attenuate, the base acute to obtuse and often slightly decurrent, the margin entire, the adaxial surface very sparsely short-strigillose, the abaxial surface evenly short-strigillose. Inflorescence usually terminal, a loose, much-branched cyme, the branches to 5 cm long, the peduncles 18–24 mm long, puberulent to strigillose. Flowers sessile, borne 1–10 mm apart, bisexual; sepals lanceolate to triangular, 0.8–2 mm long, strigillose; corolla pale yellow-green, 5-merous, the lobes filiform, 1.5–3 mm long, the tube 3.3–5 mm long, densely strigillose; stamens 5, the anthers lanceoloid, 0.8–1 mm long, connate apically, nearly sessile, inserted in the mouth of the corolla tube; ovary ovoid, 0.8–1 mm long, the disc crateriform to scarcely evident, the style 0.8–4 mm long, the stigma capitate. Fruits 4-lobed, 2.5–4 mm long, glabrous, white with black markings.

Distribution. *Tournefortia maculata* ranges from Mexico to South America and the West Indies and is found in a wide variety of habitats from sea level to 1,500 m in elevation. In Panama it is known from most provinces and probably occurs in all of them.

Tournefortia maculata is distinctive, with its four-lobed fruits and glabrous leaves. The only other Central American *Tournefortia* with four-lobed fruit is *T. volubilis*, which differs in having sericeous leaves. These two belong to sect. *Cyphocyema* I. M. Johnston, a complex group of species centered in South America and characterized by four-lobed fruits and apically connate anthers.

Additional specimens examined. PANAMA. CANAL AREA: Río Abajo, *Bartlett & Lasser 16398* (GH, MO); low woods E of Bella Vista, a suburb of Panama City, *Maxon & Valentine 6942* (GH); Fort San Lorenzo, Fort Sherman Military Reservation, *Maxon & Valentine 7011* (GH); vicinity of Salamanca Hydrographic Station, Río Pequeni, 80 m, *Woodson et al. 1630* (GH, MO). CHIRIQUÍ: Boquete, 4,000 ft., *Davidson 853* (MO); Bajo Mona, mouth of Quebrada Chiquara, along Río Caldera, 1,500–2,000 m, *Woodson 1007* (GH). COCLÉ: between Las Margaritas and El Valles, *Woodson et al. 1279* (GH, MO). COLÓN: Santa Rita Ridge Road, 4 mi. from Transisthmian Highway to Agua Clara weather station, 500 m, *Gentry et al. 8835* (MO (2)); Santa Rita Ridge, ca. 5.5–6 mi. E of Transisthmian Highway, *Lewis et al. 5387* (MO); along Río Viejo, between the Portobelo Road and Quebrada Ruíz, 4 km NE of Puerto Pilón, 5 m, *Nee 7171* (MO). DARIÉN: Río Tuqueza below Quebrada Venado, *Bristan 1076* (MO); Cerro Pirre, 2,500–4,500 ft., *Duke & Elias 13665* (MO). LOS SANTOS: Loma Prieta, 800–900 m, *Duke 11879* (MO); Pocri, *Dwyer 1193* (MO); Guarare, *Dwyer 2469* (MO); Loma Prieta, Cerro Grande, 2,400–2,800 ft., *Lewis et al. 2241* (MO). PANAMÁ: Cerro Azul, Goofy Lake, *Dwyer 2412* (MO); San José Island, *Erlanson 114, 150, 241, 249, 379, 388, 501* (GH); Taboga Island, 0–25 m, *Pittier 3536* (GH); Cerro Jefe, 850–900 m, *Sytsma 1979* (MO); on road from Chepo to El Llano, *Tyson & Smith 4119* (MO), Isla Taboga, 0–186 m, *Woodson et al. 1474* (GH, MO). SAN BLAS: to Udirbi, El Llano–Carti Road, 200–350 m, *D'Arcy et al. 16037* (MO). VERAGUAS: along road between Santa Fe and Escuela Agricola Alto Piedra, 600–800 m, *Croat 26007* (GH, MO); Río de Jesus, *Dwyer 339* (MO); Isla de Coiba (Penal Colony), *Dwyer 2330* (MO); 5 mi. E of Santiago, *Tyson et al. 4284* (MO).

Tournefortia multiflora James S. Miller, sp. nov. TYPE: Panama. Veraguas: NW of Santa Fe, 8.8 km from Escuela Agricola Alto de Piedra, on road to Calovebora, elev. 1,900 ft., *S. Mori 6659* (holotype, MO 3386967). Figure 7.

Frutex vel arbor parva ad 5 m alta, ramulis glabris. Folia alterna sed saepe prope apices caulis conferta, paene sessilia vel in petiolis ad 2(–7) cm longis, suffultis; lamina elliptica, 16–50 cm longa, 8–18 cm lata, apice obtuso ad rotundato et saepe abrupta brevi-acuminato, base attenuata quasi glabra. Inflorescentia terminalis, paniculata,

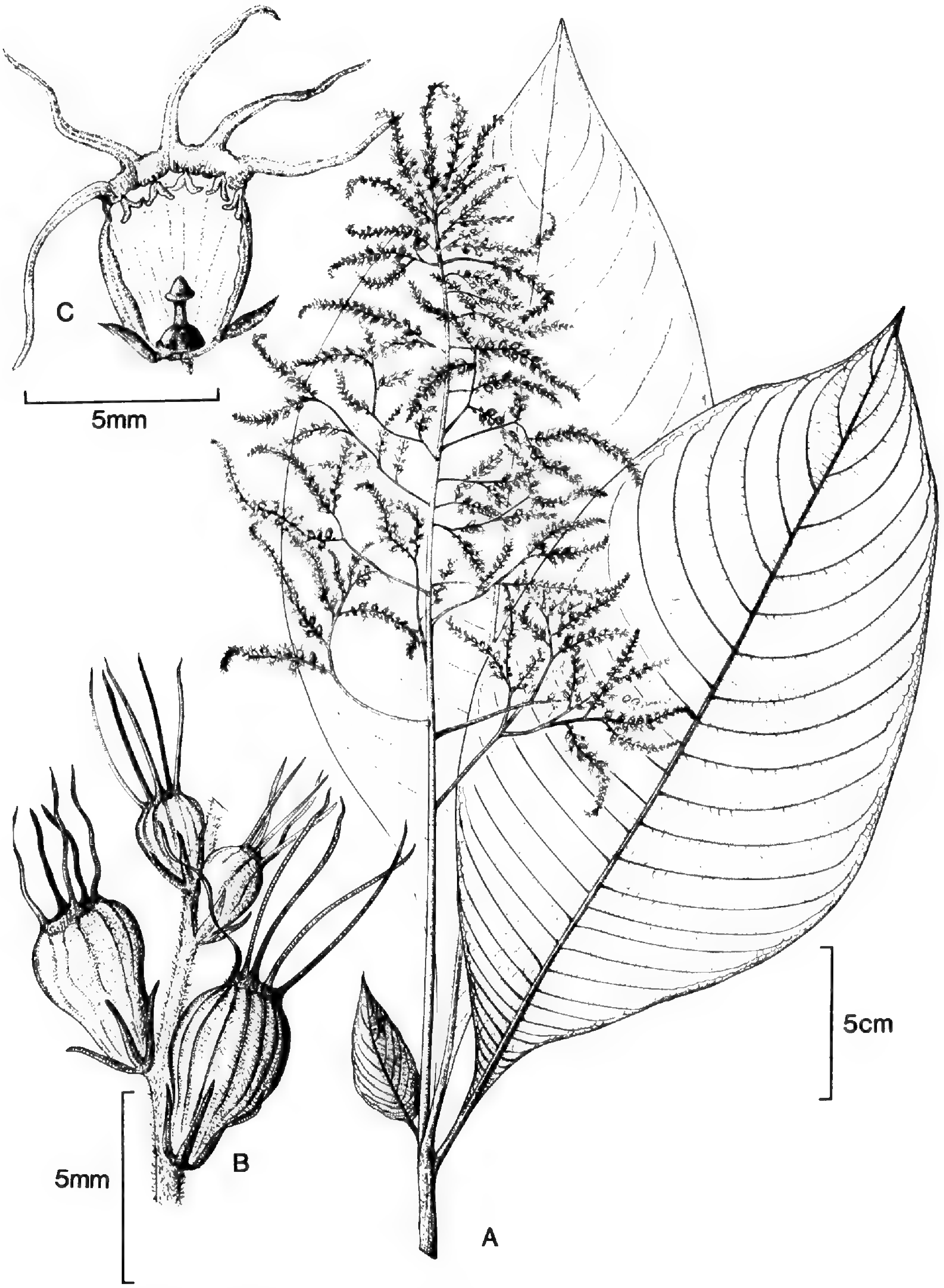

FIGURE 7. Tournefortia multiflora.—*A. Flowering branch.—B. Flowers.—C. Flower with corolla opened showing pendent anthers. From* Mori 6659 *(MO), Veraguas, Panama.*

20–40 cm longa, 16–30 cm lata, pedunculo 10–19 cm longo, fusco-puberulo. Flores sessiles, seorsum 2–5 mm dispositi; sepala 5, lanceolata, 1.7–3.2 mm longa; corolla viridi-alba, striis atroviridibus ornata, urceolata lobis patulis, pentameris, lobis linearibus, 3–4.5 mm longis, tubo 3.5–5 mm longo, extus puberulo; stamina 5, antheris conspicua bilobatis et in ore corollae tube pendentibus, 0.5–0.8 mm longis; stylus 0.5–1.6 mm longus, stigmate conoidi, puberulo. Fructus albi, ovoidei, 4.5–5.5 mm longi, 3–4 mm lati, glabro.

Shrub or small tree to 5 m tall, the twigs glabrous. Leaves alternate but often crowded near the stem apices, nearly sessile or on petioles to 2(–7) cm long; blade elliptic, 16–

50 cm long, 8–18 cm wide, the apex obtuse to rounded and often abruptly short-acuminate, the base attenuate, the margin entire, the adaxial surface essentially glabrous with widely scattered, short, appressed hairs, the abaxial surface glabrous, strigillose along the midrib and the 15–22 arcuate secondary veins, the tertiary and quaternary veins clearly evident. Inflorescence terminal, paniculate, 20–40 cm long, 16–30 cm broad, the peduncle 10–19 cm long, the peduncle and branches brown-puberulent. Flowers sessile, borne 2–5 mm apart; sepals lanceolate, 1.7–3.2 mm long, puberulent or strigillose to glabrous; corolla urceolate with spreading lobes, greenish white with darker green stripes, the lobes linear, 3–4.5 mm long, the tube 3.5–5 mm long, puberulent outside; stamens 5, the anthers distinctly bilobed and pendent in the mouth of the corolla tube, 0.5–0.8 mm long; ovary globose, 0.5–0.9 mm long, the disc crateriform, the style 0.5–1.6 mm long, the stigma conical, puberulent. Fruits ovoid, white, 4.5–5.5 mm long, 3–4 mm broad, glabrous.

Distribution. *Tournefortia multiflora* is known only from Panama, where it occurs in wet forest in the provinces of Veraguas and Colón from 400–900 m in elevation.

Tournefortia multiflora is distinctive with its large leaves to 50 cm long and unique in the genus in its large, many-flowered inflorescence, unusual striped flowers with linear corolla lobes, pendent anthers, and puberulent stigma. Despite these distinctions, it does have a gynoecium with a conical stigma and the two-lobed fruits that characterize the genus. It also has pollen grains that are similar to the majority of other species of *Tournefortia* (Nowicke & Miller, unpubl.). Johnston (1954) noted that pollen morphology seems to be a valuable generic character in the Boraginaceae, and, although unique in some characters, *T. multiflora* clearly falls within the morphological and palynological boundaries of the genus.

Additional specimens examined. PANAMA. COLÓN: Santa Rita Ridge trail, beyond end of Santa Rita Ridge Road (Panamanian Highway (R20D)), 17–35 km from Boyd–Roosevelt Highway, 400–800 m, *Mori & Crosby 6413* (MO). VERAGUAS: along Río Primero Braso, *Croat 25976* (MO); N of Santa Fe, 6.5 km from Escuela Agricola Alto de Piedra, *Mori & Kallunki 3067* (MO).

Tournefortia ramonensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 992. 1938. TYPE: Costa Rica. Alajuela: Los Angeles de San Ramón, Apr. 1928, *Brenes 6118* (holotype, F 851176; isotype, NY).

Shrub to 3 m tall, the twigs densely puberulent. Leaves opposite; petioles 13–28 mm long, densely puberulent; leaf blades widely ovate to lance-ovate, 8.9–15 cm long, 3.5–9 cm wide, the apex acuminate, the base acute and decurrent, the margin entire to unevenly dentate, the adaxial surface sparsely strigillose, the abaxial surface sparsely pubescent, lighter in color than above, the tertiary and quaternary veins clearly visible. Inflorescence terminal or axillary, a once- or twice-branched cyme, the branches 3–7.5 mm long, the peduncle 6–9 cm long, brown puberulent. Flowers sessile, borne 2–4 mm apart, bisexual; sepals lanceolate, ca. 6 mm long, strigillose; corolla tubular with spreading lobes, greenish white, the lobes ovate, 2 mm long, the tube 9.5 mm long, puberulent outside; ovary ovoid, 1 mm long, the disc crateriform, the style 4 mm long, the stigma pyramidal. Fruits broadly ovoid, white, 4–5 mm long, 3–4.5 mm broad, glabrous, the style often persisting.

Distribution. *Tournefortia ramonensis* is known only from high elevations in cloud forests in Costa Rica and the provinces of Bocas del Toro and Chiriquí in Panama.

Tournefortia ramonensis is distinctive in being one of only two Panamanian members of the genus with opposite leaves. The other, *T. johnstonii*, is a low shrub rather than a tree and has coarse velutinous twigs compared with the puberulent twigs of *T. ramonensis*.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Robalo Trail, northern slopes of Cerro Horqueta, 6,000–7,000 ft., *Allen 4919* (GH, MO). CHIRIQUÍ: vicinity of Bajo Chorro, 1,900 m, *Woodson & Schery 609* (GH (2), MO).

Tournefortia tacarcunensis A. Gentry & Nowicke, Ann. Missouri Bot. Gard. 64: 134. 1977. TYPE: Panama. Darién: Cerro Tacarcuna, west ridge, trail from summit camp to waterfall east of camp, 1,550–1,700 m, *A. H. Gentry & S. Mori 14114* (holotype, MO 2280271).

Low subshrub to 0.5 m tall, the twigs glabrous or nearly so. Leaves alternate; petioles 2–3 mm long, glabrous or nearly so; leaf blade elliptic to elliptic-ovate, 8.3–23 cm long, 3.2–8 cm wide, the apex acuminate, the base cuneate, the margin entire to unevenly undulate, the adaxial surface glabrous, the abaxial surface glabrous, much lighter than above, tertiary and quaternary veins obscure. Inflorescence terminal, a once- or twice-branched dichotomous cyme, the peduncle 2–6 cm long, brown-strigillose. Flowers borne 2–3 mm apart, bisexual; sepals lanceolate, 3.5–4.5 mm long, sparsely brown-puberulent; corolla tubular, white or greenish white, the lobes spreading, very widely ovate, rounded at the apex, 2–2.2 mm long, the tube 9–9.5 mm long; stamens 5, the anthers ovoid to lanceoloid, 1.3–1.5 mm long, sessile, inserted just below the mouth of the corolla tube; ovary globose to ovoid, 1–1.7 mm long, the disc scarcely evident, the style 6–7 mm long, the stigma conical. Fruits broadly ovoid, white, 4–6 mm long, 4–5.5 mm broad, glabrous.

Distribution. *Tournefortia tacarcunensis* is known only from Darién in Panama and Valle in Colombia in cloud forests of the Serranía del Darién above 1,500 m in elevation.

Tournefortia tacarcunensis is poorly understood, being known from only the type and a collection from adjacent Colombia, both from Cerro Tacarcuna. While it appears to be endemic in this region, this is one of the most poorly known areas of both Panama and Colombia.

Tournefortia urceolata James S. Miller, sp. nov. TYPE: Panama. Bocas del Toro: along continental divide from road branching N off main Fortuna–Chiriquí Grande Highway near continental divide, 1.1 mi. from main highway, ca. 1,200 m, *T. B. Croat & M. H. Grayum 60301* (holotype, MO 3386968). Figure 8.

Frutex ad 2 m altus, ramulis glabris vel fere glabris. Folia alterna, petiolis 8–32 mm longis; lamina lanceolata vel angusto-elliptica ad elliptica, (10.7–)13.5–31(–38) cm longa, (3.2–)4–14(–17.5) cm lata, apice acuminata, basi attenuata, glabris vel fere glabra. Inflorescentia terminalis, pyramidalis cymis parvis praedita, 13–28 cm longa, pedunculo (5–)9–21 cm longo. Flores sessiles vel in pedunculis brevibus ad 1 mm longis, seorsum 1–3 mm dispositis; sepala lanceolata, 3.5–5 mm longa; corolla viridis ad viridi-flava, tubularis ad urceolata lobis patulis, lanceolatis, 3–4 mm longis; antheris 1–2 mm longis, sessilibus, infra faucem fere ad medium corollae tubi insertis; stylus 1.7–2.5 mm longus, stigmate spinulo ad puberulo. Fructus late ovoidei, albi, 4–6 mm longi, 4–6 mm lati, glabri.

Shrub to 2 m tall, the twigs glabrous to brown puberulent. Leaves alternate; petioles 8–32 mm long, glabrous to brown-puberulent, the blade lanceolate or narrowly elliptic to elliptic, (10.7–)13.5–31(–38) cm long, (3.2–)4–14(–17.5) cm wide, the apex acuminate, the base attenuate, the margin entire, the adaxial surface glabrous, the abaxial surface essentially glabrous, strigillose along the major veins and papillose between them, the secondary veins 9–15, the tertiary and quaternary veins clearly evident. Inflorescence terminal, pyramidal, a panicle of small cymes, 13–28 cm long, the peduncle (5–)9–21 cm long, brown strigillose to puberulent. Flowers sessile or on short petioles to 1 mm long, borne 1–3 mm apart; sepals 5, lanceolate, 3.5–5 mm long, sparsely to evenly strigillose; corolla green to greenish yellow, tubular to urceolate with spreading lobes, 5-merous, the lobes lanceolate, 3–4 mm long, the tube 7–10 mm long, strigillose outside; stamens 5, the anthers lanceoloid, 1–2 mm long, sessile, inserted from just below the mouth to just above the middle of the corolla tube; ovary ovoid, 0.5–0.8 mm long, the disc scarcely evident to crateriform, the style 1.7–2.5 mm long, the stigma conical, spinulose to puberulent. Fruits broadly ovoid, white, 4–6 mm long, 4–6 mm broad, glabrous.

Distribution. *Tournefortia urceolata* is

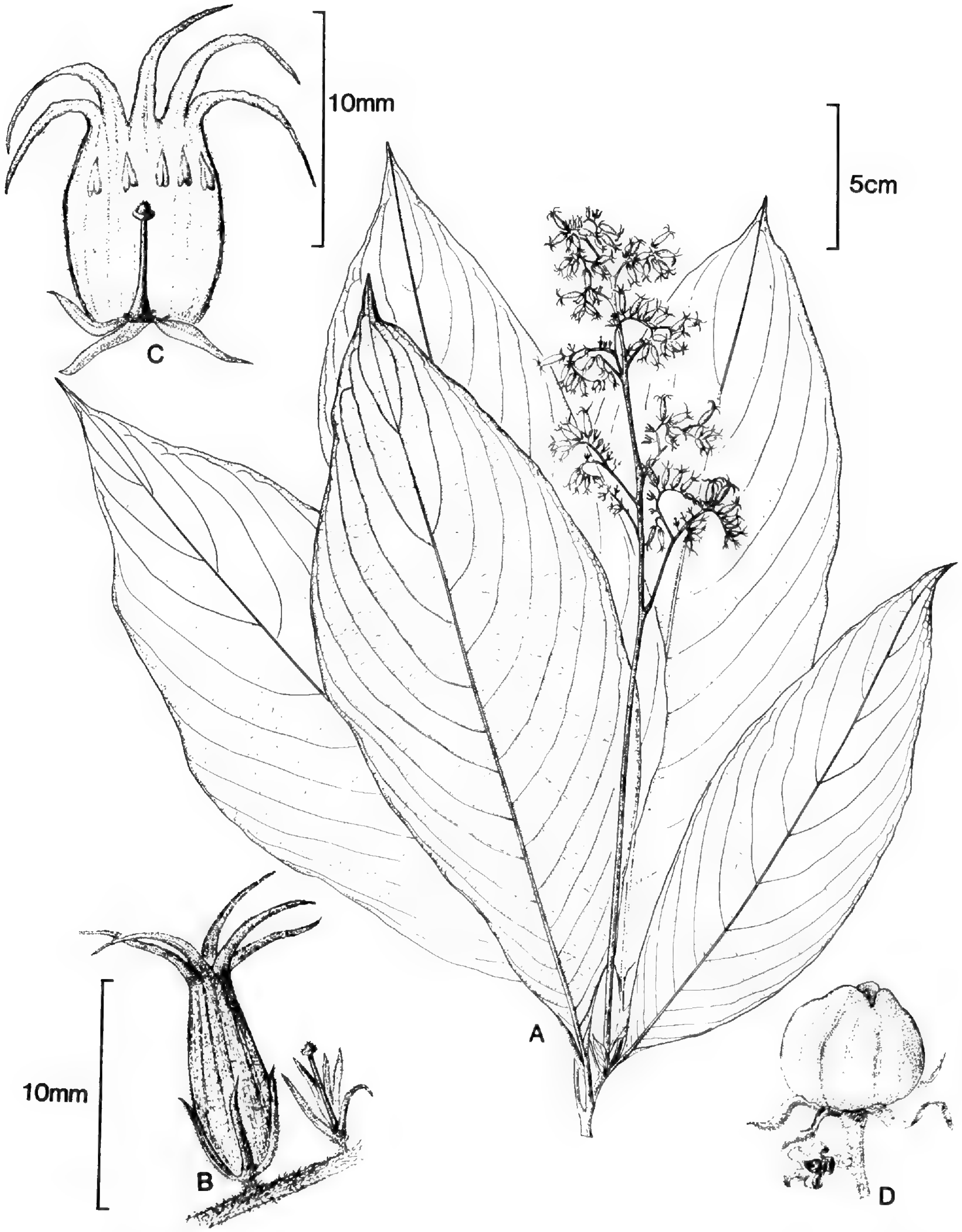

FIGURE 8. Tournefortia urceolata.—*A. Flowering branch.—B. Flower.—C. Flower with corolla opened.—D. Fruit. A–C from* Croat & Grayum 60301 *(MO), Bocas del Toro, Panama; D from* Croat 37301 *(MO)*.

known only from Panamá in Chiriquí, Colón, and San Blas, where it occurs in cloud forests at elevations of 400–2,300 m.

Tournefortia urceolata is distinct in its large glabrous leaves with relatively obscure venation and urceolate corollas. Vegetatively it somewhat resembles *T. glabra* but can be distinguished by its less prominent tertiary veins, sepals longer than 3 mm, and corolla longer than 7 mm.

Additional specimens examined. PANAMA. CHIRIQUÍ: Fortuna Dam area, on Kaolin hill, just N of reservoir, 1,100–1,400 m, *D'Arcy et al. 15919* (MO); forested slopes below divide ridge near Cerro Pate Macho, 6,200 ft., *Hammel 5817* (MO); Palo Alto, 4.5 mi. NE of Boquete, forest along western branch of headwaters of Río Palo Alto, 6,300 ft., *Hammel 7414* (MO); S slopes of Cerro Pate Macho, along Río Palo Alto, 1,300–1,800 m, *Knapp et al. 2077* (MO); ca. 0.5 km E of Cerro Pate Macho, headwaters of Río Palo Alto, 1,800–2,100 m, *Knapp et al. 2121* (MO); SE slopes and summit of Cerro Pate Macho, trail from Río Palo Alto, 4 km NE of Boquete, 1,700–2,100 m, *Sytsma et al. 4845* (MO). COLÓN: on Santa Rita Ridge Road, 17–35 km from Boyd-Roosevelt Highway, 400–800 m, *Mori & Crosby 6413* (MO). SAN BLAS: Cerro Brewster, headwaters of Río Cangandí, 2,300 ft., *De Nevers et al. 5500* (MO).

Tournefortia volubilis L., Sp. Pl. 140. 1753. TYPE: without locality or collector (holotype, LINN (Savage Catalog number 193.3), not seen; microfiche, MO).

Tournefortia floribunda Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 79. 1818. TYPE: Venezuela. Sucre: prope Cumaná (holotype, B-WILLD, not seen; microfiche, MO).

Tournefortia velutina Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 79, t. 201. 1818. TYPE: Mexico. Guerrero: Acapulco, *collector unknown 3863* (holotype, P, not seen; microfiche, MO).

Tournefortia potosina Standley, Contr. U. S. Natl. Herb. 23: 1230. 1924. TYPE: Mexico, San Luis Potosí: Tamasopo Canyon, 750 m, *C. G. Pringle 3518* (holotype, US 316801; isotype, CAS).

Woody vine or occasionally a small shrub, the twigs densely puberulent. Leaves alternate; petioles 4–8(–12) mm long, densely puberulent; leaf blade lanceolate to lance-ovate, (2.7–)5–7(–10.4) cm long, (1–)2–3.5(–5) cm wide, the apex acuminate, the base obtuse to rounded, the margin entire, the adaxial surface strigillose, the abaxial surface densely puberulent to nearly tomentose. Inflorescence terminal or internodal, a loosely branched cyme, the peduncle 3–16 mm long, the fertile branches 3–5(–10) cm long. Flowers sessile, borne 1–5 mm apart; sepals linear-lanceolate, 1.2–1.8 mm long, densely strigillose; corolla dull yellow or white to pale green, the lobes linear-lanceolate, ca. 1.5 mm long, the tube 2–2.3 mm long, densely strigillose outside; stamens 5, the anthers ovoid, 0.5–0.7 mm long, connate apically, sessile, inserted near mouth of corolla tube; ovary ovoid, 0.6–0.8 mm long, the stigma conical, exceeding the calyx lobes, elongate. Fruits distinctly 4-lobed, 2–3 mm long, glabrous, white with dark brown to black spots at the apex.

Distribution. *Tournefortia volubilis* is widely distributed in dry, disturbed areas from sea level to 600 m in elevation from Mexico throughout Central America to Panama, and is found in the West Indies. In Panama it is known only from the provinces of Los Santos and Panamá.

Tournefortia volubilis is a member of the complex sect. *Cyphocyema* I. M. Johnston, a group centered in South America. It differs from the only other Central American species of the section, *T. maculata,* in having pubescent leaves (discussion under *T. maculata*).

Additional specimens examined. PANAMA. LOS SANTOS: Monagre Beach, *Dwyer 4182* (MO (2)). PANAMÁ: Coronado Beach, 6 mi. E of San Carlos, *Croat 14261* (MO); near Playa Río Mar, 10–100 ft., *Duke 11761* (MO).

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THE GENUS *XYRIS* (XYRIDACEAE) IN VENEZUELA AND CONTIGUOUS NORTHERN SOUTH AMERICA[1]

Robert Kral[2]

ABSTRACT

This work is a taxonomic treatment of those species of Xyris *(Xyridaceae) now known to occur in Venezuela and contiguous northern South America, including parts of Brazilian Amazonia. A general discussion of the morphology of* Xyris *is given, particularly as to the construction of the inflorescence and flower. Problems with the previously accepted sections of* Xyris *are stated; it appears that the major distinguishing feature for these sections (placentation type) breaks down when Guayanan material is studied. The taxonomy is done for 87 species (14 newly described), including 4 subspecies (one newly described) and 7 varieties. Synonymy and full descriptions are presented, along with diagnostic keys. Nearly all taxa are illustrated with full plates.*

The first comprehensive treatment of *Xyris* of the Guayana Highland was authored by Dr. Bassett Maguire of the New York Botanical Garden and Dr. Lyman B. Smith of the Smithsonian Institution (Botany of the Guyana Highland V, *Memoirs of the New York Botanical Garden* 10: 8–72. 1963). That excellent work has provided a basis for this supplemental study, which includes new information on species already described and descriptions of several new *Xyris*. Also, the coverage is extended to include Andean species from western Venezuela and Colombia as well as those from the Guayanas to the east and the contiguous territories of Brazil. Useful sourceworks for this have been: J. M. Idrobo, "Xyridaceas de Colombia," *Caldasia* VI(29): 185–245. 1954; J. Lanjouw, Xyridaceae *in Flora of Suriname* I(1): 225–244. 1966; L. B. Smith & R. J. Downs, Xyridaceae *in Flora Brasilica* IX(11): 1–211 + index. 1968; L. B. Smith & R. J. Downs, "Las especies Peruanas de la Familia Xyridaceae," *Publicaciones del Museo de Historia Natural "Javier Prado," Serie B. Botanica* (15)1–13, + figs. 1963.

As was stated by Maguire & Smith (l.c.), Brazilia, to the south of the Amazon, and Guayana, to the north, comprise the two largest centers for *Xyris* in the world; each major area has large numbers of endemics, with new ones being discovered on any major expedition into these regions. The authors continue:

> It is suggested that *Xyris* in South America, with its present bicentric distribution, may have occupied at one time an essentially identical and continuous area, and that in subsequent history, by the intervention of the Amazon Basin, the original area became divided, and that since then a parallel evolution has proceeded without appreciable interchange.

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[1] *Many hundreds of specimens have been examined in the preparation of the work and I acknowledge the assistance of curators and staffs of F, GH, K, L, MO, NY, P, U, and US who kindly made loans and facilities available. I could not have done the work were it not for Dr. Lyman B. Smith, who provided me the opportunity to undertake the project in the first place, who reviewed descriptions of most of the new species, and who is therefore coauthor of them; Dr. Otto Huber, ecologist and authority on the botany of tropical American savanna, who has provided specimens for study, who led me to a grand, albeit short, trip into the Yapacana savannas, and who has provided friendly criticisms along the way; and Dr. Julian A. Steyermark, whose experience with and knowledge of Venezuelan botany is unsurpassed, and who has made specimens and information available. To all of the above I am deeply grateful. Special thanks are due to Dr. George Rogers, Editor, and to Ms. Janice Wilson, Editorial Assistant, for their patient, thorough, and tactful processing of my work. Their constructive editing has much enhanced the study, and is therefore very gratefully acknowledged.*

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ANN. MISSOURI BOT. GARD. 75: 522–722. 1988.

My observations in no way conflict with the above. I can only add that, since the addition of the monotypic *Aratitiyopea* by Steyermark (*Ann. Missouri Bot. Gard.* 71: 298–300. 1984), there are now five genera known for the Xyridaceae, all occurring in, if not solely confined to, the Venezuelan Guayana, with the greatest diversity being in the high sandstone tepuis of the region. *Xyris* is by far the largest of the five. At the rate new species are now being found it will probably well exceed 300 species worldwide. Prior workers have organized these into three subgenera, namely *Pomatoxyris* Endl. with ca. 20 species, Australian, distinguished by axile placentation; *Xyris* (*Euxyris* Endl.) with ca. 100 species, pantropic and North American, distinguished by marginal or parietal placentation; and *Nematopus* Seub., with probably more than 200 species, mainly South American and distinguished by basal or free-central placentation. In dissecting ovularies of Guayanan xyrids preparatory to describing them, I discovered that many of these species, placed by prior workers in *Nematopus*, actually have axile placentation or are transitional from axile, this evidenced by the presence of complete or partial septa in the ovary and fruit. Out of slightly more than 80 taxa studied, 33 show evidence of some septation; some show completely axile placentation.

I suggest that sectionalization of *Xyris* based on mode of placentation perhaps does not reflect the real situation and that there appear to be no other solid characters by which to place species within sections or subgenera consistently. Certainly the sections are arbitrary. Alternatives would be to put the more than 30 Guayanan species with partial or complete septation into *Pomatoxyris*, a perhaps more realistic alternative, even though it eliminates the geographic integrity of that section. Another would be to dispense with *Pomatoxyris*, since subgenus *Xyris*, even as represented in the southeastern United States, may show transition from axile to parietal placentation (*X. elliottii* Chapman, *X. baldwiniana* Schultes, *X. brevifolia* Michaux); therefore, the limits of section *Xyris* could be amplified to accommodate the situation. A third alternative, namely to eliminate the sections altogether, would in my view be best, in that mode of placentation has been nearly the entire basis.

In any event, it would appear that in regard to a phylogeny the Guayana Highland show the greatest diversity in xyrids, with placentation in all genera except *Xyris* wholly axile. It seems that distichous-leaved xyrids with axile placentation have evolved from polystichous-leaved ancestors with axile placentation, at least if Abolbodaceae are to be considered as part of Xyridaceae, a generally accepted classification based on the sound anatomical analyses of Carlquist and others. That being so, *Xyris* may have had its origin in the Guayana Highland.

No further introduction is needed here save to relate what appears to be the basic morphology in *Xyris*.

Species of *Xyris* are mostly high hydroperiod, rosulate plants of acid boggy sites, their alternate, equitant, distichous, lineal leaves approximate and arising from contracted or elongated stems or from scaly rhizomes; some rise from bulbous axillary offshoots; the roots are simple and fibrous (Fig. I).

Leaves are highly variable in structure but are similar to those of *Iris*. The leaf base is open-sheathing, the sheath edges broad and thin, often scarious or hyaline, and entire or variously ciliate; the sheath base is frequently abruptly orbicular-dilated, this most obvious in species with bulbous bases. Above the clasping sheath base, the sides narrow abruptly or gradually to the blade, there converging and merging with it as the ventral margins close. At this point there may be a simple transition to the inner margin of the blade (most species), or the transition may be abrupt, with a ligule of various proportion being produced (Fig. IIb, c). Often in ligulate species the inner edge of the leaf blade may show a strong sulcus or groove for some distance above this junction (Fig. IIc). The leaf blade then shows a convergence of leaf sheath edges to form either a set of ventral edges (as in sulcate-bladed

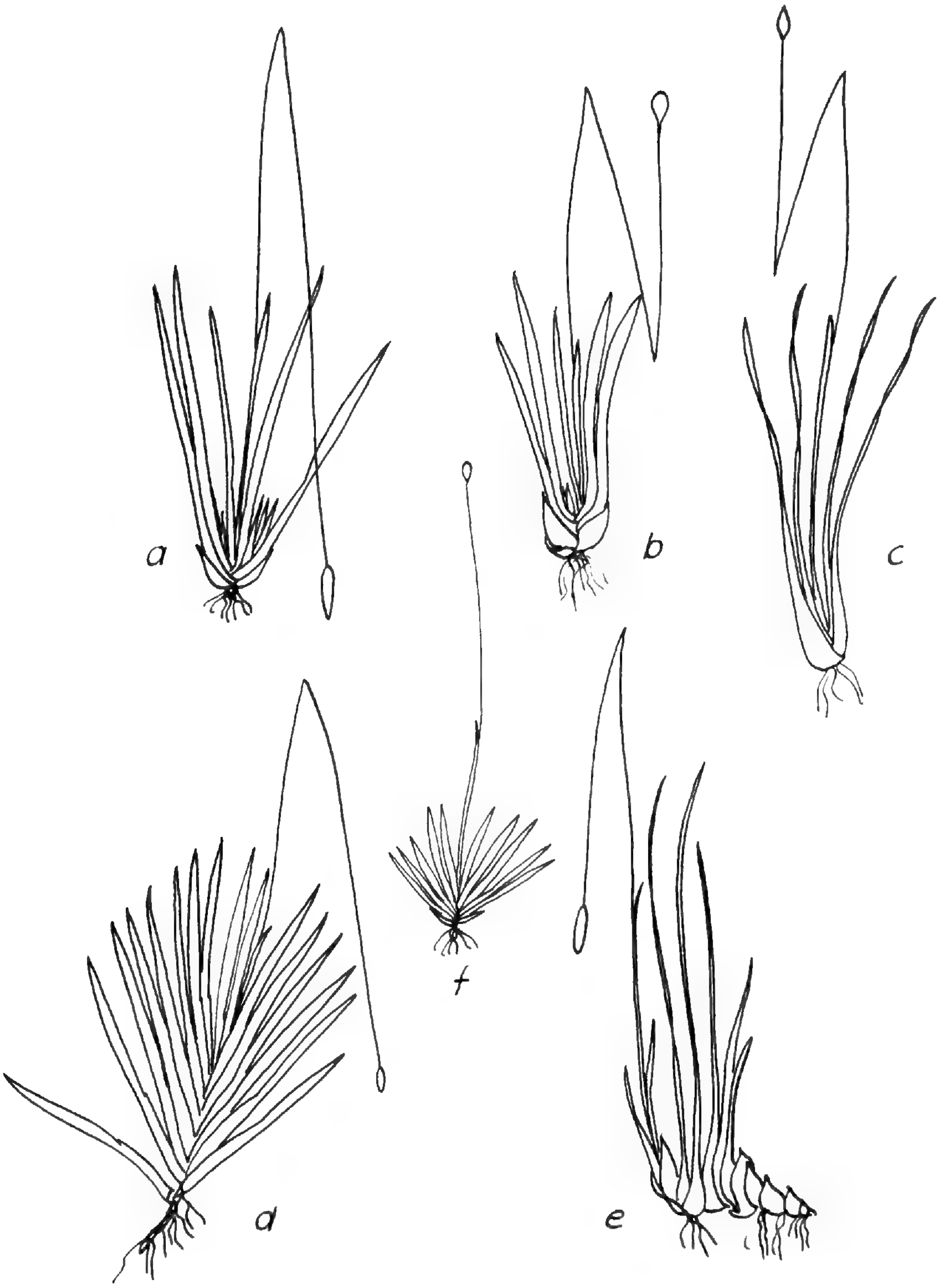

FIGURE I. *Sketches of some common habits in* Xyris.—*a. Base soft, leaves flattened, sheaths keeled.*—*b. Base bulbous, sheaths fleshy-based, blades curvate, flattened.*—*c. Base elongate-bulbous, sheaths firm, blades flexuous and twisted.*—*d. Plant caulescent and rhizomatous, leafy shoots frondlike.*—*e. Plant stout-rhizomatous.*—*f. Annual, leaves spreading flabellately; scape sheaths longer than principal leaves.*

species), or the ventral edges have joined into a single, compound-traced, ventral edge (Fig. IIa). Much *Xyris* taxonomy centers around the characters of the leaf sheath and blade, which tend to be more consistent than most, outside of flower and fruit features. For example, *Xyris* leaf blades may be terete or angulate or flattened; their tips may be extremely varied, with everything from emarginate to conic-subulate, even setiform; their edges and borders are incrassate to thin and variously pubescent or totally smooth; the

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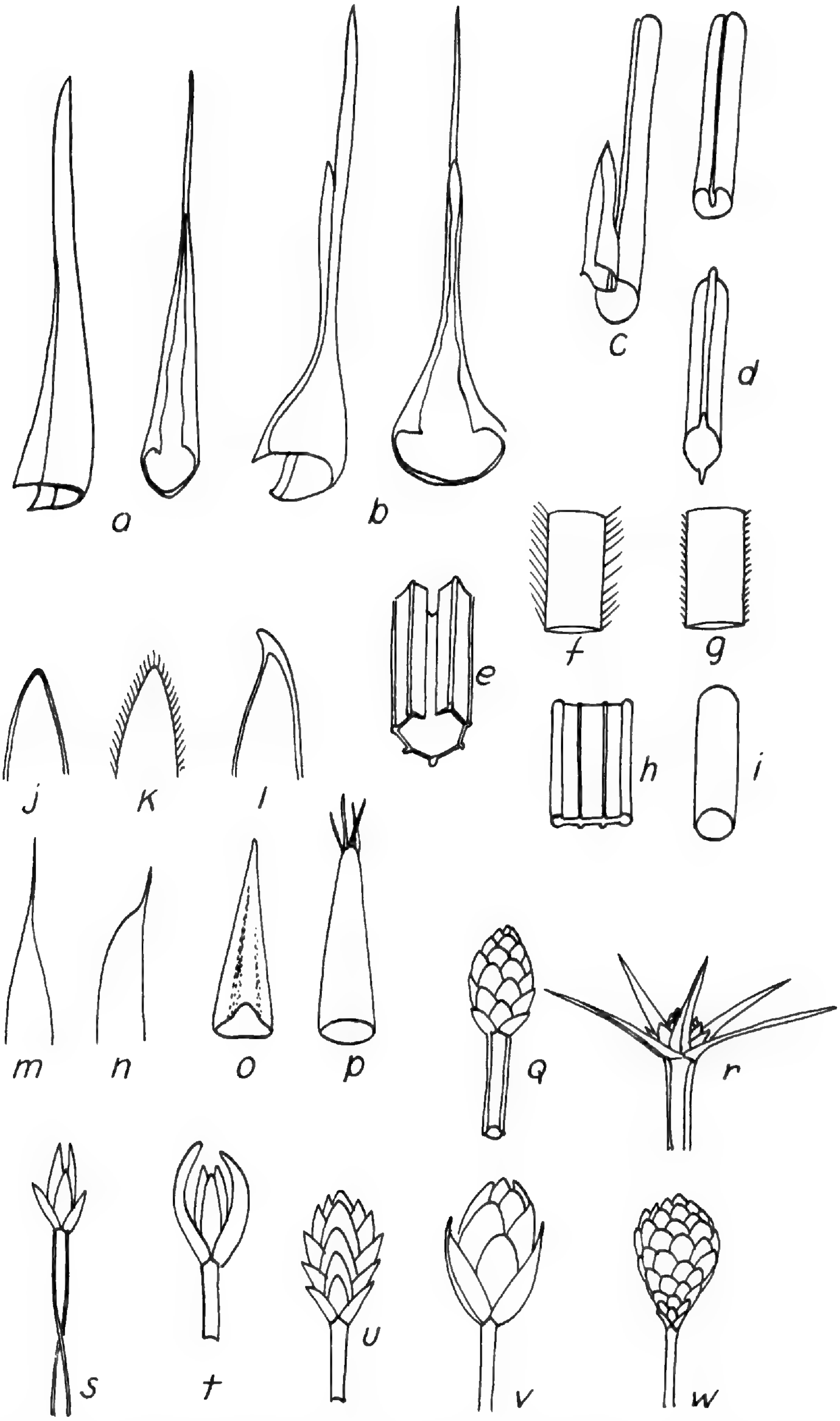
FIGURE II. *Leaves, spikes, and upper scapes.*—*a. Side and ventral views of leaf with sheath gradually dilated to base, eligulate, blade flattened.*—*b. Side and ventral views of leaf with sheath abruptly dilated at base (a bulbous type), ligulate, blade flattened.*—*c. Sector of leaf at junction of ligule and blade, blade subterete, with*



ventral sulcus.—d. Sector of leaf blade, this subterete and bicostate.—e. Thin, involute, multicostate blade.—f. Sector of flattened, ciliate leaf blade.—g. Sector of flattened, scabrid leaf blade.—h. Sector of flattened leaf blade with incrassate edges.—i. Sector of terete leaf blade.—j. Acute, incrassate-edged leaf apex.—k. Acute, ciliate leaf apex.—l. Acuminate, incrassate-edged, incurved leaf apex.—m. Acuminate, spinulose-tipped leaf apex.—n. Asymmetrically spinulose-tipped, acute leaf apex.—o. Trigonous-acute leaf apex.—p. Leaf apex narrowly and bluntly conic, trichomiferous.—q. Ovoid spike with spirally imbricate bracts (commonest type with little bract gradation); scape subterete, bicostate.—r. Broadly ovoid spike, sterile bracts involucrate, scape ancipital.—s. Spike biflorous, decussate, scape flattened, incrassate-bordered, twisted.—t. Spike biflorous, decussate, lowest bracts exceeding spike, incurvate.—u. Spike ellipsoid, bracts decussate, 5-ranked, little graded.—v. Spike ovoid, bracts spirally imbricate, lowest pair of bracts distinctly longer than the fertile bracts.—w. Spike obovoid, sterile bracts many, grading gradually into the fertile bracts.

surfaces are variously pigmented, smooth to variously rugose, with raised or sunken or flush stomates, or even quite pubescent (Fig. IId–p). Most of such external characters have long been noted in the literature, particularly by G. O. A. Malme, A. Nilsson, M. Seubert, and others in the late 19th and early 20th centuries.

Xyris plants have scapes arising in axillary fashion enfolded in closed-based, distally open and bladed scape sheaths. The scapes are also quite diverse, usually terete and solid basally and variously multicostate. Distally they vary the most, from terete and ecostate to multicostate, variously flattened, even ancipital; they range from smooth to variously scabrid or ciliate, particularly on the costae (Fig. IIq–w).

Usually the scape terminates in a single spike (most exceptions being either the Guayanan *X. bicephala* Gleason or anomalous examples). The spike is mostly conelike with either spirally or decussately imbricate bracts. Subsections have been developed on the character of the bracts. One direction of evolution has been toward species with the lower bracts elongate, even leaflike (*X. cipoensis, X. hystrix, X. involucrata, X. uleana*, etc.) with the fertile bracts much shorter and abruptly reduced. Another is toward sterile bracts few at the spike base, somewhat larger than the fertile bracts and transitional to them. A third trend has been for sterile bracts to be many, the lowermost very small, gradually passing into the larger fertile ones. The commonest condition is for there to be a few sterile bracts somewhat smaller than the spirally imbricate fertile ones. Significant also is a bract zone that may run the length of the midbract or be variously apical, the dorsal area. Doubtlessly homologous to the leaf blade in *Xyris*, this is frequently photosynthetic and is mostly distinctly different from the usually chaffy bract matrix. As mentioned above, some bracts in *Xyris* are elongated and may have blades, and when this is so, such are mostly extensions of dorsal area tissue, or at least of midrib tissue (Fig. IVa–h). Bracts on yet other species may lack a dorsal area, and a few species may be versatile in this character. Some examples of *X. tenella* Kunth have bracts with and others without dorsal areas on the same plant, or may have them on the sterile bracts but lack them on the fertile ones. Backs of bracts also vary considerably, from rounded-convex and ecostate (carinate) to strongly folded, navicular, or costate, while the usually thin edges vary from strongly bordered and variously ciliate, lacerate, or fimbriate to entire.

In the axils of the fertile bracts the flowers are solitary, the axis of the indeterminate inflorescence being contracted and headlike or conelike, or quite elongate (as in *X. stenostachya* Steyerm., the most extreme). These flowers are conspicuous at anthesis, usually but a few hours for a single bloom, a given spike producing usually only one or two flowers simultaneously (in the species with contracted spikes several flowers may be open at once, e.g., *X. involucrata* Nees).

A dissection of the flower bud just prior to its expansion is the best approach to understanding the *Xyris* flower (Fig. IIIa–f). The usual *Xyris* bud is narrowly obovoid and planoconvex. There are three sepals. The lateral sepals are boatlike, their keels directed outward, their concave sides clasping the edges of the compressed corolla bud as well as the edges of the inner (dorsal) sepal, which forms a cap over the corolla with its two edges overlapping on the ventral side. The lateral sepals (Fig. IVl, m) are the bonanza for xyridologists in that they vary little from biotype to biotype in a species. In most cases they are free; in fewer instances they are connate;

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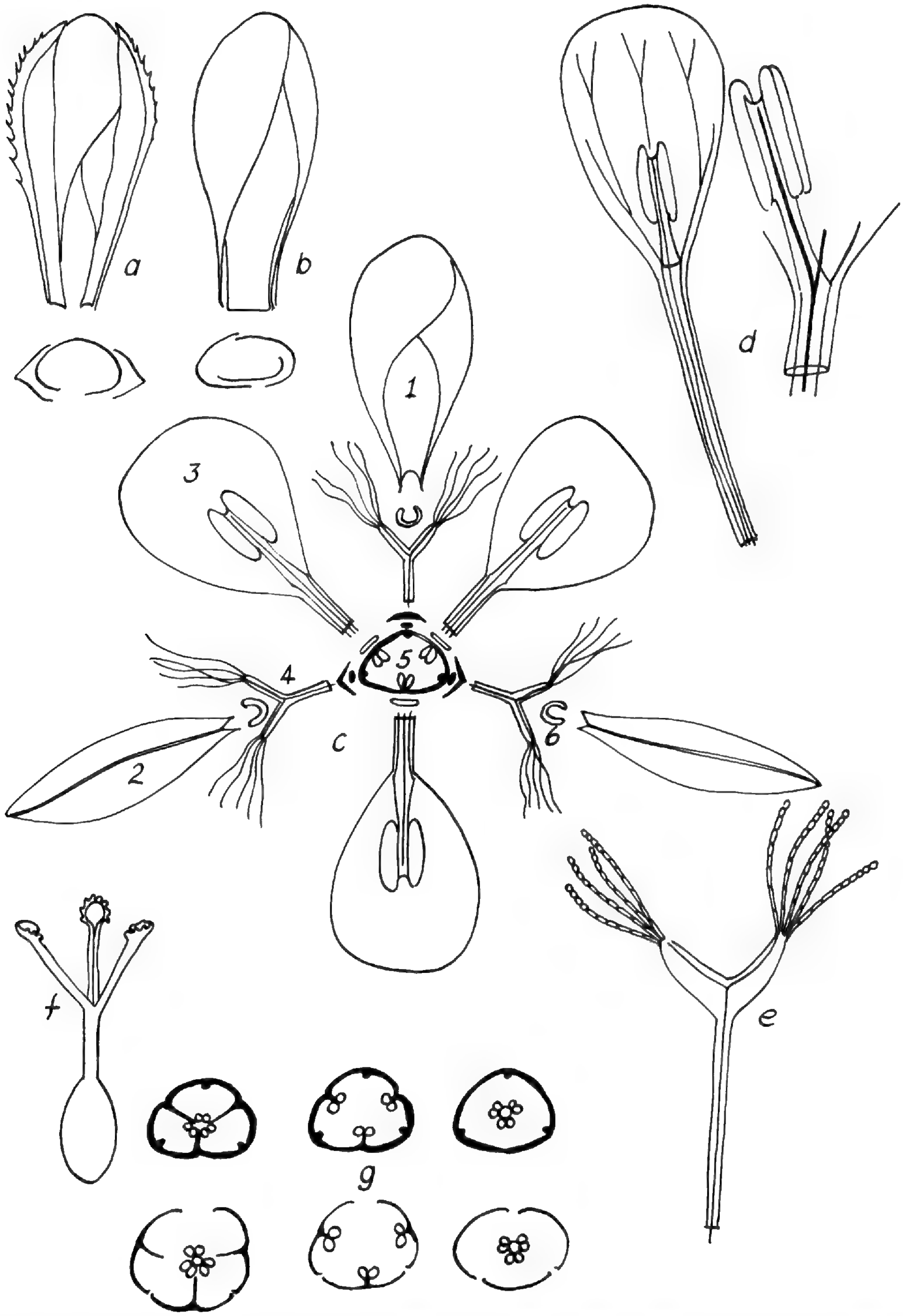
FIGURE III. *Flower and fruit structure.—a. Ventral and cross-sectional view of sepals in bud, lateral sepals enfolding inner (dorsal) thin sepal.—b. Ventral and cross-sectional view of petals in bud, lateral petals enfolding ventral petal.—c. "Exploded"* Xyris *flower. 1. disarticulated dorsal sepal; 2. lateral sepals; 3. petal blades (claws foreshortened) with adnate stamens; 4. staminodia, claws foreshortened, showing flattened, bifurcate*



blades and terminal tufts of trichomes; 5. cross section of flower toward base as parts are oriented in bud, placentation parietal; 6. stylar apex, showing horseshoelike stigma pattern at about level of staminode tip.—d. At left petal blade, claw, adnate stamen (note 3 traces in claw); at right an upper sector of petal claw, oblique view showing branching of median claw trace: one branch into filament base, the other forward into mid-base of petal blade.—e. Staminode showing yokelike blade, bifurcated trace, and moniliform staminodial beard hairs.—f. Gynoecium, showing style base, tubular style branches, and stigmas.—g. Placentation types. Left rank: above—axile placentation in ovary; below—cross section of dehiscing fruit showing septa pulling away from axis. Middle rank: above—parietal placentation in ovary; below—cross section of dehiscing fruit. Right rank: above—central placentation in ovary; below—cross section of dehiscing fruit, valves lacking septa.

very infrequently they may be free toward a spike base, increasingly connate toward that spike apex (e.g., the *X. thysanolepis* complex). The sides of a lateral sepal are mostly very thin; in some cases they are equal or approximately so, and the sepal is equilateral; in fewer instances they are inequilateral (Fig. IVi, j). In all cases the sepal has a midrib (costa or carinal keel) that usually conforms with the angle of the sepal fold; in some cases this keel is thick and firm, made up of many strands of cells oriented longitudinally and breaking outward. The crest of such keels may range from entire to variously scabrid or ciliate (Fig. IVl). In other cases the keel may be produced into a sheet of cells one layer thick, its border made up of simple or compound strands of cells, these forming a lacerate or fimbriate outline (Fig. IVm). The best stage for seeing these characters comes after mature fruit has just formed and the sepals are hardened to produce a typical border.

At anthesis the outer (dorsal) sepal abscisses, falling away calyptralike as the corolla expands (Fig. IIIa). In the bud, the anterior (inner) petal is enfolded by the right (observing the bud from the adaxial side) edge of the left lateral petal and is enfolded by the left edge of the other lateral petal, the right edge of which overlaps the right side of the ventral (inner) petal (Fig. IIIb). All petals are roughly equal in size and usually separate to the base. Each has a long claw and a broad, usually yellow (in Africa there are blue-flowered species) spreading blade, this of a distinctive outline and apical border. There are three functional stamens adnate along the length of the claw. What appear to be three traces run the length of the claw, but the median trace is compound, branching at the blade base, the adaxial branch departing into the divergent filament base and going up into the anther connective (Fig. IIId), the dorsal branch supplying the middle of the petal blade.

Xyris anthers are mostly tetrasporangiate and bilocular, variously separated by a flattened connective, usually bifid distally, and sagittate proximally; their dehiscence is longitudinal, either lateral or extrorse. Alternating with the petal claws and slightly inside them is a whorl of three staminodes in most *Xyris* flowers (in a few these are reduced to nubs of tissue at the floral base or are totally absent, e.g., *X. savanensis* Miq.). The staminode is usually made up of an elongate slender claw about as long as the petal claw, and a yokelike flattened blade wherein the single trace bifurcates, tailing out toward the spreading staminodial branch tip, where there are usually borders of slender, moniliform hairs. The character of the cells making up the beard hairs deserves more attention than it has gotten heretofore and may well be reliable to determine complexes of species (Fig. IIIc-4, e). The ovary is superior, the style tubular, branching midway into three subequal branches whose involute edges are pollen receptive distally. Placentation varies; in most *Nematopus* it is either plainly basal with a brush of long funiculi or free-central with shorter, ascending funiculi. In other *Xyris* the placentation is plainly parietal or appears marginal. But in a significant number of Guayanan species it may be axile and the ovary distinctly trilocular, or it may be axile toward the base and parietal upward in the ovary, or the septa may pull away so that the axis is left with the ovules (Fig. IIIg).

The fruit is usually thin-valved, though there are some definite exceptions in which the walls are hard. Dehiscence is loculicidal along the dorsal side of the carpel.

The seeds may be few or very numerous, diverse in shape and size, 0.3–5 mm long. The outer integument is usually raised into a variously longitudinally ribbed, sometimes also cross-lined surface which is specific in character; distally it may form an empty ribbed beak or it may separate into a crown of narrow scales (e.g., *X. teinosperma* Idrobo & Smith). The contents of the seed are a starchy and proteinaceous, translucent or farinose endosperm and a small basal–lateral embryo.

The type for the genus is *Xyris indica* L. This was based by Linnaeus on an east Indian element and a North American element. J. E. Smith (*Rees' Cycl.* 39. 1818) designated

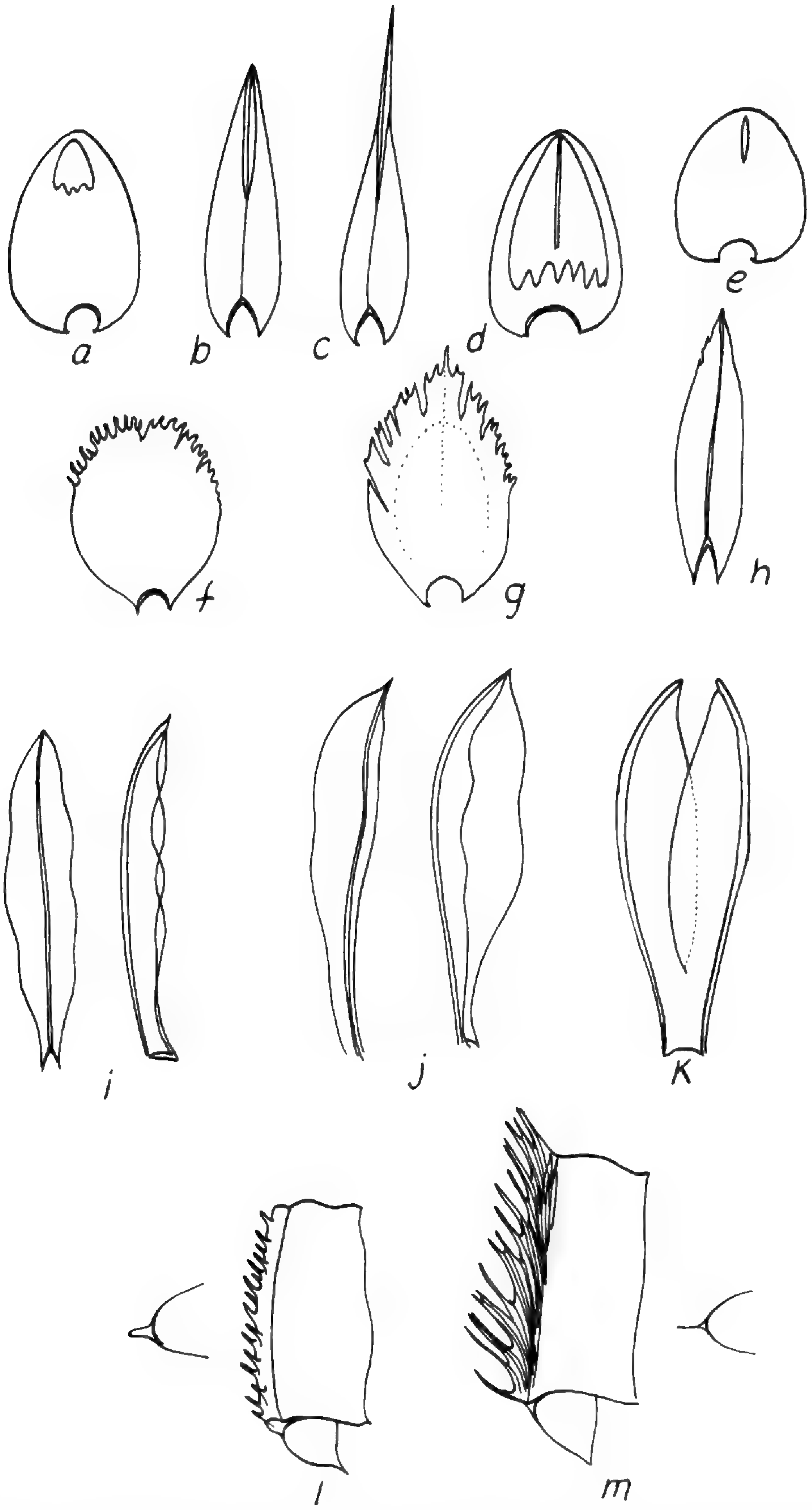


FIGURE IV. *Bract and lateral sepal types.—a. Ovate bract with ovate, subapical dorsal area.—b. Lanciform bract, keeled, with elliptic-linear dorsal area.—c. Lanciform bract, keeled, bladed, the blade comprising a cusp and dorsal area.—d. Ovate bract, mostly dorsal area, the convex bract medially-apically carinate.—e. Broadly ovate bract with narrow, subapical dorsal area.—f. Broadly obovate bract, border thin, lacerate; dorsal area lacking.—g. Broadly elliptic bract, border thin, laciniate, friable; dorsal area lacking.—h. Lanceolate bract, keeled; dorsal area lacking.—i. Dorsal and lateral views of lateral sepal, this oblong-elliptic, equilateral, slightly curvate, with narrow, thick, entire keel.—j. Dorsal and lateral views of lateral sepal, this oblanceolate, inequilateral, with narrow, thick, entire keel.—k. Connate lateral sepals.—l. Midsector of lateral sepal showing thickened, scabro-ciliate keel.—m. Midsector of lateral sepal showing thin (made up of a single layer of cells), ciliate-fimbriate keel.*

the Indian element as *X. indica* while using the North American element for *X. torta* Smith.

In the key below, the characters are based on principal leaves from healthy plants, spikes at seeding time, lateral sepals at seeding time, and on mature fruit and seed. Any attempt to determine sterile or depauperate material, or specimens with immature flowers, fruit, or seed is virtually impossible in a group of this sort.

The key below applies primarily to the *Xyris* of Venezuela, Colombia, and the Guianas. Some taxa discovered in contiguous Brazil, if in habitat likely to be found in Venezuela and the Guianas, are likewise included.

The key applies to healthy material with normally developed, seeding spikes. Principal, not juvenile, leaves are to be used. Overlaps in variation—particularly in trichome characters, lateral sepal and dorsal area color or accrescence, and plant pigmentation—often have necessitated the same species coming out in two or more leads.

KEY TO *XYRIS* OF GUAYANA AND AMAZONIAN NORTHERN SOUTH AMERICA

I. Placentation evidently marginal or parietal, the capsule valves on dehiscence retaining placentae and seeds .... Section *Xyris* (conventional)

II. Placentation free-central or basal or apparently axile, capsule valves on dehiscence with or without septa, but not retaining seeds .... other *Xyris*

I. Section *Xyris* (conventional).

1a. Keel of lateral sepals at least in part lacerate or irregular.

2a. Seeds fully 1 mm long; dorsal area venose and/or midnerve conspicuous; scapes terete distally with (usually) 3 or more strong costae, occasionally multistriate; leaf sheath sometimes long-ciliate.

3a. Principal foliage leaves longer than scape sheaths; spike bracts when dry inrolling and excurving, all with tips lacking tufts of long trichomes .... 1. *X. fallax*

3b. Principal foliage leaves poorly developed, exceeded by scape sheaths; spike bracts when dry not excurving, the lower ones with apical tufts of slender trichomes .... 6. *X. brachyfolia*

2b. Seeds 0.4–0.8(–0.9) mm long; dorsal area not venose or costate as in above; scapes seldom more than bicostate; leaf sheath never ciliate.

4a. Plant base strongly tinged with red or purple; scapes ecostate distally or with costae smooth; seeds fusiform or narrowly ellipsoid, mostly opaque, dark-ribbed, farinous, 0.7–0.9 mm long; plants perennial .... 2. *X. laxifolia*

4b. Plant base greenish, stramineous, dull brown or tan; scapes always with 1–2 (rarely a few more) costae, these usually papillose or scaberulous; seeds ovoid or broadly ellipsoid, amber, translucent, 0.4–0.7 mm long; plants annual .... 3. *X. jupicai*

1b. Keel of lateral sepals either ciliate or entire.

5a. Lateral sepals with keel ciliate; bracts dark dull brown, at maturity strongly spreading, the dorsal area unkeeled, paler but indistinct .... 4. *X. navicularis*

5b. Lateral sepals with keel eciliate, entire; bracts pale greenish tan, lustrous, the indistinct dorsal areas strongly keeled .... 5. *X. anceps*

II. Other *Xyris*.

1a. Margins of leaf sheaths entire.

2a. Plants mostly densely cespitose, evidently perennial; leaf sheaths hard, lustrous, castaneous to reddish brown, usually in strong contrast to leaf blades both in color and texture.

3a. Leaf blades not flattened or 2-edged, for most of their length either terete or very thickened and deeply ribbed and sulcate; ligules prominent, abruptly narrowed to blades.

4a. Dorsal area distinguishable.

5a. Plant bases nearly black .... 7. *X. neblinae*

5b. Plant bases deep brown, pale brown, or reddish brown.

6a. Mature spikes mostly over 1.5 cm long, fusiform or distinctly broadest above middle; leaf blades at least 1 mm thick .... 8. *X. juncifolia*

6b. Mature spikes mostly under 1.5 cm long, ovoid to cylindrical or subglobose; leaf blades less than 1 mm thick.

7a. Bract edges densely pale-villose; plants lacking stout, scaly rhizomes .... 9. *X. lanulobractea*

7b. Bract edges not densely pale-villose; plants with short, stout, ascending, scaly rhizomes .... 10. *X. terrestris*

4b. Dorsal area imperceptible.

8a. Leaf blades and upper sheaths coarsely ribbed and sulcate; sheath bases brown (bases of blades and apices of sheaths mostly rose-purple) .... 11. *X. scabridula*

8b. Leaf blades not deeply ribbed and sulcate; sheath bases (usually tips also) nearly black .... 12. *X. atriceps*

3b. Leaf blades flattened, for most of their length 2-edged, the edges either thickened or sharp; ligules evident or not.

9a. Dorsal area evident.

10a. Scapes strongly flattened, at least 2–2.5 mm broad distally, ancipital.

11a. Several bracts leaflike, forming an involucre .... 13. *X. involucrata*

11b. No bracts leaflike.

12a. Scapes bispicate; seeds under 2 mm long .... 15. *X. bicephala*

12b. Scapes unispicate; seeds over 2 mm long .... 16. *X. teinosperma*

10b. Scapes distally round or if strongly flattened distally not as wide as 2 mm there, not ancipital.

13a. Lowermost sterile bracts distinctly shorter than the fertile ones and grading gradually into them.

14a. Leaf blade edge cartilaginous-thickened, entire or ciliolate; bract borders pale villosulous (low-elevation savanna) .... 17. *X. lomatophylla*

14b. Leaf blade edge not cartilaginous-bordered, smooth; bract borders not pale villosulous, sometimes sparsely short-brown ciliolate .... 18. *X. contracta*

13b. Lowermost sterile bracts as long as or longer than the fertile ones.

15a. Lateral sepals connate, crested with a red villous keel apex; plants glaucous; dorsal area of lowest 1–2 bracts often excurrent as a green blade .... 19. *X. seubertii*

15b. Lateral sepals free, not crested as above; plants not glaucous; dorsal areas bladeless.

16a. Dorsal area large, triangular, punctate, occupying most of bract above middle; low-elevation savanna or granite outcrops, T. F. Amazonas, Venezuela.

17a. Bract borders reddish, long-ciliate; keel of lateral sepals and leaf blade edges ciliate; seeds 1.3–1.4 mm long .... 20. *X. huberi*

17b. Bract borders not reddish, eciliate; keel of lateral sepals sparsely scabrid and leaf blade edges scabrociliate only toward base; seeds ca. 0.5 mm long .... 21. *X. graniticola*

16b. Dorsal area narrower, less conspicuous, not evidently punctate; high savanna of tepuis .... 22. *X. frondosa*

9b. Dorsal area not evident.

18a. Longest leaves rarely with sheaths over ½ as long as blades, mostly ⅓ as long or shorter.

19a. Leaf blades under 3 mm wide.

20a. Keel of lateral sepals toward apex red villous-ciliate; edges of young bracts toward apex red villose .... 23. *X. chimantae*

20b. Keel of lateral sepals ciliate or lacerate but not as above; bract tips entire or brown ciliolate.

21a. Tips of leaf blades strongly callused, thick, blunt; leaf blades coarsely few-ribbed; high tepuis of Amazonas.

22a. Foliage smooth; leaf sheath apex tan to stramineous, lustrous; sheath edge forming a strong, broad ligule apically; keel of lateral sepals narrow, entire or subentire .... 24. *X. stenophylloides*

22b. Foliage harsh, particularly leaf blades toward base; leaf sheath apex and blade bases strongly tinged with red or rose; sheath tending gradually to merge with blade base .... 11. *X. scabridula*

21b. Tips of leaf blades acute or acuminate, sometimes spinulose; leaf blades not coarsely ribbed; high elevations.

23a. Flowers/spike 5–14; lateral sepals inequilateral, the keel long-ciliate above middle .... 25. *X. columbiana*

23b. Flowers/spike 4 or fewer; lateral sepals subequilateral, the keel either not evident or entire, papillate, or distantly scabrociliate.

24a. Lateral sepals ca. 5 mm long; bracts ovate to orbicular, ecarinate, nearly black; seeds ca. 1 mm long .... 26. *X. subulata* (complex)

24b. Lateral sepals ca. 7–8 mm long; bracts narrower, carinate, brown; seeds ca. 2 mm long .... 27. *X. valdeapiculata*

19b. Leaf blades mostly over 3 mm wide.

25a. Scapes ancipital (flattened and sharp-edged) distally, mostly 2.5 mm or more wide (variously scabrid, ciliate, or smooth).
    26a. Spikes obovoid or hemispheric, ca. as broad as long or broader; scape edges scabrid; bracts dark lustrous brown (Duida tepui and adjacent highlands) .... 28. *X. tatei*
    26b. Spikes ovoid-cylindric, distinctly longer than wide; scape edges smooth to pale ascending-ciliate; bracts dull, dark greenish black .... 29. *X. melanovaginata*
25b. Scapes not sharp-edged distally, mostly less than 2.5 mm wide.
    27a. Leaf blades with a rusty border, ciliate (often with reddish vein intervals) .... 30. *X. culmenicola*
    27b. Leaf blades without a rusty border, eciliate .... 31. *X. lugubris*

18b. Longest leaves commonly with sheaths over ½ as long as blades, frequently ⅔ as long or longer.
    28a. Basal bracts forming a leafy involucre longer than the spike .... 14. *X. pallidula*
    28b. Basal bracts not forming a leafy involucre.
        29a. Bracts toward apex with a scarious, lacerate, pale or reddish border; bases of leaf sheaths abruptly orbicular-dilated.
            30a. Scarious bract borders pale to deep red or red-brown; seeds ca. 1 mm long .... 32. *X. thysanolepis* (complex)
            30b. Scarious bract borders almost always pale, off-white; seeds 0.5–0.7 mm long.
                31a. Apices of most bracts acute and distinctly folded; stem bases cloaked with very numerous, closely overlapping leaf sheath bases, these a lustrous brown; endemic to summit elevations, Roraima and adjacent tepuis .... 33. *X. concinna*
                31b. Apices of most bracts broader, often broadly rounded; stem bases usually not as elongate, not as above; widely distributed from medium to high elevations .... 34. *X. hymenachne*
        29b. Bracts not bordered as above; bases of leaf sheaths not abruptly orbicular-dilated.
            32a. Scapes ancipital and strongly ciliate distally.
                33a. Scapes bispicate .... 15. *X. bicephala*
                33b. Scapes unispicate.
                    34a. Hairs of leaf and scape edges rusty, forming a dense border; apices of leaves erect; seeds ca. 1.5 mm long.
                        35a. Main stems rebranching, the branches elongate, forming frondlike plates of leaves; tips of leaves narrowly acute; spikes ellipsoid or obovoid .... 38. *X. ptariana* (extreme)
                        35b. Main stems not rebranching; tips of leaves rounded; spikes hemispheric or subglobose .... 35. *X. decussata*
                    34b. Hairs of leaf and scape pale, usually white or blonde; apices of leaves various; seeds various.
                        36a. Seeds at least 2 mm long; spikes hemispheric or subglobose; bracts very lustrous with subcucullate tips; tips of most leaves incurved-blunt .... 36. *X. albescens*
                        36b. Seeds ca. 1.5 mm long; spikes obovoid or oblong; bracts dull, sooty brown, with flat tips; tips of most leaves erect and acute .... 37. *X. fuliginea*
            32b. Scapes ancipital or not, never ciliate, at most scabridulous along edges; stems forming frondlike plates of leaves (like giant *Fissidens*).
                37a. Spikes 1.5 cm long or shorter, ovoid or broadly obovoid; lateral sepals under 1 cm long, strongly curved, blunt.
                    38a. Ligular apex often excurved; scapes strongly flattened distally, mostly 2.5 mm broad or wider; leaf blades commonly over 4 mm wide .... 38. *X. ptariana*
                    38b. Ligular apex commonly erect or ascending; scapes narrower, usually 2 mm broad or narrower distally; leaf blades usually under 4 mm wide .... 39. *X. witsenioides*
                37b. Spikes mostly 2–2.5 cm long, ellipsoid-cylindric or narrowly obovoid; lateral sepals over 1 cm long, narrowly acute .... 40. *X. xiphophylla*

2b. Plants either aquatic perennials or short-lived perennials or annuals of low- or moderate-elevation savanna, mostly low of habit and slender-scaped, and with small or narrow spikes; leaf sheaths mostly softer, paler, their bases not in sharp contrast to blades in color and texture.

39a. Scapes ancipital, edges at least in combination broader than the scape body; dorsal area and midrib of at least one of the lowest sterile bracts excurrent as a strong cusp or blade (body of lower bracts with a strong keel).

40a. Basal bracts foliaceous, slightly to much longer than the fertile bracts, sharply alate-keeled, spreading or ascending and often forming an involucre; sepals acute .... 41. *X. spruceana*

40b. Basal bracts tending to be incurved, cucullate, the lowest slightly to much longer than the fertile bracts, thus spikes not as noticeably involucrate and spreading-foliaceous; sepals obtuse .... 42. *X. uleana* (complex)

39b. Scapes flattened or terete, but not winged as above; lowest bracts shorter in relation to fertile bracts.

41a. Florets 4 or fewer.

42a. Lateral sepals connate.

43a. Fertile florets 1 per spike.

44a. Leaf blades with edges cartilaginous-thickened; scapes flattened distally with costae making edges .... 44. *X. esmeraldae*

44b. Leaf blades filiform, the edges not noticeably cartilaginous-thickened; scapes filiform-terete, ecostate .... 45. *X. subuniflora*

43b. Fertile florets more than 1 per spike .... 46. *X. connosepala*

42b. Lateral sepals free.

45a. Leaf blades strongly flattened, with narrow, pale, incrassate borders .... 47. *X. guianensis*

45b. Leaf blades terete or somewhat flattened, without pale, incrassate borders.

46a. Leaf sheath apically with a broad ligule, this narrowing abruptly to a terete blade; spikes frequently proliferous; aquatic or emergent plants with foliage often maroon and soft .... 48. *X. spathacea*

46b. Leaf sheath with borders narrowing more gradually to a more flattened, often strongly ribbed blade; spikes not proliferous.

47a. Mature scapes equalled or exceeded by larger leaves; bracts at maturity strongly excurved, thus spikes broadly turbinate .... 49. *X. cyperoides*

47b. Mature scapes definitely longer than leaves; bracts and spikes not as above.

48a. Seeds ca. 1 mm long, including an apical pale coma of short squamellae; scapes and leaf blades rugose or rugulose .... 58. *X. mima*

48b. Seeds 0.4–0.7 mm long, lacking apical squamellae; scapes and leaf blades smooth or nearly so.

49a. Lateral sepals narrow, acute, entire; bract tips acute, with narrow dorsal areas .... 50. *X. toronoana*

49b. Lateral sepals broad, ciliate or ciliolate; bract tips broader, with broader dorsal areas (see no. 47).

41b. Florets 4–many.

50a. Leaf blades filiform and flaccid; sheath bases broadly scarious-bordered, the scarious borders distally producing a strong ligule much broader than the leaf blade base; rhizomatous soft aquatics or marsh emergents.

51a. Leaf blade terete; scapes arising from long, stout, scaly rhizomes; seeds ca. 0.5 mm long .... 51. *X. aquatica*

51b. Leaf blade flattened, strongly nerved; scapes arising from slender rhizomes; seeds ca. 1 mm long .... 52. *X. apureana*

50b. Leaf blades wider and/or firmer; sheath at apex not as above; erhizomatous plants of drier sites.

52a. Spike elongate, more than 4 times as long as wide.

53a. Bracts distichous, spikes flattened .... 53. *X. stenostachya*

53b. Bracts polystichous, spikes terete.

54a. Leaf blades at least toward base with thickened, lustrous cartilaginous margins; leaf sheath keels distally with cartilaginous dark costa.

55a. Spikes sharply acute, fusiform or ellipsoid; seeds 1.2–1.7 mm long .... 54. *X. stenocephala*

55b. Spikes blunt, the mature ones cylindric; seeds 0.6–0.7 mm long .... 55. *X. cylindrostachya*

54b. Leaf blades lacking thickened, lustrous, cartilaginous margins; leaf sheath keels lacking cartilaginous dark costa.

56a. Spike lanceoloid to fusiform, acuminate; fertile bracts at apex with lanceolate dorsal area forming a sharp subapical keel; leaf blades terete most of their length above base .... 56. *X. brachysepala*

56b. Spike ovoid to ellipsoid, lanceoloid, or cylindric, blunt or acute; fertile bracts with broad dorsal areas not forming a sharp subapical keel; leaf blades usually terete only at or toward tips (if at all) .... 57. *X. paraensis* (complex)

52b. Spikes of a broader, shorter outline.

57a. Lateral sepals subequilateral or slightly inequilateral.

58a. Scapes scabrid, tuberculate-rugose, strongly bicostate distally; seeds apically with coma of pale, narrow scales .... 58. *X. mima*

58b. Scapes smooth or at most papillate, usually ecostate or at most striate; seeds without coma.

59a. Spikes broadest at or above middle; leaf blades with strong red border; lateral sepals strongly curved, the keel evenly ciliate .... 59. *X. rubrolimbata*

59b. Spikes ovoid, acute; leaf blades lacking strong red border; lateral sepals not strongly curved, the narrow keel entire or subentire .... 60. *X. cuatrecasana*

57b. Lateral sepals either connate or very inequilateral.

60a. The lateral sepals connate; fertile bracts pectinate-bordered .... 61. *X. pectinata*

60b. The lateral sepals free; fertile bracts not pectinate-bordered.

61a. Staminodia lacking beard; foliage prevalently (one var. excepted) papillose or rugulose, the leaf blades strongly nerved; dorsal areas of fertile bracts mostly narrowly elliptic or linear; seed tips truncate, with a central low apiculus .... 62. *X. savanensis*

61b. Staminodia bearded; foliage prevalently smooth, the leaf blades either less strongly nerved or smooth; dorsal areas of fertile bracts broader or more raised; seed tips not truncate.

62a. Backs of bracts strongly papillose-tuberculate; bract edges at least apically villous or pilose-ciliate.

63a. Lowest pair of bracts incurved-cucullate at tips not much if at all exceeding spike .... 42. *X. uleana* (complex)

63b. Lowest pair of bracts with spreading, trigonous-subulate tips many times longer than spike .... 43. *X. calderonii*

62b. Backs and edges of bracts smooth and entire.

64a. Leaf blades with cartilaginous-thickened borders; seeds 1.2–1.7 mm long .... 54. *X. stenocephala*

64b. Leaf blades without cartilaginous-thickened borders; seeds less than 1 mm long .... 57. *X. paraensis* (complex)

1b. Margins of leaf sheaths at some or all levels variously ciliate with various sorts of hairs.

65a. Dorsal area evident on some or all spike bracts.

66a. Leaves at junction of sheath and blade definitely flattened.

67a. Scapes either strongly flattened distally or with 2 costae making 2 strong edges.

68a. Leaf blade edges and/or scape edges usually with long, straight cilia, rarely smooth, if so then thickened.

69a. Spikes broad; dorsal area broadly triangular, occupying most of upper part of bract; scapes mostly 2 mm wide or more .... 63. *X. surinamensis*

69b. Spikes narrow; dorsal area narrower; scape narrower .... 64. *X. pratensis*

68b. Leaf blade and scape edges scabrociliate with shorter, stiffer hairs .... 65. *X. bicostata*

67b. Scapes distally terete or at least thickened in cross section, 0–many-costate, costae in bicostate types not ciliate or scabrociliate, not making 2 strong edges.

70a. Scapes smooth, without strong costae or merely fluted

71a. Flowers usually more than 4.

72a. Bracts, or some of them, with long hairs on margins or backs or on both.

73a. Bracts rounded, edges villous-ciliate ... 66. *X. globosa*

73b. Bracts acute, some bract backs with white hairs ... 67. *X. arachnoidea*

72b. Bracts without pubescent margins or backs.

74a. Matrix of bracts (at level of dorsal areas) pale brown or pale red-brown, thin, lacerate or entire.

75a. Leaf sheath bases abruptly dilated; plant base thus bulbous.

76a. Fertile bracts apically carinate, acute; leaf blades coarsely few-nerved ... 69. *X. araracuare*

76b. Fertile bracts more rounded, less carinate at apex; leaf blades more flattened, less coarsely nerved ... 70. *X. lacerata*

75b. Leaf sheath bases not abruptly dilated; plant base not bulbous (spike oblate, often proliferous) ... 71. *X. oblata*

74b. Matrix of bracts dark brown, spikes dark; scapes usually lustrous, deep brown or olivaceous or reddish (leaf tip excentrically spinulose) ... 81. *X. setigera* (complex)

71b. Flowers almost always 4 or fewer (spikes mostly narrow; dorsal area narrow, often streaklike, absent on some bracts).

77a. Sheath cilia long and spreading but firm; seeds ovoid, ca. 0.5 mm long; leaf blades linear ... 72. *X. tenella* (complex)

77b. Sheath cilia arachnoid; seeds ellipsoid or cylindric, ca. 1 mm long; leaf blades filiform ... 73. *X. byssacea*

70b. Scapes with strong costae.

78a. Scapes sharply 3-or-more-costate; plant base sub-bulbous; spike broadly ovoid or ellipsoid ... 68. *X. malmeana*

78b. Scapes with costae fewer if multicostate; papillate-scabrid plant base not bulbous (the plants annual and low); spike ellipsoid to lanceoloid ... 72. *X. tenella* (complex)

66b. Leaves at junction of sheath and blade definitely not flattened, at most elliptic in cross section, mostly terete or oval, often with a ventral sulcus.

79a. Spikes few-flowered and narrow (narrowly oblong to linear-lanceoloid).

80a. One pair of lower (sterile) bracts longer than the rest and connivent over spike top ... 74. *X. cryptantha*

80b. Lower bracts not as above, the lowest pair slightly to considerably shorter than the spike ... 75. *X. oxylepis*

79b. Spikes several–many-flowered and broader.

81a. Bract tips narrowly or bluntly acute.

82a. Outer bracts densely hirsute-tomentose or hirsute-ciliate with white hairs; bract tips straight, erect or ascending, bract matrix dark-castaneous ... 76. *X. wurdackii*

82b. Outer bracts not hirsute-tomentose or hirsute-ciliate, mostly smooth; bract tips becoming excurved, bract matrix brown ... 77. *X. frequens*

81b. Bract tips broadly angled to rounded.

83a. Dorsal area broad, comprising most of the bract above middle; leaves strongly angulately ribbed; mostly plants of low-altitude savanna ... 78. *X. subglabrata*

83b. Dorsal area narrower; leaves not strongly ribbed; mostly plants of medium- to high-altitude tepuis.

84a. Scapes smooth, usually lustrous, at most punctate.

85a. Bracts dark brown or dark red-brown, dorsal areas pale and inconspicuous ... 81. *X. setigera* (complex)

85b. Bracts pale brown with darker dorsal areas ... 79. *X. lithophila*

84b. Scapes papillate or tuberculate, usually rugulose or rugose, at least above middle ... 80. *X. carinata*

65b. Dorsal area not evident.

86a. Leaves distinctly compressed at junction of sheath and blade, with the ventral edges about as narrow as the dorsal edge.

87a. Scapes terete distally, ecostate, smooth and also punctate; leaf apex usually excentrically spinulose-tipped.

88a. Leaves 0.5–3 mm wide; lateral sepals 5–6 mm long; seeds 0.5–0.6 mm long ... 81. *X. setigera* (complex)

88b. Leaves 2–3 mm wide; lateral sepals 6.5–7 mm long; seeds 0.9–1 mm long ... 82. *X. riparia*

87b. Scapes terete or somewhat flattened distally, there costate, usually tuberculate-scabrid, ciliate, papillose and/or rugulose at least on the costae; leaf apex not excentrically spinulose-subulate.

89a. Bracts with scarious and lacerate borders different abruptly in texture and color from main bract body.
  90a. Borders of bracts red or red-brown.
    91a. Spikes ellipsoid to broad-cylindric; foliage above dilated base yellow-green, scabrid-papillose-rugulose; scapes ancipital distally .... 83. *X. roraimae*
    91b. Spikes broadly obovoid or turbinate to subglobose; foliage except for leaf edges and costae not yellow-green, smooth; scapes not ancipital .... 32. *X. thysanolepis* (complex)
  90b. Borders of bracts pale.
    92a. Apices of bracts, particularly basal and inner ones, acute, folded; spikes ovoid .... 33. *X. concinna*
    92b. Apices of bracts mostly obtuse, not folded; spikes broadly ellipsoid, obovoid, or subglobose .... 34. *X. hymenachne*
89b. Bracts very dark, usually deep olive-brown, the borders entire and not much contrasting in color.
  93a. Surfaces of leaves and scapes completely rugulose-papillose-tuberculate.
    94a. Lateral sepals all free; capsule valves with strong septa .... 84. *X. schneeana*
    94b. Lateral sepals connate; capsule valves lacking septa .... 85. *X. consolida*
  93b. Surfaces of leaves and scapes smooth or at most papillate only toward leaf sheath base, but edges of leaf blades and of ancipital scape white-ciliolate; lateral sepals free, capsule valves with septa .... 86. *X. kukenaniana*
86b. Leaves definitely thickened at junction of sheath and blade, not 2-edged.
  95a. Tips of leaf blades blunt; scapes rugose-tuberculate or rugulose-papillate .... 87. *X. delicatula*
  95b. Tips of leaf blades subulate-spinulose; scapes totally smooth, or smooth and puncticulate .... 81. *X. setigera* (complex)

1. Xyris fallax Malme, Bih. Svensk. Vet.-Akad. Handl. 22, Afd. 3, no. 2: 12, pl. 1, f. 5. 1896. TYPE: Brazil. Mato Grosso: Sta. Anna da Chapada, *G. Malme 1432* (lectotype, S). Figure 1.

X. dolichosperma Lanjouw, Rec. Trav. Bot. Neerl. 34: 488, f. 5. 1937. TYPE: Suriname: in savannis humidis prope Zanderij I, Suriname, *Pulle 39* (holotype, U).

X. erythema Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 12, fig. 1A–F. 1963. TYPE: Guyana: infrequent in wet places, scrub and low forest (8–10 m) on shoulder of east flank above Thompson Camp, 1,418–1,525 m, 10 Aug. 1960, Upper Mazaruni River Basin, Mt. Ayanganna, British Guiana, *S. S. & C. L. Tillett & R. Boyan 45074* (holotype, N; isotype, US).

Low and slender to robust, solitary or cespitose, glabrous or papillose-rugulose perennial to 1 m high, the stems contracted, sometimes perennating by stout (–4 mm thick) horizontal rhizome. Leaves erect to spreading flabellately, (5–)10–30(–40) cm long, often suffused with maroon pigment; sheaths ½ to under ¼ as long as blades, soft, pale lustrous brown, the dilated base entire, multicostate, gradually narrowing and carinate upward, the carina often papillose or ciliate-scabrid, the margins frequently sparsely to densely spreading-pilose-ciliate, gradually narrowing to blade or there producing a broadly triangular, incurved ligule to 2 mm long; blades ensiform-linear, 1–5(–7) mm wide, much flattened, sometimes slightly twisted, the apex narrowly incurved-acute, the margins thin or (usually) lustrous-incrassate, often papillate or minutely scabrociliate, more often smooth. Scape sheaths shorter than main foliage leaves, loosely tubular, multicostate, deep reddish brown proximally, distally opening and broadening, apically with short, erect blades. Scapes straight or somewhat flexuous, twisted, terete and multicostate distally, 1–2 mm thick, the costae smooth or papillate. Spikes lance-cylindric to broadly ellipsoid or ovoid, mostly 1–2 cm long, acute, the base short-attenuate, multiflorous; sterile bracts several, the lowest much smaller than the fertile bracts, narrowly triangular-ovate, carinate, grading gradually upward into the fertile bracts, these mostly broadly ovate or obovate, 5–7 mm long, subentire, apically narrowly rounded, the back with distinct elliptic dorsal areas, convex and ecarinate, the dorsal area bisected by a narrow, low but distinct midnerve. Lateral sepals

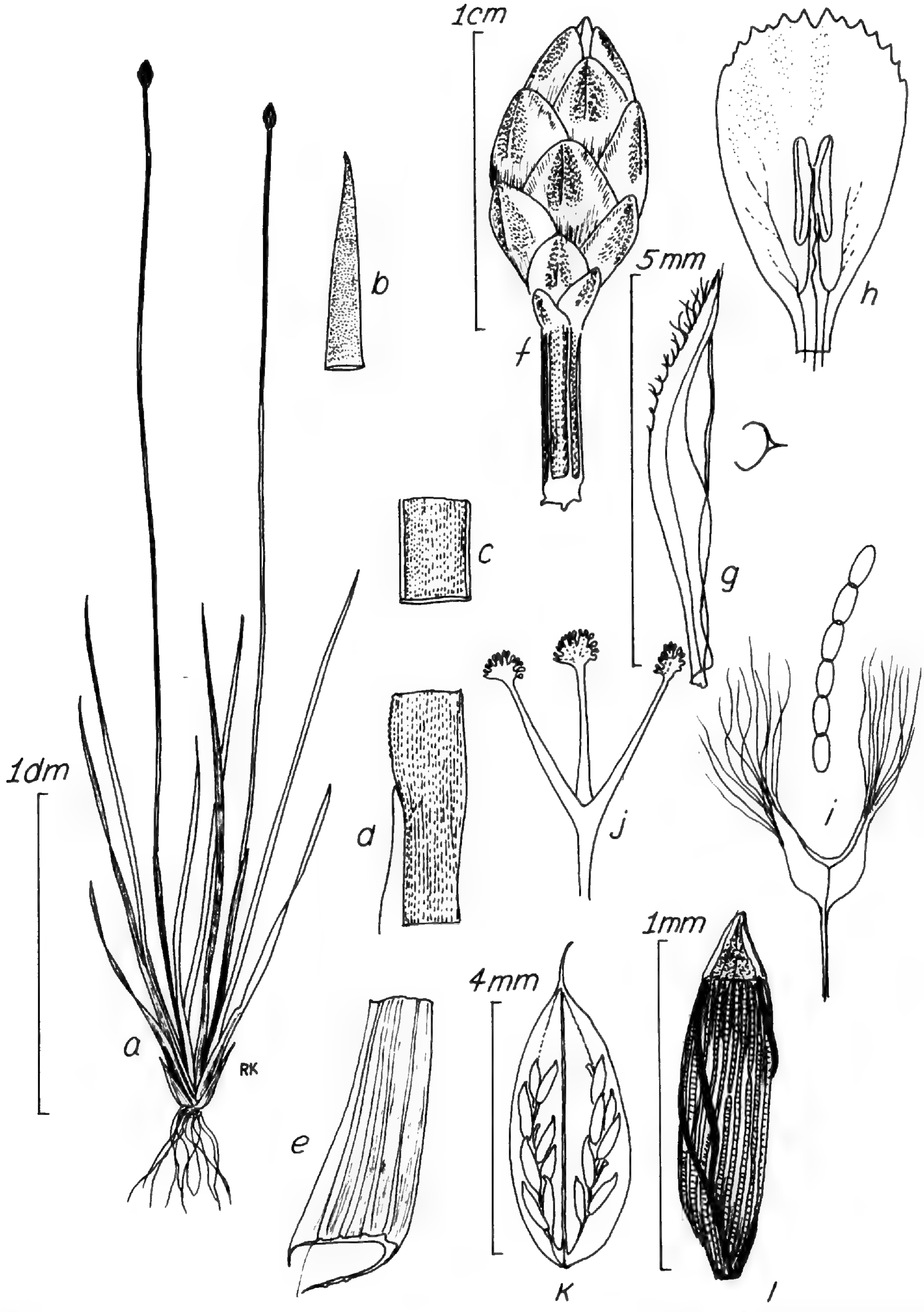


FIGURE 1. Xyris fallax (Davidse et al. 1785).—*a. Habit sketch.—b. Leaf tip.—c. Sector of leaf midblade.—d. Leaf base–blade junction.—e. Leaf base.—f. Spike.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode, enlarged part of beard hair.—j. Stylar apex.—k. Capsule with one valve removed, showing two lines of placentation.—l. Seed.*

free, subequilateral, linear-oblanceolate, 4.5–5 mm long (often much reduced in length even in fruit), acute, red-brown, the firm broad keel lacerociliate from ca. middle to apex, sometimes villous-ciliate at apex. Petal blades unfolding in morning, broadly obovate, 4–5 mm long, yellow, the broadly rounded apex lacerodentate. Staminodia bibrachiate, the broad branches long-penicillate toward tips. Anthers oblong, ca. 1.5 mm long, deeply bifid and sagittate, on filaments ca. 1 mm long. Capsule ellipsoid or narrowly obovoid, 3–5 mm long, the placentae parietal and extending ½–⅔ up the ovulary. Seeds numerous, 1–1.5 mm long, asymmetrically cylindrical or fusiform, deep red-brown and translucent, longitudinally distinctly and closely multiribbed, the ribs often crossed or overlain by an occasional broader, deeper-brown rib.

Distribution. Trinidad South to Mato Grosso (Norte), westward into the Andean foothills; Africa.

This xyrid shows weedy tendencies, is often abundant in recently disturbed wetlands, if acid, and along fluctuating shorelines and banks. While commonest in low-elevation savanna, it may be found in wetlands at elevations of nearly 1,500 meters. In ciliation of sheath it varies considerably from totally entire to densely long-brown-ciliate.

2. Xyris laxifolia C. Martius, Fl. Bras. 24(2): 58. 1841. TYPE: Brazil. Without definite locality: Mart. Herb. no. 540 (holotype, M). Figure 2.

?*X. macrocephala* M. Vahl, Enum. Pl. 2: 204. 1805. TYPE: French Guiana, "e Cayenne Vahl" (lectotype, C; this a mixture of *X. ambigua* Beyr. and *X. jupicai* Rich.).

X. macrocephala var. *major* (C. Martius) Nilsson, Kgl. Sv. Vet. Akad. Handl. 24(14): 30. 1892.

X. caroliniana Walt. var. *major* (C. Martius) Idrobo & Smith, Caldasia 6(29): 199, fig. 4. 1954.

X. jupicai Rich. var. *major* (C. Martius) Smith & Downs in Reitz, Fl. Ill. Catarinensis, Pt. 1, fasc. xii: 9. 1965.

Robust, solitary or cespitose perennial 0.5–1.5 m tall, the bases usually suffused with red or purple, all surfaces smooth. Principal leaves erect or spreading flabellately, 4–7 dm long, the sheaths over ½ as long to longer than blades, at very base broad with scarious entire margins, red to purple or charcoal, tapering gradually, keeled into junction with blades, these broadly linear, mostly 1–2 cm wide, strongly flattened, straight, the apex abruptly incurved-acute or erect-acute, the margins thin and hyaline or slightly incrassate, the surfaces deep lustrous green. Scape sheaths shorter than leaves, proximally loosely tubular, multiribbed, deeply tinted with red, purple, or lustrous brown, distally opening and keeled, producing a short, flat, green blade. Scapes straight, stiffly linear, distally terete to oval or elliptic in cross section, sometimes 2-edged but usually ecostate, smooth, green. Spikes ovoid to cylindrical, 3–3.5 cm long, blunt to acute, green-brown, of many tightly and spirally imbricate firm bracts, the sterile ones much smaller than and grading into the fertile ones, keeled, all with distinct and usually greenish dorsal areas; fertile bracts obovate to ovate or suborbicular, convex-backed and ecarinate, 7–10 mm long, apically narrowly rounded, entire, the matrix deep to pale reddish brown, lustrous, in sharp contrast to the paler and dull dorsal areas. Lateral sepals free, oblong-curvate, 5–6.5 mm long, acute, the pale brown, thin sides subequilateral, the dark reddish brown keel wide but thin, lacerate or lacerofimbriate from ca. middle to tip. Petal blades broadly obovate, ca. 5 mm long, yellow, the broadly rounded apex erose, the base broadly cuneate. Staminodia bibrachiate, the broad, flat branches apically rebranched and long-penicillate, the cells congested with dark material, the terminal few often double. Anthers ca. 2.5 mm long, lance-oblong, shallowly bifid, deeply sagittate, on filaments 0.5–0.6 mm long. Capsule plano-convex, broadly to narrowly obovoid, 5.5–6.5 mm long, often longer than the sepals; placentation parietal. Seeds ellipsoid-fusiform, 0.7–0.9 mm long, slightly to conspicuously farinose or translucent, with 6–8 conspicuous, minutely pebbled, dark, longitudinal ribs and many slightly less prominent cross-lines.

Distribution. Southern Mexico southward through Central America and at the

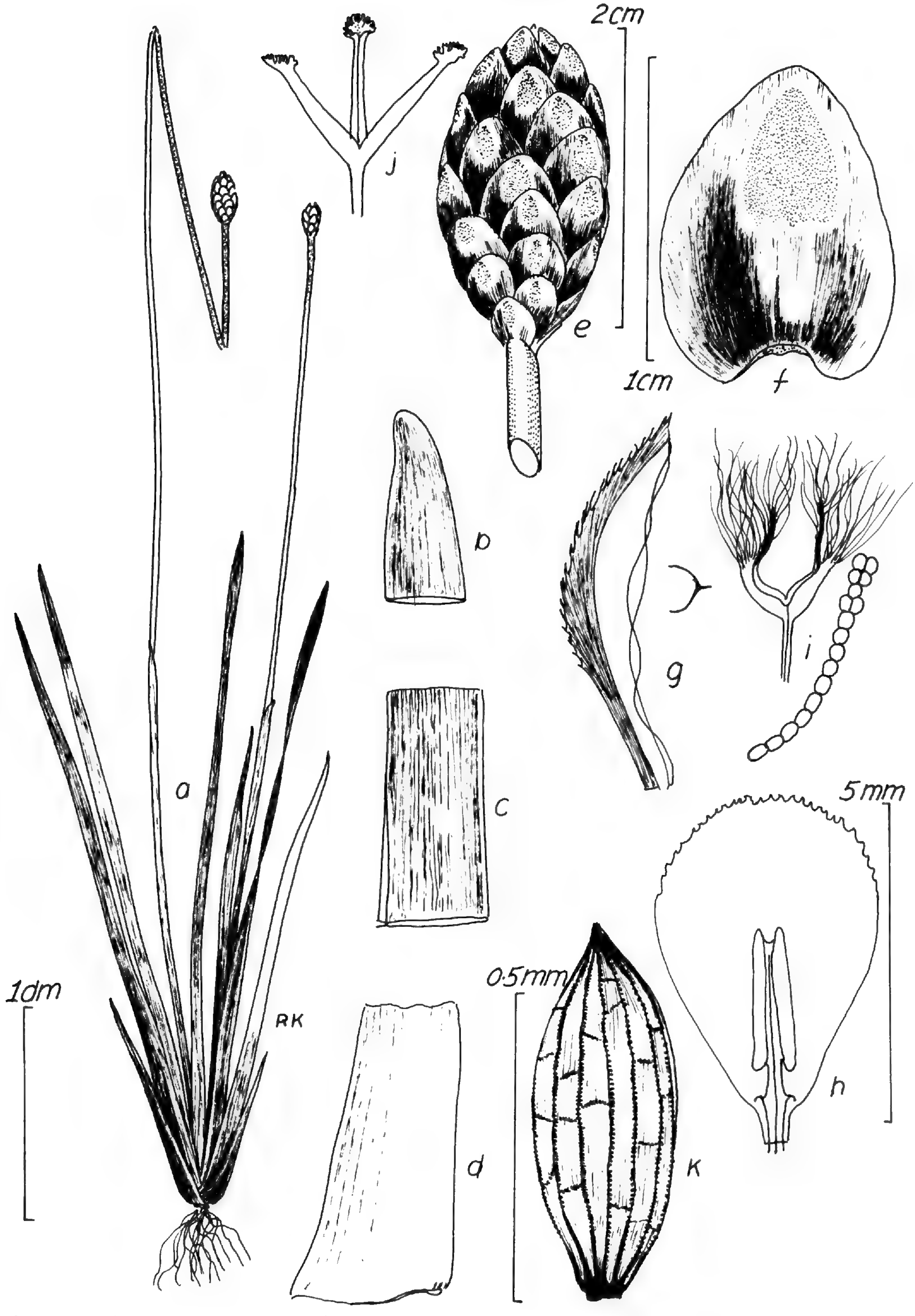


FIGURE 2. Xyris laxifolia (Davidse & Gonzales 15946).—*a. Habit sketch.—b. Leaf tip.—c. Leaf blade-sheath junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode.—j. Stylar apex.—k. Seed.*

lower elevations south into Argentina. Coastal Plain of the southeastern United States (var. *iridifolia*).

The specimen sent from C in the type folder representing *X. macrocephala* Vahl and bearing Vahl's identification as *X. macrocephala* (Vahl script) should bear the oldest name for this species. However, the sheet has two elements on it: one is a spike of *X. ambigua* Beyr., a Mesoamerican, Caribbean, and North American species but definitely not from the type area (Cayenne, French Guiana); the other is *X. jupicai* L. C. Richard, a previously named species. This situation appears to be best handled by selecting the earliest available indisputably typified name. Material at Florence of the type collection of *X. macrocephala* (which I have seen only as photographs) appears likewise to be mixed. The main difficulty here is one of deciding the appropriate whereabouts of the lectotype and the varied interpretations of Vahl's original, and cryptic comments add much to the problem.

Xyris laxifolia, like *X. jupicai,* is a common weed of disturbed, mildly to very acid open areas and riverine forest borders. In North America it ranges from southeastern Virginia southward into northern Florida, thence west in the Coastal Plain into south-central Texas, with an outlier in Tabasco, Mexico. These northern populations are designated var. *iridifolia* (Chapm.), but even varietal distinction is difficult. In South America the species is general in wetlands, particularly at lower elevations from the Andean foothills to the Atlantic. Its most common associate xyrid is *X. jupicai* from which *X. laxifolia* differs primarily by having taller habit, broader and purple-based leaves, wider and smooth-edged scapes, larger and darker spikes with narrower bract apices. The seeds are mostly farinose. Much confusion in identification comes from larger specimens of the former and smaller specimens of the latter, also from the fact that the red pigments that so definitely mark *X. laxifolia* in the field do not persist for very many years on herbarium material or are entirely lost when specimens are treated with alcohol or formalin (as they so often are in the tropics).

3. Xyris jupicai Rich., Act. Soc. Hist. Nat. Paris I: 100. 1792. TYPE: French Guiana: "Cayenne," *LeBlond* (lectotype, P). Figure 3.

X. anceps Pers., Syn. Pl. I: 56. 1805, non Lamarck, 1791.
X. jupicae Michaux, Fl. Bor. Am. I: 23. 1803.
X. communis Kunth, Enum. Pl. 4: 12. 1843. TYPE: Brazil: without precise locality, "Amazonas, Pará, *Poeppig*" (isotype, L).
X. arenicola Miq., Linn. 18: 75. 1844.
X. gymnoptera Griseb., Cat. Pl. Cub. 223. 1866, in part (and in part *X. ambigua* Beyr.). TYPE: Cuba: without definite locality, 1865, *C. Wright 3228* (isotypes, NY, US).
X. acuminata Miq. ex. Steud., Syn. Pl. Glum. 2: 284. 1855.
X. jupicai var. *brachylepis* Malme, Sv. Bot. Tidskr. 21: 394. 1927.
X. macrocephala f. *minor* (C. Martius) M. Kuhlmann & Kuhn, Fl. Dist. Ibiti. 34. 1947.

Annual or short-lived, perennial, solitary or tufted, 1–10 dm high, the stems contracted, mostly dying by end of season, rarely perennating by bulbous overwintering lateral buds. Leaves mostly erect or ascending, 1–6 dm long; sheaths entire, often as long as the blades, tapering gradually from a dilated, pale green, dull brown or stramineous, keeled, ribbed base to the blade, there with edges convergent and merging with blade or with a short, erect triangular ligule; blades linear, strongly flattened, straight, the apex acuminate, erect or incurved, the margins thin or narrowly incrassate, smooth or papillate, the surface yellow-green with short streaks of maroon, finely nerved. Scape sheaths much shorter than leaves, the tubular bases multicostate and twisted, stramineous, pale green or pale brown, upwardly dilating and open, keeled, then narrowing to a slightly divergent, cusplike flat blade. Scapes straight, erect, rarely somewhat twisted, proximally terete, multistriate and 1–2-costate, tan or stramineous, distally slightly compressed and 1–2-costate, green, the costae narrow but strong, usually papillose-tuberculate, rarely smooth. Mature spikes ovoid, ellipsoid or oblong, 0.5–

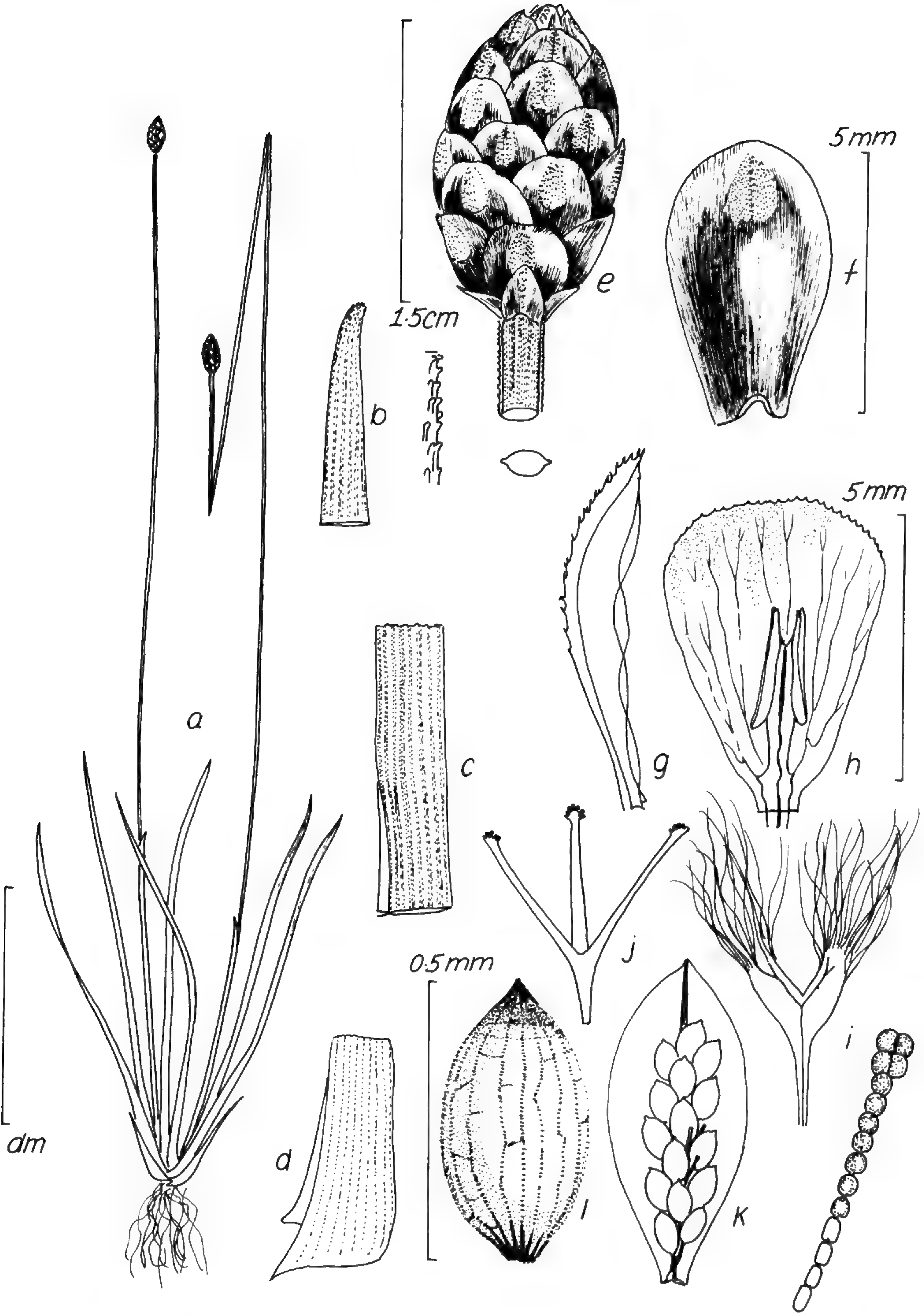


FIGURE 3. Xyris jupicai (Kral 25970). —*a. Habit sketch.—b. Leaf apex.—c. Leaf at blade-sheath junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode, enlarged hair.—j. Stylar apex.—k. One valve of capsule.—l. Seed.*

1.5(−2.5) cm long, blunt or rarely acute, of many (several in depauperate individuals) rather loosely and spirally imbricate bracts, several of the lower ones sterile, narrower and shorter than the fertile bracts and grading into them; fertile bracts obovate to ovate, 5–7 mm long, apically rounded to broadly acute, the margin entire, aging erose, the backs strongly rounded, ecarinate, pale to dark red-brown, lustrous, the dorsal areas rectangular to elliptic, green, aging brown. Lateral sepals linear-oblanceolate, slightly curvate, from 3 mm long to equaling bracts, equilateral, very thin, usually pale green-tan, the thin but broad brownish keel lacerate from ca. middle to acute apex. Petal blades broadly obovate, ca. 3–4(−5) mm long, yellow, the broadly rounded to subtruncate apex denticulate-erose, the base cuneate. Staminodia bibrachiate with 2 broad flat branches terminally penicillate, most of the cells congested with dark material. Anthers lance-oblong, ca. 1.5 mm long, deeply bifid and auriculate on filaments ca. 1 mm long. Capsule thin, narrowly obovoid or ellipsoid, plano-convex, ca. 3–4 mm long, the placentae parietal, continuous to locule summit. Seeds broadly ellipsoid, ca. 0.4–0.5 mm long, pale amber, longitudinally with several papillate straight or anastomosing ribs and with several weaker cross-lines.

Distribution. Throughout the southeastern United States southward through the Caribbean and Central America, mostly at lower elevations, south into Argentina.

This morning-bloomer is a common wetlands weed over much of its range, generally in Central and South America, sharing its habitat with *X. laxifolia*, with which larger specimens are confused. Original material of "*X. macrocephala*" Vahl is largely *X. jupicai* (see discussion of species 2).

4. **Xyris navicularis** Griseb., Cat. Pl. Cub. 223. 1866. TYPE: Cuba: "savannas Dayanigua, *C. Wright 3229*" (presumed location of lectotype, HAC; isotypes, NY, US). Figure 4.

X. subnavicularis Malme, Ark. Bot. 13^8: 15. 1913. TYPE: Belize: Stann Creek, Honduras, Rev. *J. Robertson* (holotype, BM).

Perennial or annual, usually cespitose, to 4.5 dm tall. Leaves flabellately spreading, (4–)10–15(−20) cm long; sheaths entire or, rarely, papillose or scabridulous-edged, the broad, clasping base maroon, brown or red-brown, often papillose, narrowing gradually into the blade, the ligule lacking or inconspicuous; blades linear-gladiate, flattened, sometimes slightly twisted, sometimes curvate, 2–5 mm wide, yellow-green or maroon-tinted, the apex incurved-acute, incrassate, the edges thin, entire or more often papillate or tuberculate-scabrid, the surface smooth or with short lines of papillae or tubercles proximally. Scape sheaths shorter than leaves, terete and multicostate, lustrous brown proximally, the blade often conspicuous, leaflike. Scapes linear, sometimes twisted, distally flattened, bicarinate, 0.8–1.2 mm broad, the costae often papillose-tuberculate. Spikes narrowly ovate to oblong (0.7–)1–2(−2.5) cm long, of several to many loosely spirally imbricated, pale brown or dark brown bracts; lowest sterile bracts distinctly smaller than the fertile bracts, narrower, mostly lanceolate, keeled, acute, grading gradually into the fertile bracts, these ovate to broadly oblong or suborbicular, ecarinate or imperceptibly so, ca. 4–5 mm long, broadly rounded, the rounded backs papillate, the edges thin, at first entire, the dorsal areas subapical, lanceolate to ovate, paler, often inconspicuous (particularly in age). Lateral sepals free, equilateral, elliptic, 3.5–4.5 mm long, strongly curvate, lustrous red-brown, the keel firm but narrow, ciliate or ciliolate from near base to acute apex. Petal blades broadly obovate, ca. 5 mm long, yellow, the rounded apex crenate-erose. Staminodia bibrachiate, the flat branches at tips long-penicillate. Anthers broadly oblong, ca. 1.5–2 mm long, deeply bifid and sagittate, on filaments ca. 1.5 mm long. Capsule obovoid, 4 mm long; placentation 3-parietal. Seeds ellipsoid or ovoid, 0.5–0.6 mm long, short-caudate, with 9–10 raised and smooth longitudinal ribs per side and sev-

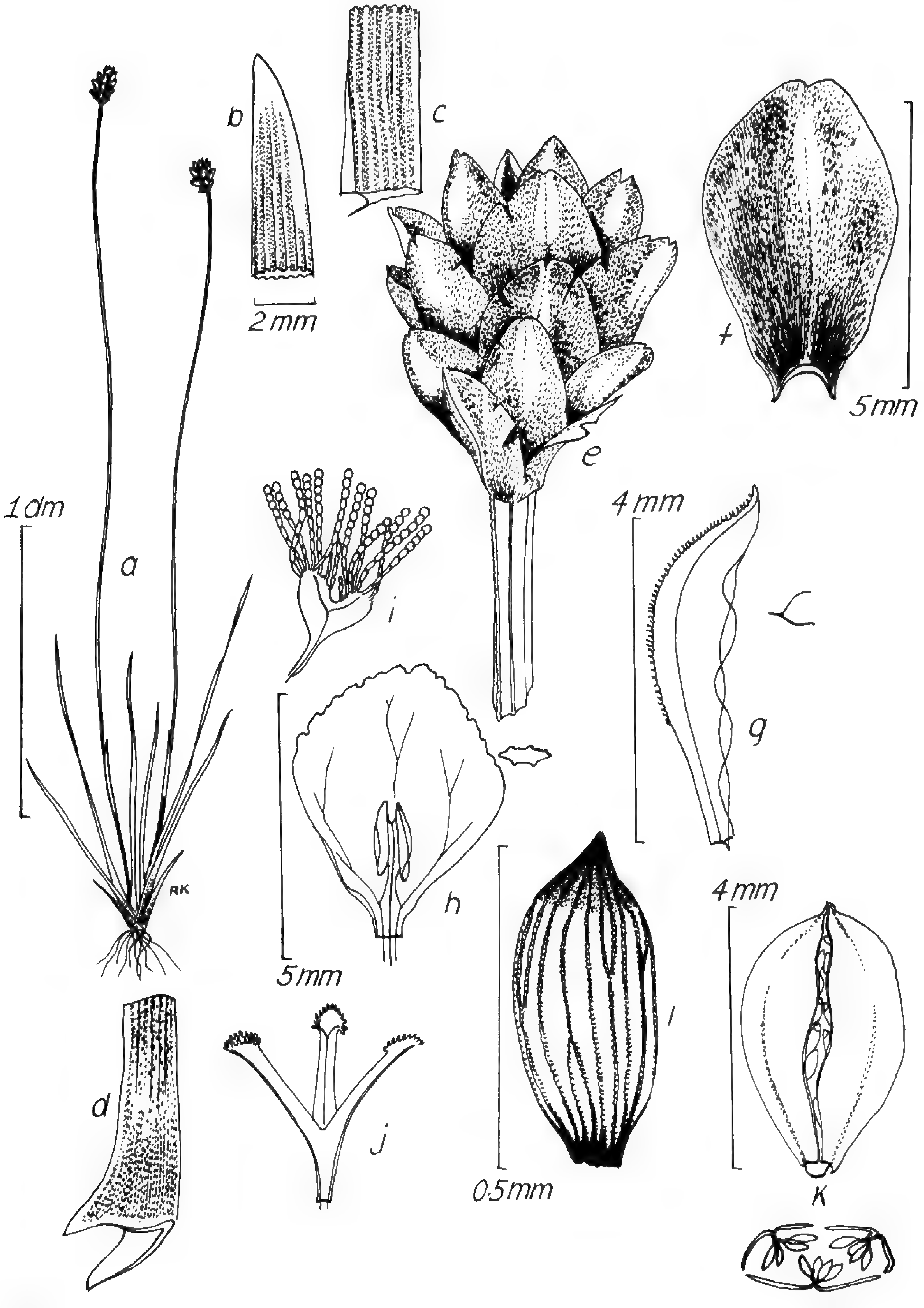


FIGURE 4. Xyris navicularis (G. Proctor 38799).—*a. Habit sketch.—b. Leaf apex.—c. Leaf blade–sheath junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode.—j. Stylar apex.—k. Capsule (outer face, showing line of dehiscence along dorsal bundle, this revealing tips of two placental lines of seeds).—l. Seed.*

eral indistinct crosslines, deep, lustrous, translucently amber.

Distribution. Low-altitude sandy palm or pine savanna from western Cuba through Belize and Honduras southward into Nicaragua (Zelaya); Colombia.

Xyris subnavicularis Malme, supposedly distinguished by having longer leaf sheaths associated with ciliate-scabrid blades and by its indistinct dorsal areas, falls in regard to these characters well within the total range of variation of *X. navicularis*. The species definitely centers in Cuba as to abundance.

5. **Xyris anceps** Lam., Illustr. I: 132. 1791. TYPE: "Guyane francaise," Herb. Hornemann (P, photo at F). Figure 5.

X. platycaulis Poiret, Encycl. 8: 820. 1808.
X. nitida Willd. ex Dietr., Sp. Pl. 2: 372. 1833.
X. pallida C. Martius, Fl. Bras. 24, Beibl. 2: 57. 1841. TYPE: Brazil. Bahia: "litoral, Camamu," 1818, *Martius s.n.* (type, M, photo at F).
X. fontanesiana Kunth, Enum. Pl. 4: 10. 1843.
?*X. bahiensis* Steudel, Syn. Pl. Glum. 2: 287. 1855.

Low to moderately robust, solitary or cespitose, glabrous, soft-based annual (1–)1.5–8 dm high. Leaves erect to spreading flabellately, the principal ones 5–40 cm long; sheaths up to ½ as long as blades, pale brown to stramineous or pink, soft, entire, multicostate, keeled just above base, the mid costa often papillose, the edges scarious, entire, gradually narrowing to the blade, there with a ligule up to 1 mm long; blades flattened, straight, ensiform-linear, pale or deep green, bluntly incurved-acute, the edges thin, or slightly incrassate and papillose-tuberculate. Scape sheaths shorter than principal leaves, loosely tubular, multicostate, proximally lustrous brown or pale brown, distally with short, erect blades. Scapes straight or flexuous, twisted, mostly bicostate distally, even ancipital, 1–3 mm wide, the costae entire or papillose. Spikes broadly ovoid, subglobose or hemispheric, 0.4–1.5 cm long, blunt, of several thin, scarious, pale to red-brown, lustrous, spirally imbricate bracts, these with short, subapical, gray-green, lanceolate dorsal areas, or the lowest bracts with elongate-lanceolate dorsal areas. Sterile bracts few, strongly keeled, about as long as the fertile bracts, these broadly obovate to suborbicular, 4–5.5 mm long, apically rounded, entire, the backs rounded, keeled strongly toward apex. Lateral sepals free, subequilateral, linear-oblanceolate, 4–5 mm long, acuminate or narrowly acute, the keel firm, smooth, slightly broadened distally. Petal blades obovate, ca. 3 mm long, coarsely dentate at broadly rounded apex. Staminodia broadly bibrachiate, the branches distally penicillate. Anthers oblong, ca. 1 mm long, deeply bifid and sagittate, on filaments ca. 0.5 mm long. Capsule oblong-obovoid or ellipsoid, ca. 3.5 mm long, umbilicate, the valves firm, lustrous brown, the placentation parietal from base to tip of fruit. Seeds broadly ovoid or ellipsoid, 3.5–4.5 mm long, translucent, pale to deep brown, biapiculate, strongly longitudinally ribbed, sparsely and finely cross-lined.

Distribution. Widespread and weedy in open, wet, acid areas and often littoral; Africa (including Madagascar); South America from the Guianas south to southern Brazil.

6. **Xyris brachyfolia** Kral & Wanderley, sp. nov. TYPE: Brazil. Amazonas: plateau of northern massif of Serra Araca, 0°51–57′N, 63°21–22′W, 1,200 m; southern extremity of northern plateau of Serra Araca, shrub forest. Growing on floor of moist shrubby forest, 15 Feb. 1984, *G. T. Prance, I. L. do Amaral, J. J. Pipoly, A. S. Tavares, M. G. da Silva, C. D. A. da Mota & A. Cress 29079* (holotype, INPA; isotypes, NY, VDB). Figure 6.

Planta perennis, caespitosa, glabra, 4–5 dm alta. Caules breves. Radices graciles. Folia principalia curta, suberecta, brunneola, nitida, vaginis scaporum breviora, persaepe stricte vagina, vel usque ad 5 cm longa, vulgo vagina; vaginae albovillosiciliatae, ad basin gradatim dilatatae, in laminas gradatim decrescentes, eligulatae; laminae leviter compressae, excurvatae, acutae, integrae. Vaginae scaporum elongatae, usque ad 1 dm longae, multicostatae, tortae, nitidae. Scapi graciles, erecti, torti, apicem versus teretes, multistriati vel valde costati, 0.7–0.9 mm crassi. Spicae pauciflorae, ellipsoideae, tum anguste obovoideae,

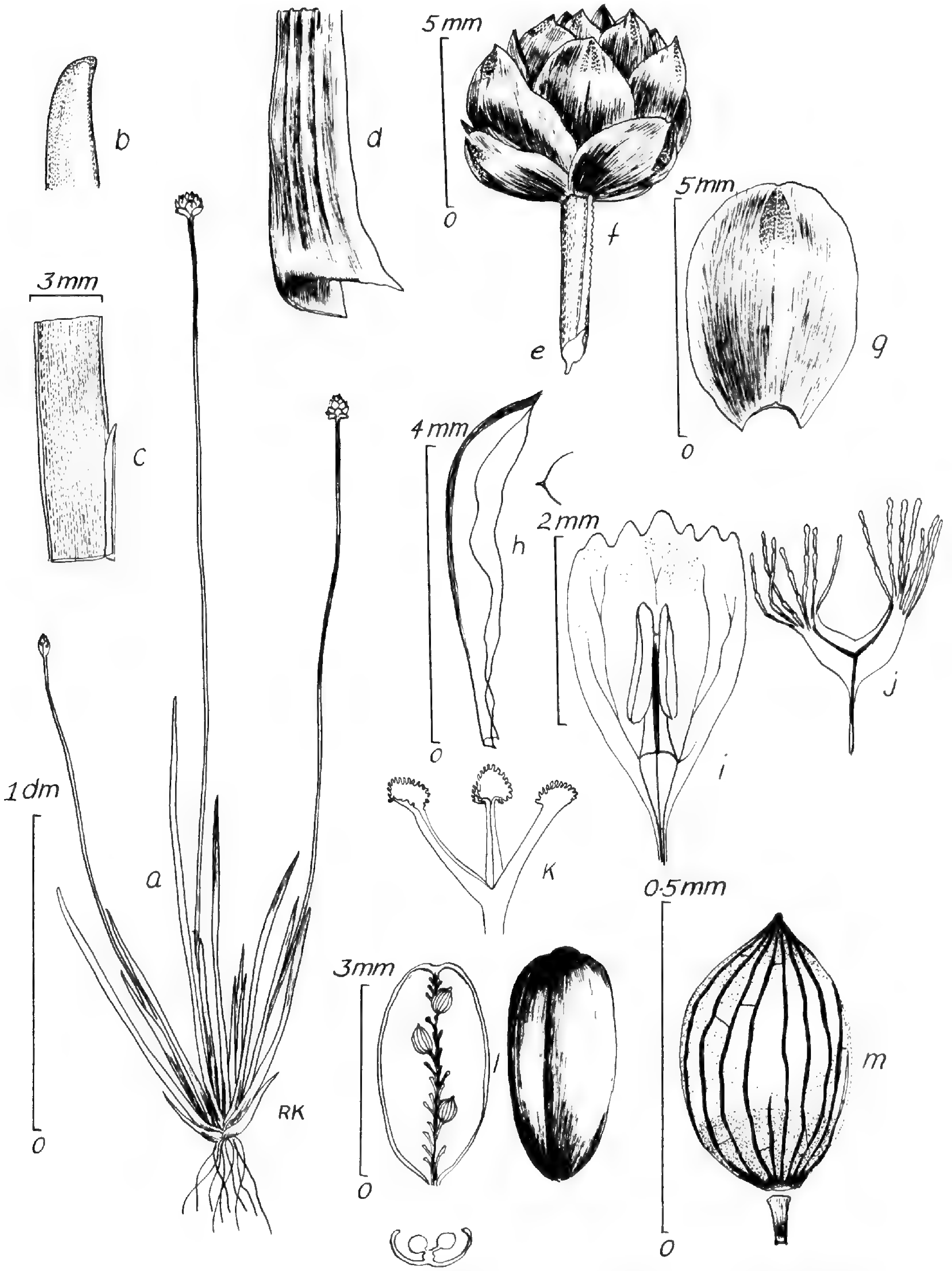


FIGURE 5. Xyris anceps (Austin et al. 6950). —*a. Habit sketch.*—*b. Leaf tip.*—*C. Leaf blade–sheath sector.*—*d. Leaf base.*—*e. Upper scape.*—*f. Spike.*—*g. Fertile bract.*—*h. Lateral sepal.*—*i. Petal blade, stamen.*—*j. Staminode.*—*k. Stylar apex.*—*l. Two views of capsule, at left one valve, at right intact capsule.*—*m. Seed.*

5–7 mm longae. Bracteae laxae spiraliter imbricatae, area dorsali conspicue; bracteae steriles 5–6, infimis late ovatis vel suborbiculatis, 1–2 mm longis, margine scariosis et dorsaliter albovillosis, superioribus ovatis, 3.5–4.5 mm longis, rotundatis, integris; bracteae fertiles ovatae, 4.5–5 mm longae, rotundatae, integrae, matrice brunneola, nitida, area dorsali ovata, viridula, mediana vadosi costali. Sepala lateralia libera, subaequilateralia, lanceolata, ca.

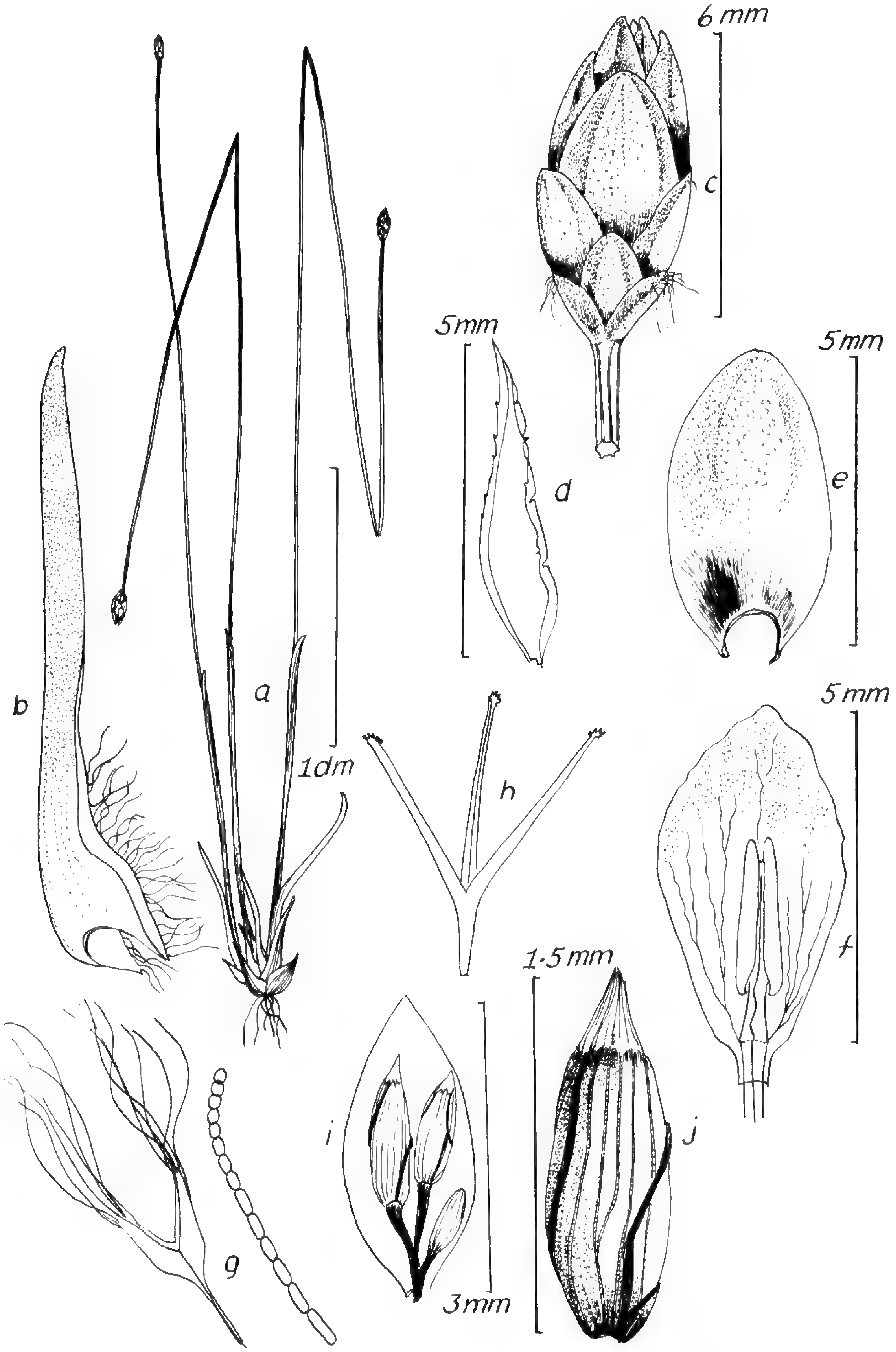


FIGURE 6. Xyris brachyfolia (Prance et al. 29079).—*a. Habit sketch.*—*b. Principal leaf.*—*c. Spike.*—*d. Lateral sepal.*—*e. Fertile bract.*—*f. Petal blade, stamen.*—*g. Staminode and beard hair.*—*h. Stylar apex.*—*i. Valve of capsule with attached placenta, seeds.*—*j. Seed.*

5 mm longa, acuta, delicatula, leviter curvata, ala carinali distaliter distante scabrolacera vel scabrida. Lamina petalorum obovata, luteola, ca. 5 mm longa, anguste rotundata, integra. Staminodia bibrachiata, brachiis longipenicillatis. Antherae lanceolatae, 1–1.2 mm longae; filiis ca. 1 mm longis. Capsula ca. 3 mm longa, ovoidea, placenta basalis-parietalis. Semina fusiformes, ca. 1.5 mm longa, translucentia, atroferruginea, valde longitudine costalis.

Cespitose perennial, smooth, 4–5 dm high. Stems short. Roots slender and fibrous. Principal leaves short, suberect, brownish, lustrous, shorter than the scape sheath, often strictly sheath, up to 5 cm long, then mostly sheath; sheaths white-villous-ciliate, gradually broadening to base, gradually narrowing to apex, eligulate; blades lightly flattened, excurvate, acute, entire. Scape sheaths elongate, to 1 cm long, multicostate, twisted, shining, short-bladed or cuspidate. Scapes slender, erect, twisted, terete toward apex, multistriate to shallowly costate, 0.7–0.9 mm thick. Spikes few-flowered, ellipsoid, becoming narrowly obovoid, 5–7 mm long. Bracts spirally and loosely imbricate, the dorsal area conspicuous; sterile bracts 5–6, the lowest broadly ovate to suborbicular, 1–2 mm long, marginally scarious and dorsally white-villose, the uppermost ovate, 3.5–4.5 mm long, rounded, entire; fertile bracts ovate, 4.5–5 mm long, rounded, entire, the matrix brown, lustrous, the dorsal area ovate, green, medially shallowly costate. Lateral sepals free, subequilateral, lanceolate, ca. 5 mm long, acute, delicate, slightly curvate, the keel distally distantly scabrolacerate or scabrid. Petal blades obovate, yellow, ca. 5 mm long, narrowly rounded, entire. Staminodes bibrachiate, the branches long-penicillate. Anthers lanceolate, 1–1.2 mm long, on filaments ca. 1 mm long. Capsule ca. 3 mm long, ovoid, the placentae basal-parietal. Seeds fusiform, ca. 1.5 mm long, translucent, deep red-brown, strongly ribbed longitudinally.

This species is morphologically closest to extremes of *X. fallax* Malme and is particularly noteworthy because of its transitional placentation type: basal-parietal. This is a further indication of the weakness of sections in *Xyris* based primarily on placentation. The long and strongly ribbed seeds with strong, irregularly raised outer seed coat are hardly distinguishable from those of *X. fallax*; pigmentation of leaves and scapes is likewise within the range of that species. However, the distinctly pale-villous patches on the spike bracts are notable and distinct. The sheath borders are consistently long-ciliate.

7. **Xyris neblinae** Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 26, fig. 11A–E. 1963. TYPE: Venezuela. T. F. Amazonas: summit savanna near west escarpment 2 km north of Cumbre Camp, occasional, 1,800 m, Cerro de La Neblina, Río Yatúa, 12 Jan. 1954, *B. Maguire, J. J. Wurdack & G. S. Bunting 37243* (holotype, NY; isotypes, US, VEN). Figure 7.

Tall, rushlike, cespitose, brittle perennial to 1 m tall, the stems contracted. Leaves erect, to 7 dm long; sheaths less than ½ as long as blades, firm, eciliate, dull-castaneous, nearly black, narrowing gradually from an abruptly dilated, deepset base to blade, at blade level with an erect, truncated ligule broader than leaf blade base; blades narrowly linear, terete except at the often narrow and dorsiventrally flattened base, ca. 1–1.5 mm thick, multiribbed; conic-subulate apically, the surface smooth except toward papillate base. Scape sheaths shorter than principal leaves, fluted, apically short-bladed. Scapes flexuous, twisted, terete distally, ca. 1 mm thick, ecostate, striate, sometimes papillate. Spikes ellipsoid to lance-ovoid, 1–2 cm long, acute and attenuate, reddish brown, of many, loosely and spirally imbricated papillose bracts with distinct, paler, red-brown to green dorsal areas, these with a low midnerve; sterile bracts several, oblong or narrowly ovate, slightly to much shorter than the fertile bracts, the lowest smallest and keeled, grading gradually into the fertile bracts, these ca. 8 mm long, broadly oblong, ciliolate, the backs convex and ecarinate, the apex broadly to narrowly rounded. Lateral sepals free, subequilateral, lineal, ca. 8–10 mm long, sometimes exsert-

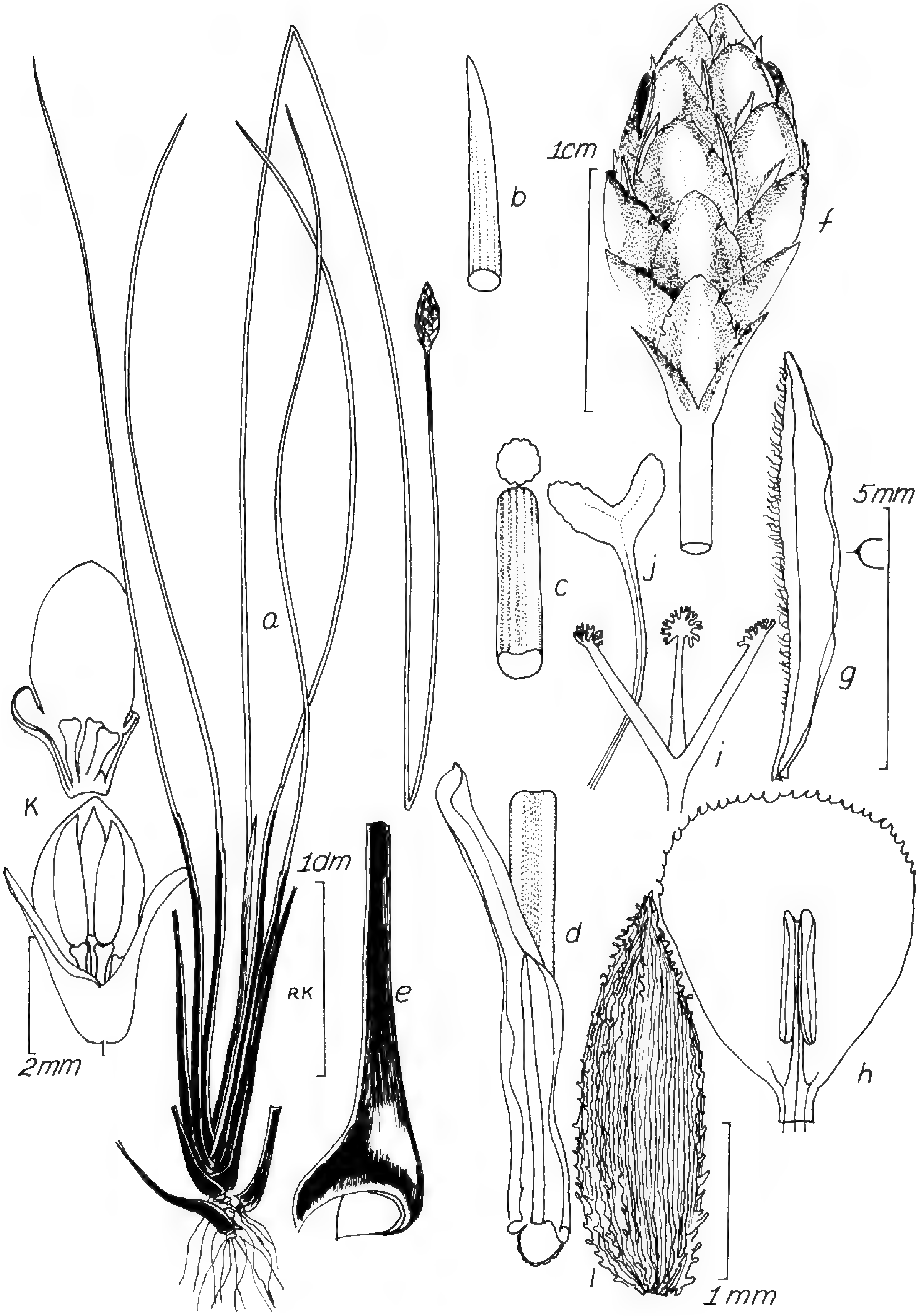


FIGURE 7. Xyris neblinae (Maguire et al. 37243).—*a. Habit sketch.—b. Leaf apex.—c. Sector of leaf blade a few cm above sheath apex.—d. Leaf sheath–blade junction.—e. Leaf base.—f. Spike.—g. Lateral sepal.—h.*

ed, the narrow, red-brown keel red-ciliolate or villosulous-ciliate from near base to the acute but blunt apex. Petal blades broadly obovate, 7–8 mm long, yellow, the broadly rounded apex lacerodentate. Staminodia bibrachiate, the short, broad, flat branches without hairs. Anthers lance-oblong, 2–2.5 mm long, emarginate, shallowly auriculate, on filaments ca. 1 mm long. Capsules obovoid, 4–4.5 mm long, the placentation basal, the funiculi stubby, the valves firm, dehiscing only ⅔ down, lacking septa. Seeds few, mostly 3–4 per capsule, cylindric, 2.5–3 mm long including a pale apiculus 0.5 mm long, the surfaces deep amber, longitudinally finely ribbed, the ribs (particularly toward base and tip of seed) muriculate, papillate or tuberculate.

Distribution. Known only from the type area, in wet rocky savanna.

This rare species, so far known only from Cerro de La Neblina, most resembles the brittle, rushlike *X. juncifolia* Maguire & Smith of Cerro Guaiquinima of neighboring Estado Bolívar in Venezuela. However, that species has leaf bases brown (rather than castaneous or near black), strongly inequilateral (versus equilateral) sepals, bearded (versus beardless) staminodia, and shorter and smoother seeds. Nonetheless, the superficial resemblance is striking.

8. **Xyris juncifolia** Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 26, fig. 10A–E. 1963. TYPE: Venezuela. Bolívar: common in Cumbre Camp, 2,000 m, Cerro Guaiquinima, Río Paragua, 25 Dec. 1951, *B. Maguire 32750* (holotype, NY; isotype, US). Figure 8.

Slender, rushlike, cespitose, brittle perennial to 1 m high, the stems contracted or short-ascending and short. Leaves erect or ascending, 4–6 dm long; sheaths dull brown or red-brown, less than ½ as long as blades, eciliate, narrowing gradually from a slightly dilated base to leaf blade, there producing an erect, firm, broad, rounded ligule to ca. 2 mm long; blades terete, fluted, narrowly lineal, to 1.5 mm thick, toward base above ligule usually deeply sulcate, toward apex narrowing to a blunt, callused tip. Scape sheaths much shorter than leaves, tubular and multiribbed proximally, opening distally, slightly dilated, with a cusplike, blunt-tipped blade. Scapes slightly flexuous and twisted, about the width of leaf blades or slightly wider, wandlike, distally terete, sometimes shallowly grooved. Spikes ellipsoid to obovoid, 1.5–2 cm long, reddish brown, acute, basally attenuate, of many tightly spirally imbricate, ciliolate bracts with distinct, deeper brown dorsal areas, the sterile bracts numerous, broadly ovate, broadly rounded, much smaller than and grading into the fertile bracts; these obovate, ca. 6 mm long, rounded-folded, ecarinate but with a pale, low midrib, the apex broadly rounded, aging lacerate. Lateral sepals free, strongly inequilateral, oblong-curvate, ca. 5 mm long, acute or blunt, the dark red-brown, firm keel ciliolate, toward apex reddish fimbriolate. Petal blades broadly elliptic or broadly obovate, ca. 5 mm long, the broadly rounded apex lacerate. Staminodia bibrachiate, the narrow flat branches distally long-penicillate. Anthers ca. 1.5 mm long, oblong, deeply bifid and sagittate, on filaments ca. 1.5 mm long. Capsule broadly obovoid, slightly compressed, ca. 3 mm long, the placentation basal, the valves producing low septa. Seeds few, ellipsoid-cylindrical, ca. 1.5 mm long, apiculate, deep amber, longitudinally rather coarsely 20–24-ribbed.

Distribution. Locally frequent, summits of tepuis Guaiquinima and Jaua, Bolívar, and tepuis Duida and Paru, Amazonas, Venezuela.

←
Petal blade, stamen.—i. Stylar apex.—j. Staminode.—k. Capsule; below with seeds on funicles, valves separating naturally, above with two valves removed, showing seedless funicles.—l. Seed showing ribbing and muriculation (seeds much darker than shown).

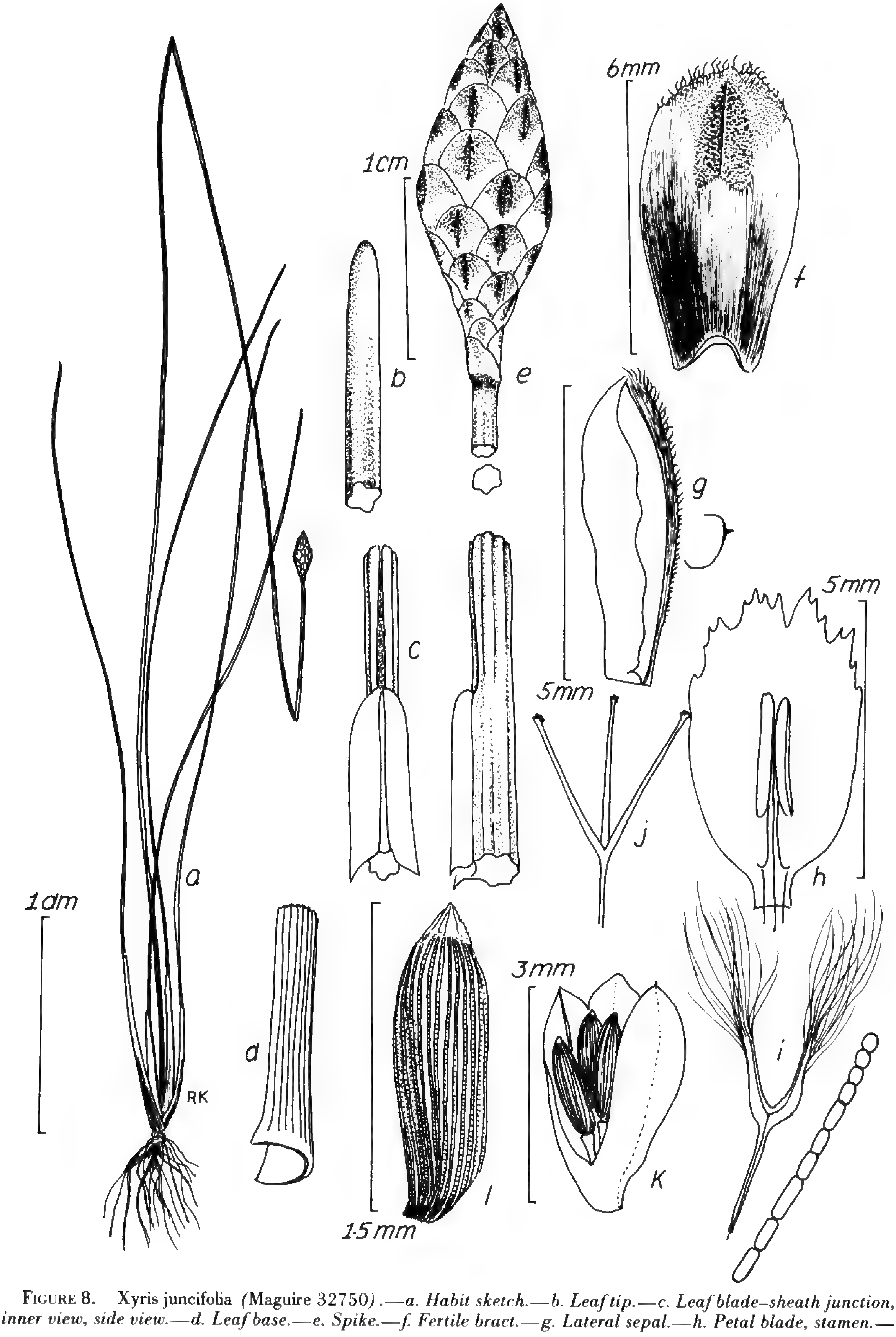


FIGURE 8. Xyris juncifolia (Maguire 32750).—*a. Habit sketch.*—*b. Leaf tip.*—*c. Leaf blade–sheath junction, inner view, side view.*—*d. Leaf base.*—*e. Spike.*—*f. Fertile bract.*—*g. Lateral sepal.*—*h. Petal blade, stamen.*—

This species, with its fusiform-ellipsoid spikes; terete, rushlike, brittle foliage; and distinct dorsal areas, most resembles *X. neblinae* of Cerro Neblina but differs in its inequilateral (rather than equilateral) lateral sepals and brownish (rather than castaneous) base. These two species and the Colombian *X. terrestris* form a complex of brittle-foliaged, rushlike xyrids closest to *X. atriceps* Malme subsp. *neblinensis*. Known until 1951 only from the type locality, *X. juncifolia* has now been collected from Cerro Jaua (*Steyermark et al. 109427*, NY, VEN), from Cerro Duida (*Steyermark 124560*, NY, VEN), and from Paru (*Cowan & Wurdack 31185*, GH, NY, US), as well as several times more from the type region.

9. **Xyris lanulobractea** Steyerm., Fieldiana, Bot. 28(1): 109, fig. 16D–H. 1951. TYPE: Venezuela. Bolívar: swampy ground, 1,200 m, Kavanayen, Gran Sabana, 26 Oct. 1944, *J. A. Steyermark 59336* (holotype, F; isotypes, US, VEN). Figure 9.

Slender, rushlike, cespitose, hard-based, glabrous perennial 4–7 dm high, the stems contracted. Leaves erect, 2–4 dm long; sheaths entire, elongate but less than ¼ of blade length, deep glossy red-brown, the backs ecarinate, the sides tapering gradually into blade, there with an erect ligule to 3 mm long; blades terete or oval in cross section, 0.5–0.7 mm thick, fluted, slightly flattened and deeply sulcate at base above ligule, apex tapering-subulate-conic or with very tip dilated clavately. Scape sheaths much shorter than leaves, tubular at base, multicostate, twisted, open at apex, keeled, stubby-bladed. Scapes slightly twisted, straight or flexuous, terete distally, ca. 1 mm thick. Spikes broadly ovoid to obovoid, 0.7–1(–1.5) cm long, blunt, dull brown, attenuate, the many spirally imbricate bracts with conspicuous dorsal areas; sterile bracts several, ovate, narrowly to broadly rounded, ecarinate, the lowest evidently much smaller than the fertile bracts, grading into them; fertile bracts broadly elliptic to obovate, ca. 6 mm long, with broadly rounded, white-villosulous borders, convex and ecarinate backs, and reddish brown, obovate or broadly elliptic dorsal areas. Lateral sepals strongly curvate, elliptic, ca. 4 mm long, thin, the broad firm keel ciliolate below middle, increasingly pale-villous-fimbriate above middle. Petal blades broadly obovate to suborbicular, yellow, ca. 5 mm long, the rounded apex serrulate-dentate. Staminodia bibrachiate, the slender recurved branches densely penicillate-pilose. Anthers oblong, 1 mm long, bifid and sagittate, on filaments ca. 1 mm long. Capsule obovoid, ca. 2 mm long, placentation basal, the valves without septa. Seeds few on short, stubby funicles, cylindrical or lance-ovoid, amber, 1.1–1.3 mm long, often angulate, finely ribbed longitudinally.

Distribution. Low to medium-elevation savanna, southeast Venezuela (Bolívar), Guayana, and contiguous northern Brazil (Amazonas).

Additional specimens examined. BRAZIL. AMAZONAS: rd. to Igarapé Preto ca. 60 km SE of Transamazon Hwy., 2 July 1979, *Calderon et al. 2743*; Mun. Humaitá, estrada da Humaitá–Jacarecanga, km 62, 17 June 1982, *Teixeira et al. 104.938* (INPA, NY, US, VDB). GUAYANA. UPPER MAZARUNI DIST.: Makwaima savanna near Mayoripai, at Kako River, 8 Feb. 1985, *J. Renz 14145* (U). VENEZUELA. BOLÍVAR: meseta norte de Serranía Caruban, 19 Feb. 1964, *G. Agostini 403* (NY, U, VEN); Auyantepui, Sept. 1937, *F. Cardona 262* (US, VEN); ca. 17 km al NE de Ikabarú, *Huber et al. 6732* (MYF, VDB, VEN); hacia Icabarú, 27 July 1983, *Huber & Alarcon 7891* (MYF, NY, VEN); 20 km NE de Uriman, *Huber 8474* (MYF, VDB); ca. 20 km NE Ikabarú, *Huber et al. 9650* (MYF, VDB, VEN); Valle de Río Karuay inferior, 18 Nov. 1984, *Huber et al. 9795* (MYF, VDB, VEN); ca. 35 km al W de Caserio de Chiguao, 23 Mar. 1985, *Huber 10355* (MYF, VDB, VEN); 46 km N of Sta. Elena, 28 July 1983, *Kral 70562*; Río Yuruani just above falls, 17 Dec. 1984, *Kral 72163*; N of Río Yuruani Ferry, *Kral 72194* (*Kral* numbers to be distributed, presently MYF, VDB); between Urarupata and Enemasic, 6 Feb. 1952, *Maguire 33234* (GH, US, VEN); 13 km NE

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i. Staminode.—j. Stylar apex.—k. Dehiscing capsule (note that dehiscence in this species is not to capsule base).—l. Seed.

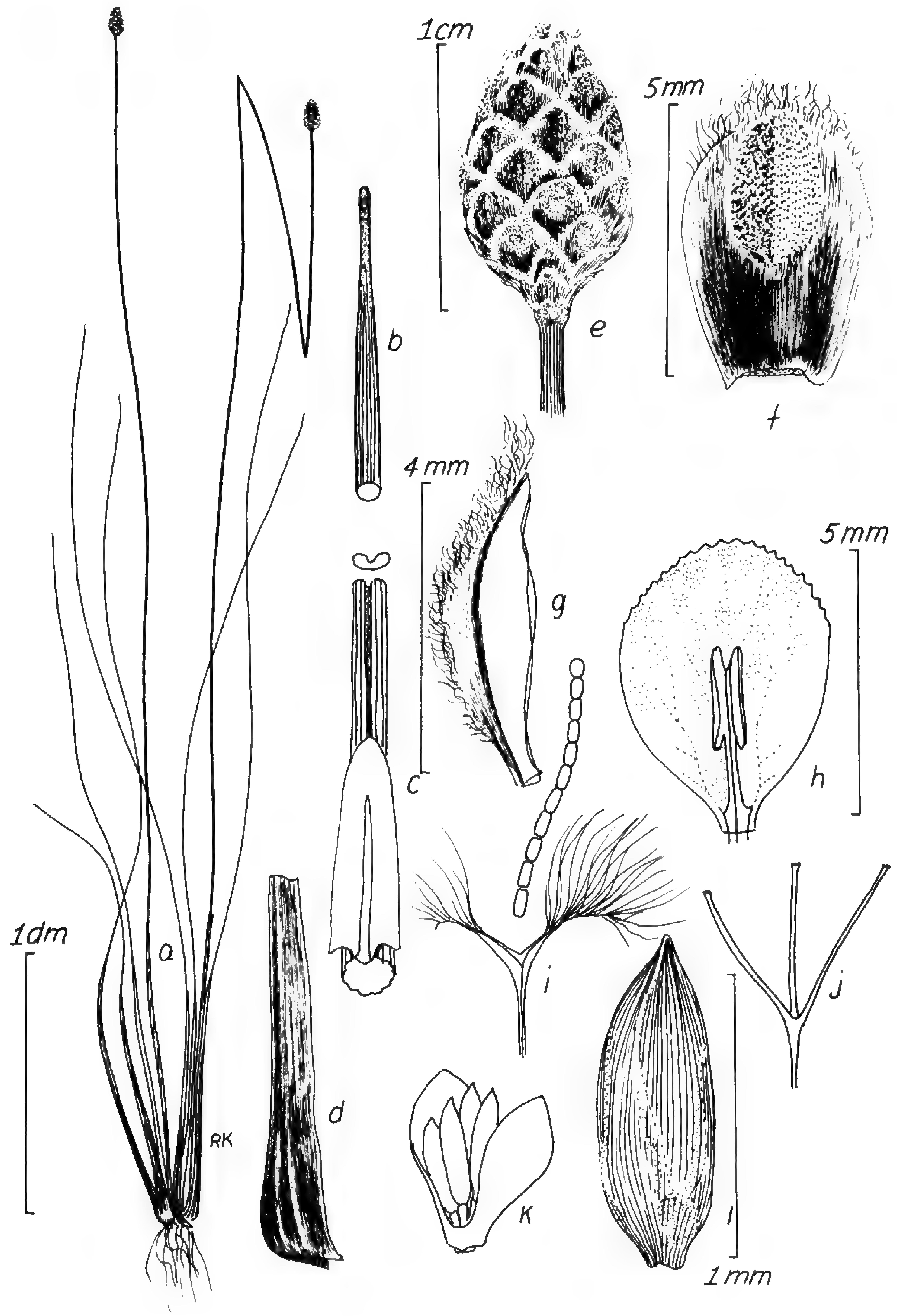


FIGURE 9. Xyris lanulobractea (Maguire 33234, Kral 70562).—*a. Habit sketch.—b. Leaf apex.—c. Leaf at sheath–blade junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal, stamen.—i. Staminode.—j. Stylar apex.—k. Capsule, one valve removed, showing placentation.—l. Seed.*

Sta. Elena, 2 Dec. 1982, *Steyermark & Liesner 127486* (VDB, VEN).

This slender morning bloomer is most similar superficially to *X. globosa* Nilsson, differing in its somewhat more slender habit, more tapering (rather than bulbous) base, more consistently terete leaf blades, ligulate sheath apex, plumose (rather than beardless) staminodes, and broader petal blades. Brazilian collections of *X. globosa* may well turn out to be *X. lanulobractea*.

10. Xyris terrestris Idrobo & Lyman B. Smith, Caldasia 6(29): 208, fig. 10. 1954. TYPE: Colombia. Vaupés: "Cerro de Caenda" (sabanas), 380–670 m, Río Kubiyu, 4 Nov. 1952, *H. García-Barriga 15090* (holotype, COL; isotypes, GH, NY, US). Figure 10.

Solitary or small-clumped, slender, smooth perennial 3–5 dm high, the stems short, erect from a short, stout, horizontal or ascending rhizome. Leaves mostly erect or ascending, twisted, 1–2.5 dm long; sheaths much less than ½ as long as blades, entire, proximally rich, lustrous red-brown or castaneous, strongly dilated at very base, thence upward gradually narrowing into an erect, narrowly triangular, chaffy ligule 3–6 mm long; blades filiform-linear, flexuous, terete or elliptic or rounded-angulate in cross section, 0.5–0.6 mm thick, yellow-green, blunt-conic at apex, longitudinally with a single, spiral, shallow to deep, papillate, usually rusty-colored sulcus. Scape sheaths shorter than leaves, with shorter blades similar to those of leaves. Scapes linear, twisted and flexuous, distally terete, ca. 0.5–0.6 mm thick, ecostate but multistriate. Spikes ellipsoid, or lance-ovoid, 0.7–2 cm long, subacute, attenuate-based, of numerous, spirally imbricate, stiff, brownish bracts, the sterile bracts numerous, the lowest lance-triangular, keeled, much smaller than, and grading into, the fertile bracts, these mostly broadly obovate, broadly to narrowly rounded apically, 4–5 mm long, the margins entire to erose in age, the back rounded, ecarinate, with strong but small, red-brown to yellow-brown, elliptic dorsal areas. Lateral sepals strongly curvate, oblong, ca. 4 mm long, free, very inequilateral, the broad, deep, reddish brown keel scabrociliate from near base to blunt apex. Petal blades obovate, ca. 4 mm long, yellow, the broadly rounded apex erose-denticulate. Staminodia bibrachiate, the flattened branches long-penicillate. Anthers oblong, ca. 2 mm long, shallowly bifid and auriculate, on filaments ca. 0.5 mm long. Capsule narrowly obovoid-apiculate, brown, 2–2.5 mm long, dehiscing only ⅔ way to base, the placenta massive and basal, the funiculi short, broadly clavate. Seeds several, cylindric-fusiform, 1.3–1.5 mm long, red-amber, irregularly anastomosing-ribbed longitudinally.

Distribution. Sandy savannas, Vaupés, southeastern Colombia, rare.

Additional specimens examined. COLOMBIA. VAUPÉS: Mesa de Yambi savanna, 15–16 Apr. 1953, *Schultes & Cabrera 14235A* (COL, GH, NY, U, US); Araracuara savannas, Río Caquéta, 6 Sept. 1959, *Maguire & Fernandez 44163* (NY).

There are so many species shared by border states in Colombia and Venezuela that it is reasonable to expect this plant to be found in T. F. Amazonas in Venezuela, where there is much savanna suitable for it.

11. Xyris scabridula Steyerm., Fieldiana, Bot. 28(1): 111. 1951. TYPE: Venezuela. T. F. Amazonas: around rills on rocky dry ridgetop, Brocchinia Hills, 1,700–1,900 m, Cerro Duida, 1 Sep. 1944, *Steyermark 58168* (holotype, F; isotypes, NY, VEN). Figure 11.

Slender, cespitose perennial 1.8–4 dm high, the stout stems mostly contracted. Leaves shorter than scape sheaths, strongly flexuous and twisted, mostly erect; sheaths eciliate, ¼ or less of blade length, firm, at very base deep red-brown or castaneous, strongly ribbed, lustrous, becoming roseate or purple above, scabridulous, narrowing gradually to blade; blades variously elongate, strongly rib-angled in cross section, also deeply sulcate, narrowly linear, ca. 1 mm thick, reddish or purplish and pale-

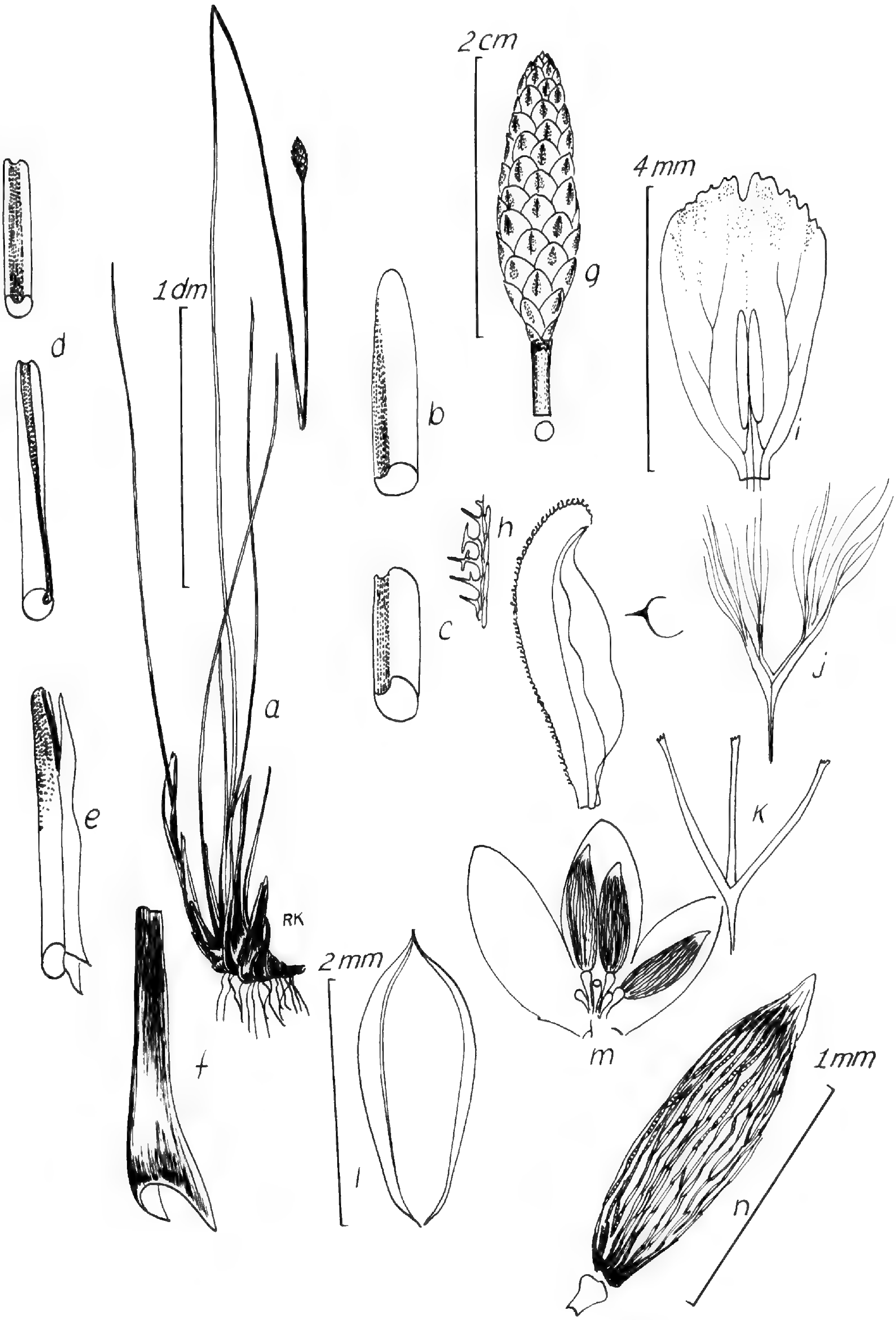


FIGURE 10. Xyris terrestris (Schultes & Cabrera 19179).—*a. Habit sketch.*—*b. Leaf apex.*—*c. Leaf blade a few cm below apex.*—*d. Further down leaf blade than c (and more reduced).*—*e. Leaf sheath–blade junction.*—*f. Leaf base.*—*g. Spike.*—*h. Lateral sepal and greatly enlarged sector of keel hairs.*—*i. Petal blade, stamen.*—*j. Staminode.*—*k. Stylar apex.*—*l. Outline of capsule.*—*m. Dehisced capsule showing basal placentation.*—*n. Seed.*

scabridulous toward base, smooth, green toward tip, narrowed abruptly to a blunt, callused apex. Scape sheath much shorter than blade, mostly tubular, twisted, strongly multicostate, reddish brown or pink at base, distally with a short, blunt cusp. Scapes twisted and flexuous, subterete toward apex, ca. 0.8 mm thick, with 1–3(–4) strong, smooth costae and some less distinct ribs, or nearly ecostate, proximally strongly multicostate. Spikes ovoid, 7–8 mm long, of several erect, spirally imbricate, ecarinate, brown, definitely papillate bracts without dorsal areas, the sterile bracts several, the lowest much smaller than the fertile bracts, orbicular or reniform, gradually grading into fertile bracts, these 4–5 mm long, broadly obovoid, broadly rounded apically, appearing entire but minutely papillate-ciliate. Lateral sepals free, equilateral, elliptic and strongly curvate, ca. 4 mm long, obtuse, the keel rusty-ciliolate.

Distribution. Cerro Duida, Territorio Federal Amazonas, and Chimantá Massif, Estado Bolívar, Venezuela.

Additional specimens examined. VENEZUELA. BOLÍVAR: savanna summit of Macizo Chimantá, *Huber & Colella 9001* (NY, VDB, VEN); *Huber & Steyermark 7162* (NY, VDB, VEN); *Huber et al. 9070* (NY, VDB, VEN); *Huber 9576* (NY, VDB, VEN); *Steyermark & Wurdack 1010* (F); *Steyermark et al. 115922* (F); *Steyermark 128429* (VDB, VEN).

This taxon has some affinity to *X. subglabrata* Malme of lower elevations in T. F. Amazonas, Venezuela, but has smoother spikes with no evident dorsal area. It also resembles *X. stenophylloides* Malme, an equally rare plant from the same area, whose leaf blades, though very narrow, are flattened. None of these species are much collected, so that comparisons of flowers and seeds are not yet made.

12. Xyris atriceps Malme, Bull. Torrey Bot. Club 58: 325. 1931. TYPE: Venezuela. T. F. Amazonas: forming tussocks, 6,700 ft., Cerro Duida, Ridge 15, Aug. 1928–Apr. 1929, *G. H. H. Tate 688* (lectotype, NY; isolectotype, US).

Densely tufted, slender, low to tall perennials 2–6 dm high, the stems short to elongate, up to 5 cm long. Leaves elongate, linear to filiform, erect or ascending, 1.5–3 dm long; sheaths deep reddish brown to nearly black, lustrous, smooth to papillose-rugulose apically, less than ½ as long as blades, entire, tapering evenly from broad, ecarinate base to distinct, firm or thin, erect, broad ligule 2–10 mm long, there broader than the usually terete blade; blades deep green, linear to filiform, 0.5–1 mm thick, sometimes fluted, usually with a median ventral sulcus, the apex blunt, broadly rounded or truncate, rarely conic, smooth, the surfaces smooth except toward the often rugulose-papillose base. Scape sheath shorter than leaves, loose, often purplish, rarely pink, the blade short, erect, blunt. Scapes flexuous or straight, twisted, terete, 0.5–1 mm thick, smooth or white-puncticulate from sunken stomata. Spike ovoid to oblong or obovate-turbinate, 0.5–1.5 cm long, the base attenuate, of several pale to deep brown or castaneous, spirally loosely imbricate bracts without distinct dorsal areas. Sterile bracts up to 6, erect or squarrose-tipped, triangular to obovate, entire to lacerate or ciliolate-villosulous-bordered, smaller than and grading into the fertile bracts, these oblong to obovate, 3.5–8 mm long, entire to villosulous-ciliate, ciliolate or pectinate-lacerate, the backs broadly rounded, smooth to papillose. Lateral sepals free, subequilateral, straight or curvate, linear or oblong-linear, 3.5–7 mm long, acute, sides pale brown, keels deep reddish brown, ciliolate to densely villous-ciliate. Petal blades broadly obovate to suborbicular, 6–7 mm long, the broadly rounded apex coarsely erose. Staminodia bibrachiate, the branches long-penicillate, or staminodia absent (subsp. *marahuacae*). Anthers oblong to lance-oblong, 2–2.5 mm long, shallowly bifid apically, deeply sagittate at base, on filaments ca. 1 mm long. Capsule cylindric to ovoid or ellipsoid, ca. 3–4 mm long, placentation appearing central but capsule valves with septa from base to near apex. Seeds several, deep reddish brown, cylindric or ellipsoid, 1.5–2 mm long, including a short-

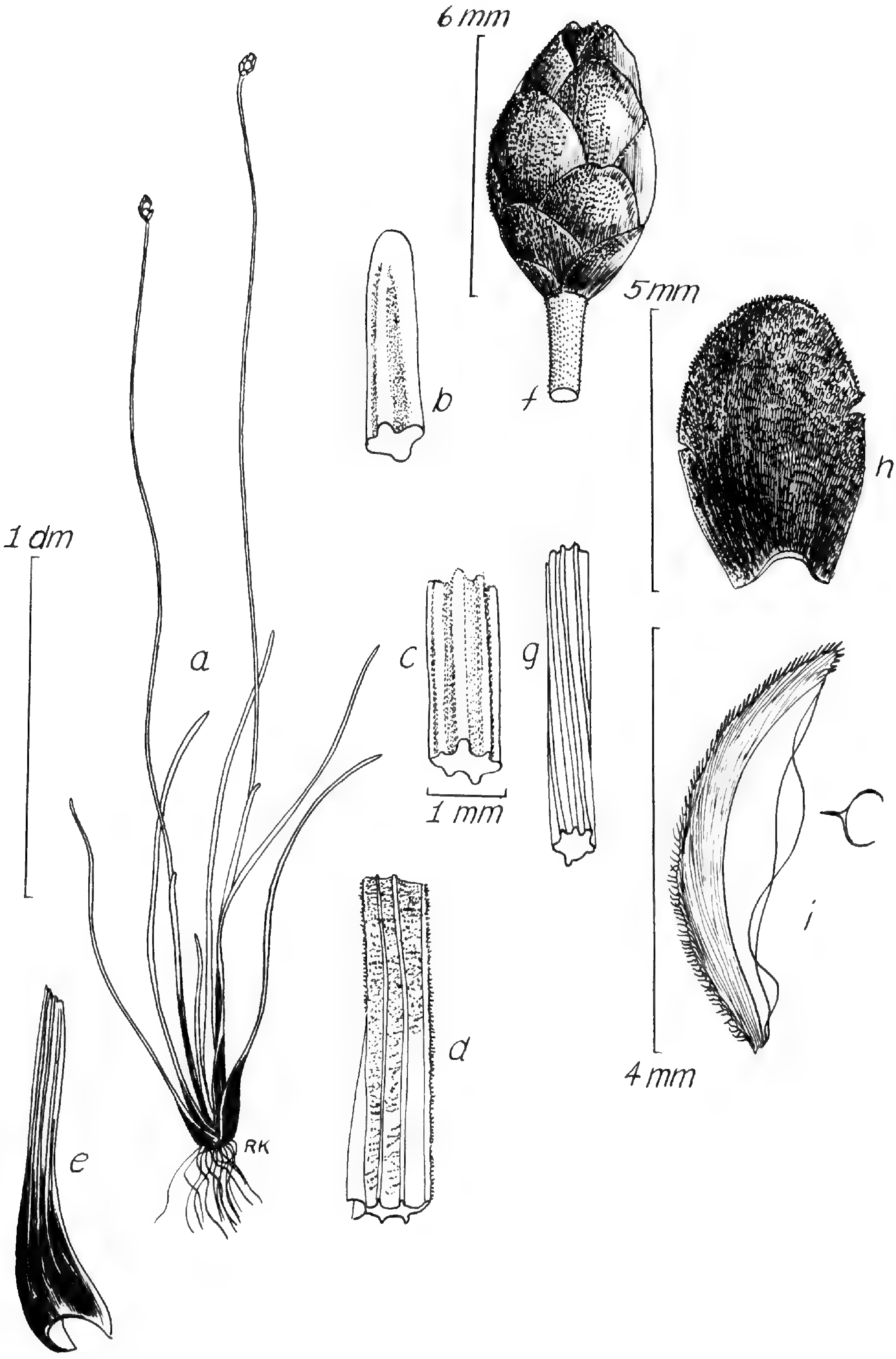


FIGURE 11. Xyris scabridula (Steyermark 58168).—*a. Habit sketch.—b. Leaf apex.—c. Leaf sector at midblade.—d. Leaf blade-sheath junction.—e. Leaf base.—f. Spike, scape apex.—g. Midscape.—h. Fertile bract.—i. Lateral sepal.*

conic, pale appendage, the seed body finely but distinctly longitudinally ribbed.

Distribution. This species appears to be confined to higher elevations in the higher tepuis of Bolívar and T. F. Amazonas, Venezuela (and probably contiguous Brazil), and sorts to four fairly distinct morphologies, here given rank of subspecies, keyed as follows:

KEY TO SUBSPECIES OF *XYRIS ATRICEPS*

1a. Spikes narrowly obovoid; leaf blades lacking sulcus; bracts subentire, with a low costa distally, the bract margins ciliolate with yellowish hairs .... subsp. *neblinensis*
1b. Spikes narrowly to broadly obovoid; leaf blades sulcate at least ventrally; bracts becoming lacerate, ecostate distally, the bract margins various.
  2a. Spikes under 1 cm long; leaf blades under 1 mm thick; bearded staminodia present.
    3a. Spike broadly obovoid, base strongly attenuate; bract edges distally white ciliate and erect .... subsp. *atriceps*
    3b. Spike narrowly obovoid or ellipsoid or ovoid, base short-attenuate if at all so; bract edges sordidly villosulous, usually becoming very lacerate, subsquarrose .... subsp. *chimantensis*
  2b. Spikes 1–1.5 cm long; leaf blades ca. 1 mm thick; staminodia absent .... subsp. *marahuacae*

12A. **Xyris atriceps** Malme subsp. **atriceps.** Figure 12A (in part).

Spikes broadly obovoid, attenuate-based, ca. 7 mm long, the bracts erect, the margins white ciliate; staminodial beard present; seeds ca. 1.5 mm long.

Distribution. This subspecies is still known only from southern Cerro Duida, the type area. Additional material from the type area is *Steyermark 58185* (F, US).

12B. **Xyris atriceps** subsp. **chimantensis** Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 19–20. 1963. TYPE: Venezuela. Bolívar: locally frequent, Río Tirica, 1,925 m, 5 Feb. 1955; Chamantá Massif, *J. A. Steyermark & J. J. Wurdack 485* (holotype, NY; isotype, US). Figure 12A, a–f, g (left)–i (left).

Spikes ellipsoid or narrowly obovoid, ca. 6–7 mm long, acute at base, the bracts loosely imbricate, narrower than in type, the margins at first sordidly villosulous, later becoming much lacerate, spreading; staminodial beard present; seeds ca. 1.5 mm long.

Distribution. Abundant locally in high savanna of Chimantá Massif and taxonomically closest to subsp. *atriceps.* Now frequently collected from the summit elevations of the Massif as follows.

Additional specimens examined. VENEZUELA. BOLÍVAR: *Huber et al. 9066* (NY, VDB, VEN); *Steyermark et al. 115852* (VEN), *128008* (VEN, VDB), *128958* (VEN, VDB), *128810* (VEN), *129908* (MYF, VDB, VEN); *Steyermark 128167* (VEN), *128854* (VEN).

12C. **Xyris atriceps** subsp. **marahuacae** Kral & Lyman B. Smith, subsp. nov. TYPE: Venezuela. T. F. Amazonas: Dept. Atabapo, Cerro Marahuaca, cumbre, parte central de la meseta Sur-Este, al lado de una grieta, a lo largo de la Quebrada Yekuana, afluente del Río Negro, 3°40′30″N, 65°26′20″W, 2,560 m, 10–12 Oct. 1983, *Steyermark 129579* (holotype, VEN; isotype, VDB). Figure 12B.

Planta fragilis, perennis, caespitosa, 4–5 dm alta, glabra. Radices graciles. Caules breves aut elongatis, usque ad 5 cm longi. Folia principalia erecta, usque ad 3 dm longa, torta, flexuosa, vaginis scaporum longiora; lamine 6–10-plo vaginis longiores, anguste lineares, teretes, 1–3-sulcatae, ca. 0.8–1.2 mm crassae, olivaceae, ad basin ventraliter profunde sulcatae; apices peranguste conici; vaginae ecarinatae, nitidae, atrocastaneae, integrae, ad basin dilatatae, in laminas gradatim, tum abrupte decrescentes, ad apicem ligulatae, ligula rigida erecta linearo-triangulata, usque ad 1 cm longa. Vaginae scaporum prope basin castaneae, apicem versus apertae, laminis elongatis, laminis foliorum similibus sed angustioribus. Scapi leviter torti, teretes, ca. 1 mm crassi, multistriati, olivacei vel brunneoli. Spicae multiflorae, anguste vel late obovoideae, ca. 1 cm longae, obtusae. Bracteae erectae, laxe spiraliter imbricatae, firmae, ecarinatae, rigidae, fuliginosae, sine area dorsali, ad apicem villosiciliatae, tum valde laceratae, eciliatae; bracteae steriles ovatae, plures, fertilibus breviores, in fertiles gradatim transientes; bracteae fertiles late obovatae, 7–8 mm longae, ad apicem late rotundatae. Sepala lateralia libera, subaequilatera, oblanceolata, atrobrunneola, 6.5–7 mm longa, leviter curvata, obtusa; ala carinali a medio ad apicem aut solum

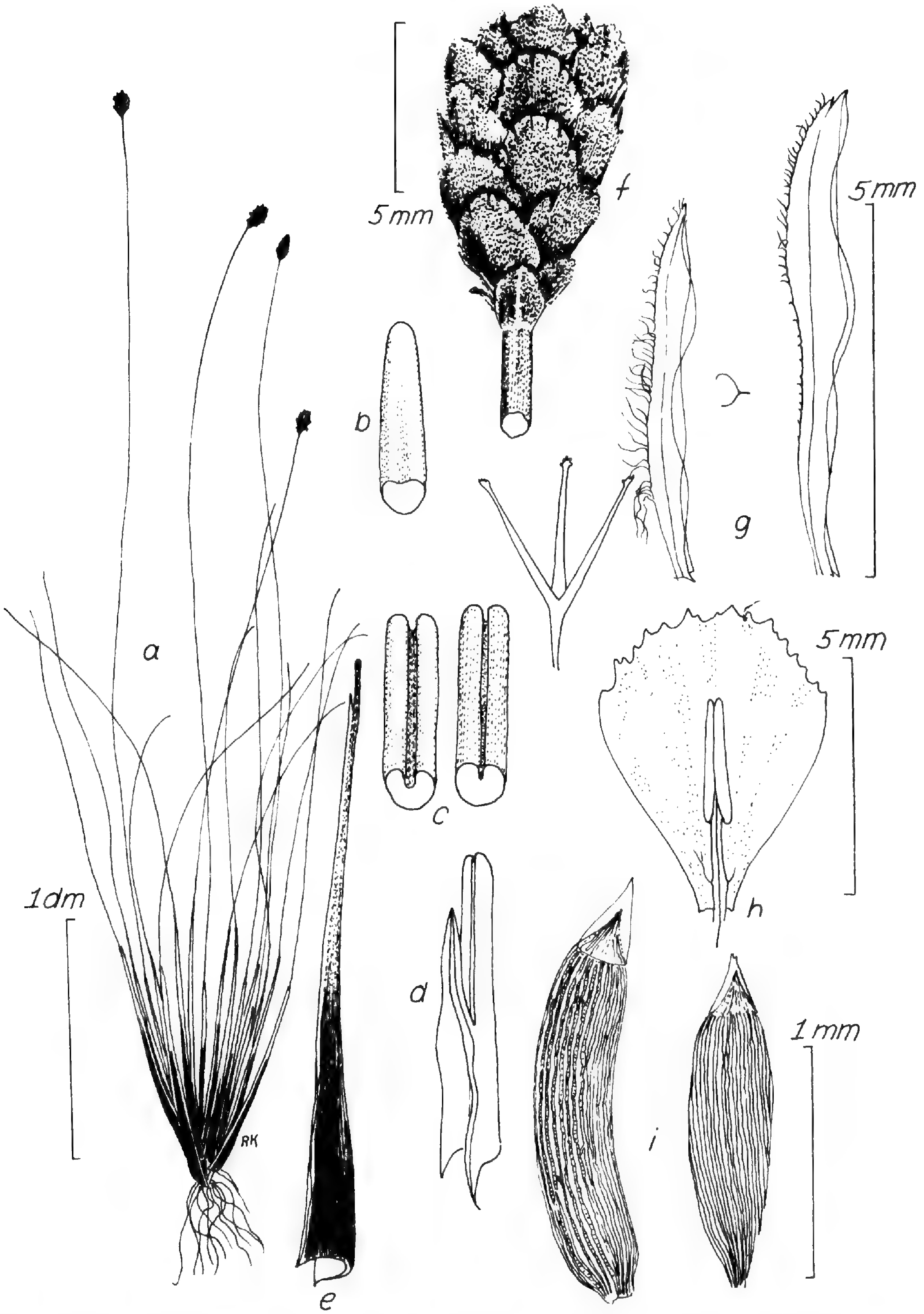
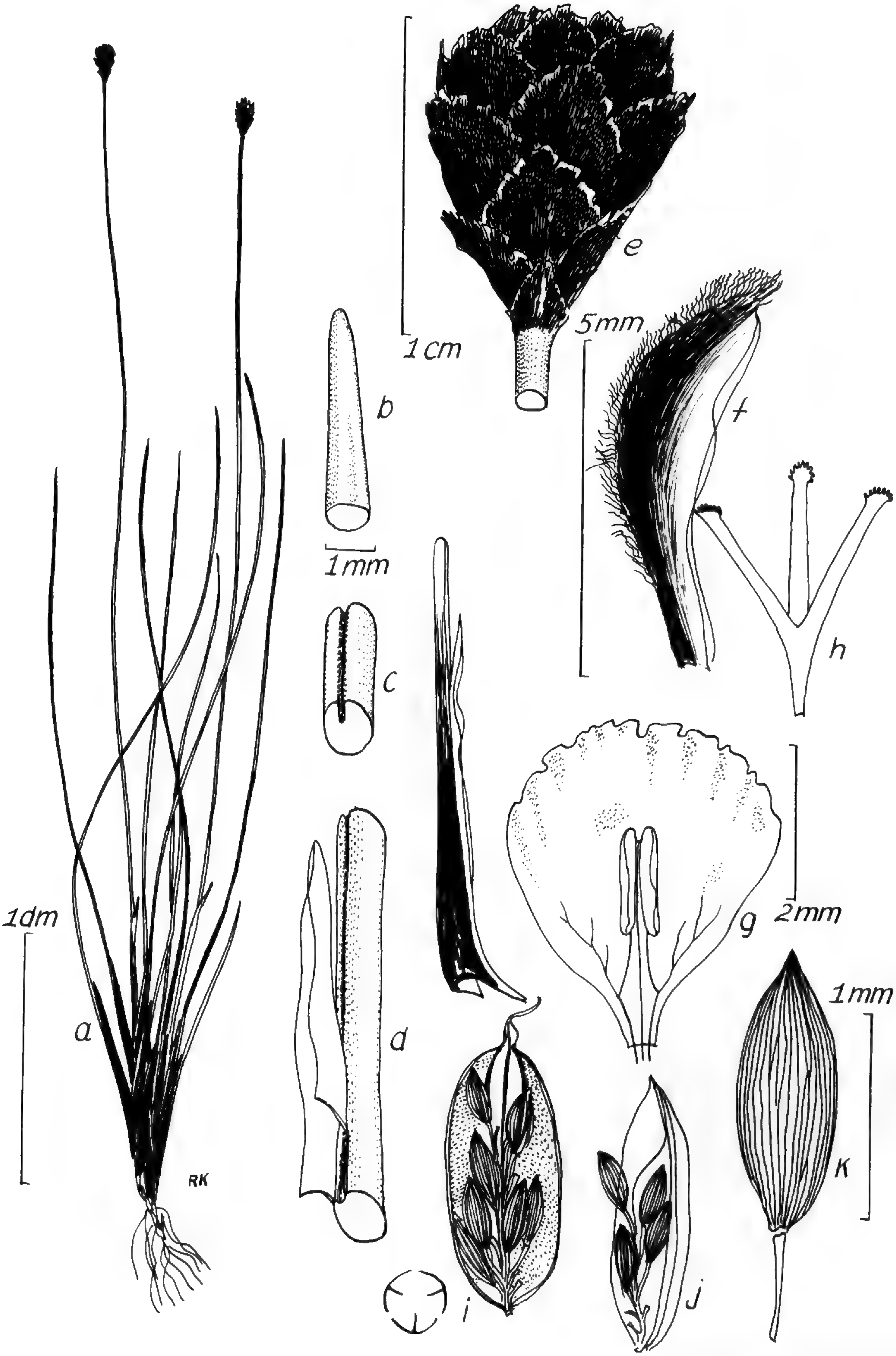


FIGURE 12A. Xyris atriceps.—*a. Habit sketch (subsp.* chimantensis*).—b. Leaf apex (general).—c. Leaf blade, midblade (general).—d. Leaf blade-sheath junction (general).—e. Leaf base (general).—f. Spike (subsp.* chimantensis*).—g. Lateral sepal (at left subsp.* chimantensis, *at right subsp.* neblinensis*).—h. Petal blade, stamen, stylar apex (general).—i. Seeds (at left subsp.* neblinensis, *at right subsp.* chimantensis, *subsp.* atriceps*).*

→

FIGURE 12B. Xyris atriceps *subsp.* marahuacae *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Leaf blade, midblade sector.—d. Leaf sheath-blade junction (at left); leaf base (at right).—e. Spike.—f. Lateral*



sepal.—g. Petal blade, stamen.—h. Stylar apex.—i. Capsule, idealized section showing two septa (stippled), placentation, vascular supply to funiculi).—j. Valve removed, showing ovular attachment to inner edge of valve septum.—k. Seed (from quasimature fruit).

ad apicem villosifimbriolata. Laminae petalorum late obovatae, ca. 6–6.5 mm longae, apice late rotundatae. Staminodia nulla. Antherae oblongae, ca. 2 mm longae, leviter emarginatae et auriculatae; filiis ca. 1.5 mm longis, latis. Capsula matura ellipsoidea, ca. 4 mm longa, valvis capsulae profunde septatis a medio ad basin. Semina numerosa, ellipsoidea, ca. 1.5 mm longa, translucida, longitudine multilineata.

Brittle, tufted, glabrous perennial 4–5 dm high. Roots slender. Stems short or elongate, up to 5 cm long. Main leaves erect, to 3 dm long, twisted, flexuous, longer than the scape sheaths; blades 6–10 times longer than the sheaths, narrowly linear, terete, 1–3-sulcate, ca. 0.8–1.2 mm thick, olive-green, deeply sulcate ventrally at base; tips narrowly conic; sheaths ecarinate, shining, deep castaneous, entire, dilated at base, narrowing gradually, then abruptly, to blades, ligulate at apex, the ligule rigid, erect, linear-triangular, to 1 cm long. Scape sheaths castaneous toward base, opening toward apex, elongate-bladed, with blades similar to those of leaves but narrower. Scapes slightly twisted, terete, ca. 1 mm thick, multistriate, olivaceous to brown. Spikes multiflorous, narrowly to broadly obovoid, ca. 1 cm long, obtuse. Bracts erect, loosely spirally imbricate, firm, ecarinate, rigid, sooty brown, without dorsal area, villous-ciliate at apex, aging strongly lacerate, eciliate; sterile bracts ovate, several, shorter than the fertile bracts and passing gradually into them; fertile bracts broadly obovate, 7–8 mm long, broadly rounded at apex. Lateral sepals free, subequilateral, oblanceolate, deep brown, 6.5–7 mm long, slightly curvate, obtuse; keel villous-fimbriolate from middle to tip or solely at tip. Petal blades broadly obovate, ca. 6–6.5 mm long, broadly rounded apically. Staminodia none. Anthers oblong, ca. 2 mm long, slightly emarginate and auriculate; filaments broad, ca. 1.5 mm long. Quasimature capsules ca. 4 mm long, ovoid, with valves deeply septate from middle to base; seeds numerous, ellipsoid, ca. 1.5 mm long, translucid, longitudinally prominently multilined.

Paratypes. All from the same massif as the type: 2–9 Feb. 1975, *S. S. Tillett et al. 752-333* (NYF, US, VEN); 16 Feb. 1981, *Steyermark et al. 124371* (NY, VDB, VEN); 1–2 Feb. 1982, *Steyermark et al. 126038* (VDB, VEN); 2 Feb. 1982, *Steyermark et al. 126038* (VDB, VEN); 1–2 Feb. 1982, *Steyermark et al. 125992* (VDB, VEN); 9–10 Feb. 1982, *Steyermark et al. 126293* (VDB, VEN); 26 Mar. 1982, *Steyermark & Delascio 129201, 129224* (VDB, VEN); 12–13 Oct. 1983, *Steyermark 129476* (MO, VDB, VEN).

This subspecies, abundant on summits of Cerro Marahuaca, is robust as is subsp. *neblinensis* and has the thickest spikes and leaves, lacks staminodia, and has very distinctively villose sepal keels and tips, with tips of young bracts also densely villous-ciliate.

12D. Xyris atriceps subsp. **neblinensis** Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 19. 1963. TYPE: Venezuela. T. F. Amazonas: Cerro de La Neblina, Río Yatua, locally abundant, east escarpment of Upper Caño Grande basin, at 1,900 m, summit, 1,200–2,200 m, *B. Maguire, J. J. Wurdack & C. K. Maguire 42416* (holotype, NY; isotypes, GH, K, US). Figure 12A, g (right), i (left),

Leaves mostly esulcate; spikes narrowly obovoid, the bracts light brown, entire, with a low costa toward apex, the margin ciliate with short, yellowish hairs. Seeds ca. 2 mm long, the longest in the complex.

Distribution and remarks. This subspecies appears to be relatively common in the high, wet open paramolike summit elevations along the Neblina Massif and has been found by several collectors.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: Neblina Massif: *Liesner 16000* (MO, NY, VDB, VEN); *Maguire et al. 37244, 42342* (NY, US); *Steyermark 103966* (NY, US, VEN); *Thomas & Plowman 3080* (MO, NY, VDB, VEN). BOLÍVAR: Chimanta Massif, *Huber et al. 10151* (MYF, VDB, VEN) (intermediate between this and the subsp. *chimantensis*).

13. Xyris involucrata Nees in J. Bot. (Hooker) 2: 397. 1840. TYPE: "British Guiana, *Schomburgk 1054*" (lectotype, K; isolectotypes, K, L). Figure 13.

X. asterocephala Seub. in C. Martius, Fl. Bras. 3(1): 219. 1855.

Solitary or tufted, rather soft-based, stiff, short-lived perennial 2–6 dm high, the stems

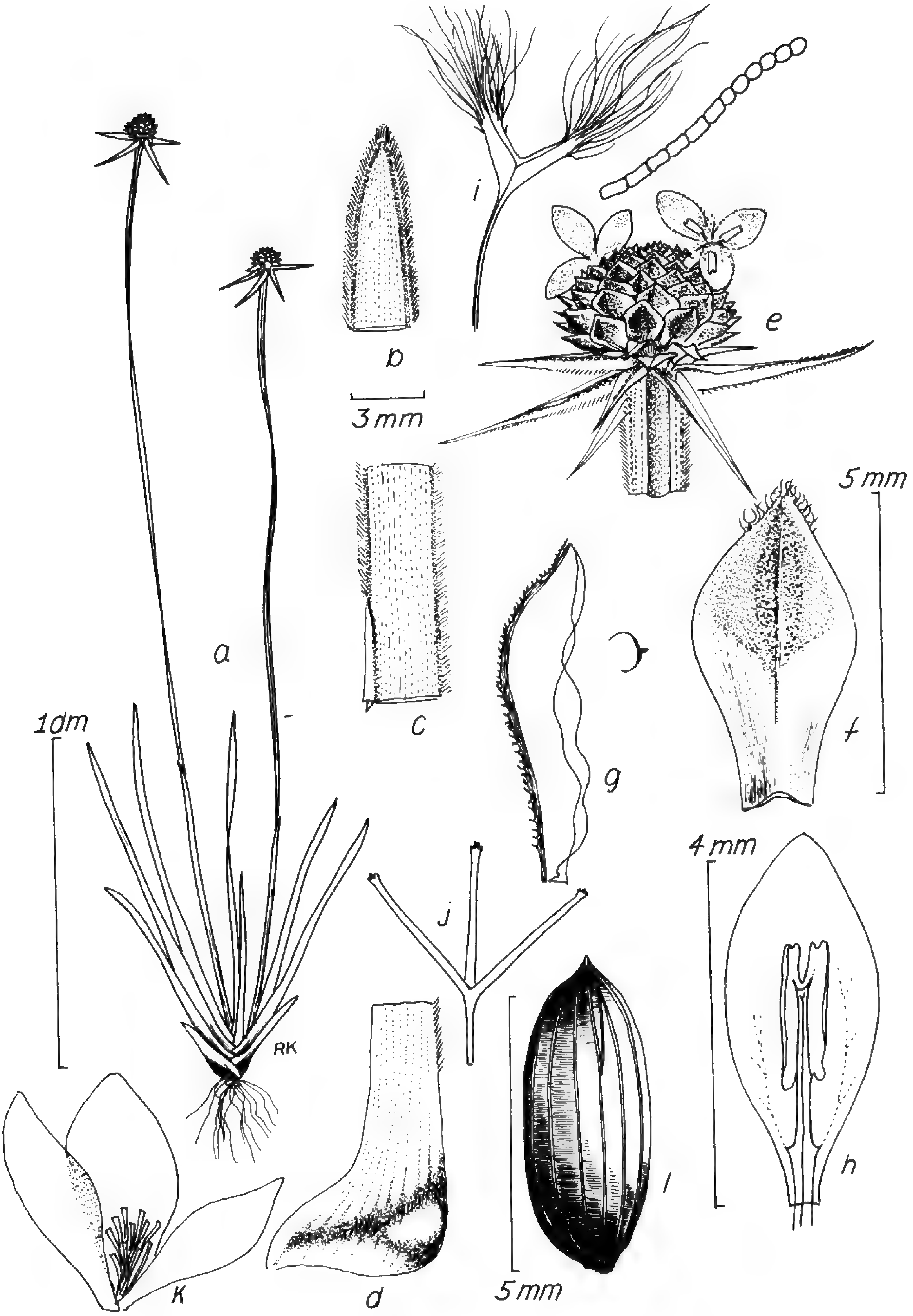


FIGURE 13. Xyris involucrata (Koyama & Agostini 7261).—*a. Habit sketch.—b. Leaf tip.—c. Leaf blade-sheath junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode.—j. Stylar apex.—k. Open capsule.—l. Seed.*

contracted. Leaves spreading flabellately 1–3 dm long, the sheaths entire, equal in length to blade or longer, sharply keeled, often castaneous at very base, abruptly dilated, green or stramineous above, narrowing gradually to blade, eligulate; blades broadly linear, flat, 3–7 mm wide, at apex abruptly rounded or broadly incurved-acute, bright pale green with submarginal reddish borders, edges white-ciliate. Scape sheaths shorter than leaves, sharply keeled, short-bladed. Scapes rigid, straight or slightly twisted, ancipital, strongly flattened distally, 3–4 mm wide, edges pale-ciliate, surface on either side of the strong and subterete scape center low-ribbed, smooth. Spikes hemispherical to broadly ovoid or subglobose, 0.5–1 cm long (sometimes longer in fruit), the bracts in tight flat spirals, the lowest several bracts sterile, foliaceous, spreading leaflike, the bases strongly ciliate-keeled, the blades ciliate as in leaves, the inner sterile bracts progressively shorter, grading into the fertile bracts, the fertile bracts ca. 4(–5) mm long, firm, erect or spreading, rhombic or oblong-obovate, acute or short-acuminate, often villosulous-ciliate at apex, the shallowly convex-rounded backs with a large, medially papillate, rhombic, reddish brown dorsal area, bisected medially by a narrow but evident midrib. Lateral sepals free, subequilateral, oblong-curvate, ca. 3 mm long, blunt, thin, the darker, firm keel reddish ciliate or ciliolate from below middle to tip. Petal blades elliptic, 4–5 mm long, acute, entire, yellow. Anthers oblong, ca. 1.5 mm long, deeply bifid and sagittate, on filaments ca. 1 mm long. Staminodia bibrachiate, the flat triangular branches apically plumose with penicillate hairs. Capsule broadly obovoid, planoconvex, ca. 2 mm long, the placentation basal, the valves not producing septa. Seeds ellipsoid-cylindric, 0.5–0.6 mm long, apiculate, dark amber, lustrous, longitudinally with a few narrow but distinct ribs and very finely cross-lined.

Distribution. Low- and high-altitude wet savanna (up to 1,500 meters), southeastern Colombia eastward across the Guayanas into Surinam, southward into the Amazon Basin of northern Brazil.

As in the capitate-spiked, involucrate xyrids, this one, which blooms from late morning into the afternoon, has several lovely pale yellow flowers simultaneously. This effect, along with that of the bright pale green, red-bordered leaves and bracts and the gaudy, eryngiumlike inflorescences, makes it one of the more handsome plants of the Guayana boglands. Its affinities are with the recently described *X. egleri* Smith & Downs of Pará, Brazil, a smoother plant with shorter involucral bracts, and with the following species, here described as *X. pallidula*, likewise from Pará.

14. Xyris pallidula Kral & Wanderley, sp. nov. TYPE: Brazil. Amazonas: Mun. Humaita, estrada Humaita–Jacarecanga, km 150, a 60 km ao Sul. Campo natural, solo arenoso. Erva de 40 cm de altura; flores amarelas, 21 June 1982, *L. O. A. Teixeira, A. J. Fife, K. McFarland, C. D. A. Mota, J. L. dos Santos, S. P. Gomes & B. W. Nelson 1263* (holotype, INPA; isotypes, NY, VDB). Figure 14.

Herba perennis, caespitosa, 6–7 dm alta, glabra. Caules breves. Radices graciles. Folia principalia leviter flabellate expansa, 10–17 cm longa, vaginis scaporum parum breviora; vaginae elongatae, integrae, laminis 1–2-plo laminis longiora, pallide rufobrunneolae, e basi ad apicem gradatim decrescentes, eligulatae; laminae valde compressae, anguste lineario-gladiatae, 2–3 mm latae, pallide olivaceae, margine pallide ferruginea, leviter incrassata, papillosa, apice incurvato-acuta. Vaginae scaporum basin versus multicostatae, ferrugineae, nitidae, apicem versus valdae carinatae, lamina ut in laminis foliorum sed breviore. Scapi rigides, lineares, leviter torti, pallide olivacei, apicem versus in sectio transversali elliptici, laterale valde acute bicostati. Spicae multiflorae, late ovoideae vel turbinatae ad hemisphericae, ca. 10 mm longae, involucratae, pallide brunneolae. Bracteae involucrales plures, expansae, subuliformes, 7–15 mm longae, abrupte in bracteas spicae transientes; bracteae spicae rhomboideo-obovatae, 5–7 mm longae, firmae, ad apicem acuminato-subulatae, integrae, sine area dorsali. Sepala lateralia libera, aequilateralia, valde curvata, oblonga, 4–5 mm longa, obtusa, ad apicem albovillosiciliata, ala carinali ciliati, apicem versus persaepe rufofimbriolati. Laminae petalorum obovatae, luteolae, ca. 5 mm longae, acutae, integrae. Staminodia bibrachiata longipenicillatis. Antherae oblongae, vadosae bifidae et sagittatae, ca. 1 mm longae, filiis ca. 0.5 mm longis. Capsula et semina non visa, sed placenta basalis.

Cespitose, smooth perennial 6–7 mm high. Stems short. Roots slender. Principal leaves

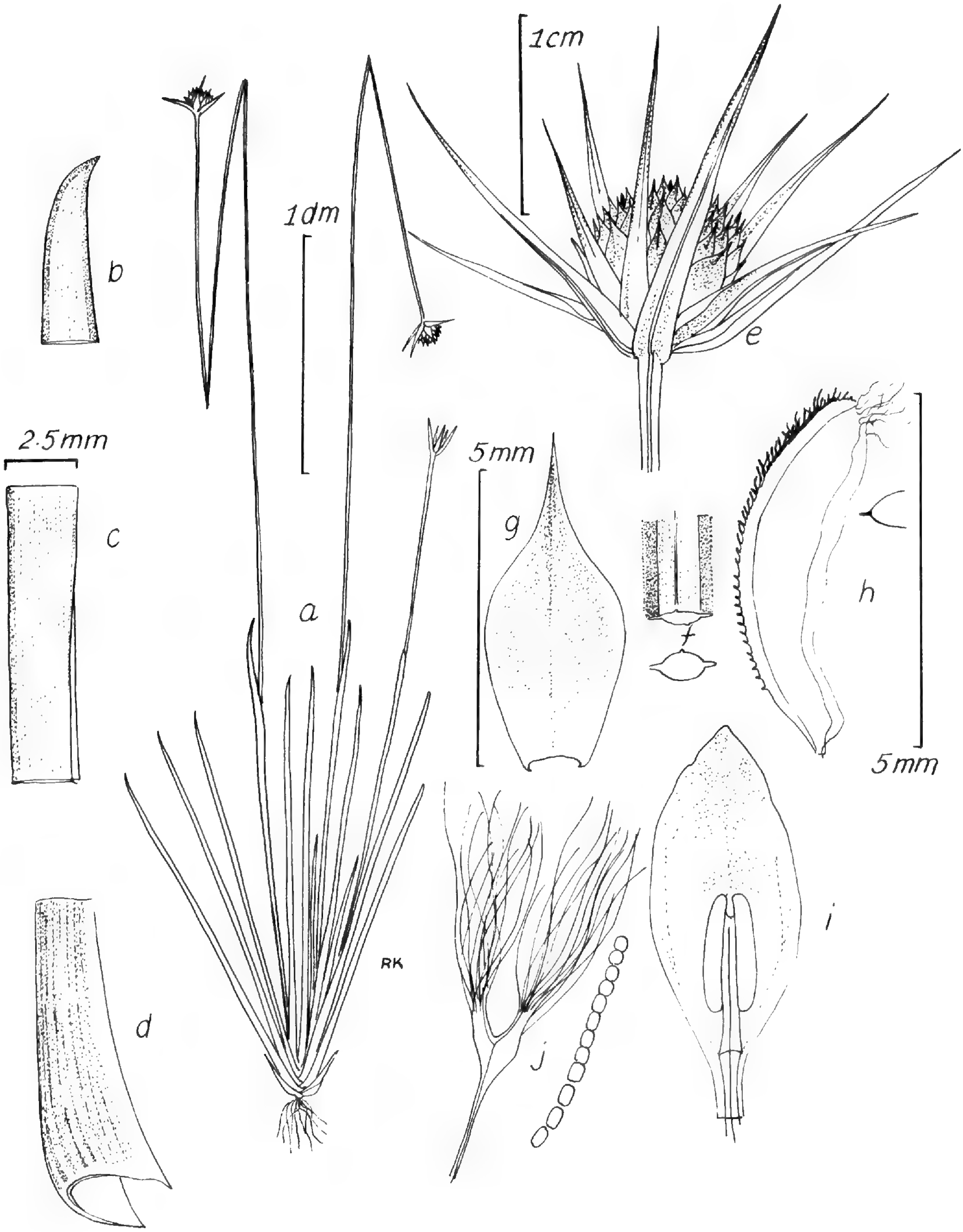


FIGURE 14. Xyris pallidula (Teixeira et al. 1263).—*a. Habit sketch.—b. Leaf tip.—c. Leaf blade–sheath junction.—d. Leaf base.—e. Spike.—f. Upper scape.—g. Fertile bract.—h. Lateral sepal.—i. Petal blade, stamen.—j. Staminode and beard hair.*

slightly spreading flabellately, 10–17 cm long, somewhat shorter than the scape sheaths; sheaths elongate, entire, 1–2 times longer than the blades, pale reddish brown, gradually narrowing from dilated base to apex, eligulate; blades strongly flattened, narrowly linear-gladiate, 2–3 mm wide, pale olive, the margins pale red-brown-bordered, slightly thickened, papillose, the apex incurved-acute. Scape sheaths multicostate toward base, reddish, shining, strongly carinate toward apex, with blade as in leaves but shorter. Scapes rigid, linear, slightly twisted, pale olive, mostly elliptic in cross section toward apex, strongly and acutely bicostate laterally. Spikes multiflorous, broadly ovoid to turbinate or hemispheric, ca. 10 mm long, involucrate, pale brown; involucral bracts several, spreading, subulate, 7–15 mm long, abruptly grading into bracts of spike; spike bracts rhombic-obovate, 5–7 mm long, firm, apically acuminate-subulate, entire, without dorsal area. Lateral sepals free, equilateral, strongly curvate, oblong, 4–5 mm long, obtuse, white-villous-ciliate at apex, the keel ciliate, frequently red-fimbriolate toward apex. Petal blades obovate, yellowish, ca. 5 mm long, acute, entire. Staminodia bibrachiate, long-penicillate. Anthers oblong, shallowly bifid and sagittate, ca. 1 mm long, the filaments ca. 0.5 mm long. Fruit and seed not seen, placentation basal.

This species, yet known only from the type material, is clearly related to the widespread *X. involucrata* but is easily distinguished by the lack of a castaneous "patch" on the leaf sheath base, by the eciliate leaf blades and bracts, and by the definitely subulate-tipped spike bracts.

15. Xyris bicephala Gleason, Brittonia 3: 155. 1939. TYPE: Venezuela. Bolívar: Auyan-tepui, 220 m, Gran Sabana, Dec. 1937–Jan. 1938, *G. H. H. Tate 1114* (holotype, NY). Figure 15.

Robust, cespitose, thick- and hard-based perennial 2.5–10 dm high, the stems stout, short or elongate to 2 dm. Leaves spreading flabellately, 2–5 dm long; sheaths with entire margins, castaneous or near black, ⅔ or more as long as blades, tapering evenly to blade, there imperceptibly short-ligulate; blades broadly linear, flat, 5–10 mm wide, the apex abruptly narrowed and rounded, incurved-acute, or narrowly rounded, the edges densely pale-pilose, densely ciliate or ciliolate, surfaces deep green, low-nerved. Scape sheath loose, shorter than leaves, distally ciliate-carinate, short-bladed. Scape flattened-ancipital, densely albociliate, 2.5–4 mm wide, bispicate (rarely monospicate). Spike broadly ovoid, obovoid or subglobose, 0.8–1.5 mm long, deep brown or castaneous, the bracts rigid, with or without a small, paler, elliptic, subapical dorsal area; sterile bracts many, ovate-triangular, smaller than and grading into the numerous fertile bracts, these broadly elliptic-ovate to oblong, 5–8 mm long, narrowly to broadly rounded, entire to erose or finely lacerate (rarely also red-ciliolate), lustrous toward base, dull toward tip, backs slightly rounded, ecarinate. Lateral sepals free, equilateral, linear-oblanceolate and often excurvate, 5.5–6.6 mm long, pale brown with firm, dark keel, this red-ciliolate or red-fimbriolate from middle to apex. Petal blades broadly obovate, 5.5–6 mm long, yellow, apically obtuse and erose. Staminodia bibrachiate, the slender branches long-villous-penicillate from base to tip. Anthers oblong, emarginate and auriculate, ca. 2 mm long, on filaments ca. 1 mm long. Capsule narrowly ellipsoid, 4–4.5 mm long, the placentation basal-axile (septa detaching from central axis and falling with valves). Seeds few, cylindric-fusiform, often curvate, 2.5–3 mm long, including a pale, narrowly conic appendage (separated outer integument), and with numerous pale, flattened, longitudinal ribs.

Distribution. Common in boggy rapateaceous savanna at medium to high elevations, the Guayana Highland of Estado Bolívar, Venezuela, eastward into the Pakaraima Mountains of Guayana.

This, the only known species of bispicate *Xyris*, unfolds its pale yellow blooms in the morning. Its dark bracts usually have inconspicuous but often detectable dorsal areas. It may intergrade with *X. decussata* Gl. and with *X. albescens* Steyerm., both of which it strongly resembles in bract and seed characters. It and several other species of the Guayana Highlands hitherto considered part of a well-defined section, "*Nematopus*," are showing septate ovary and fruit, and axile placentation.

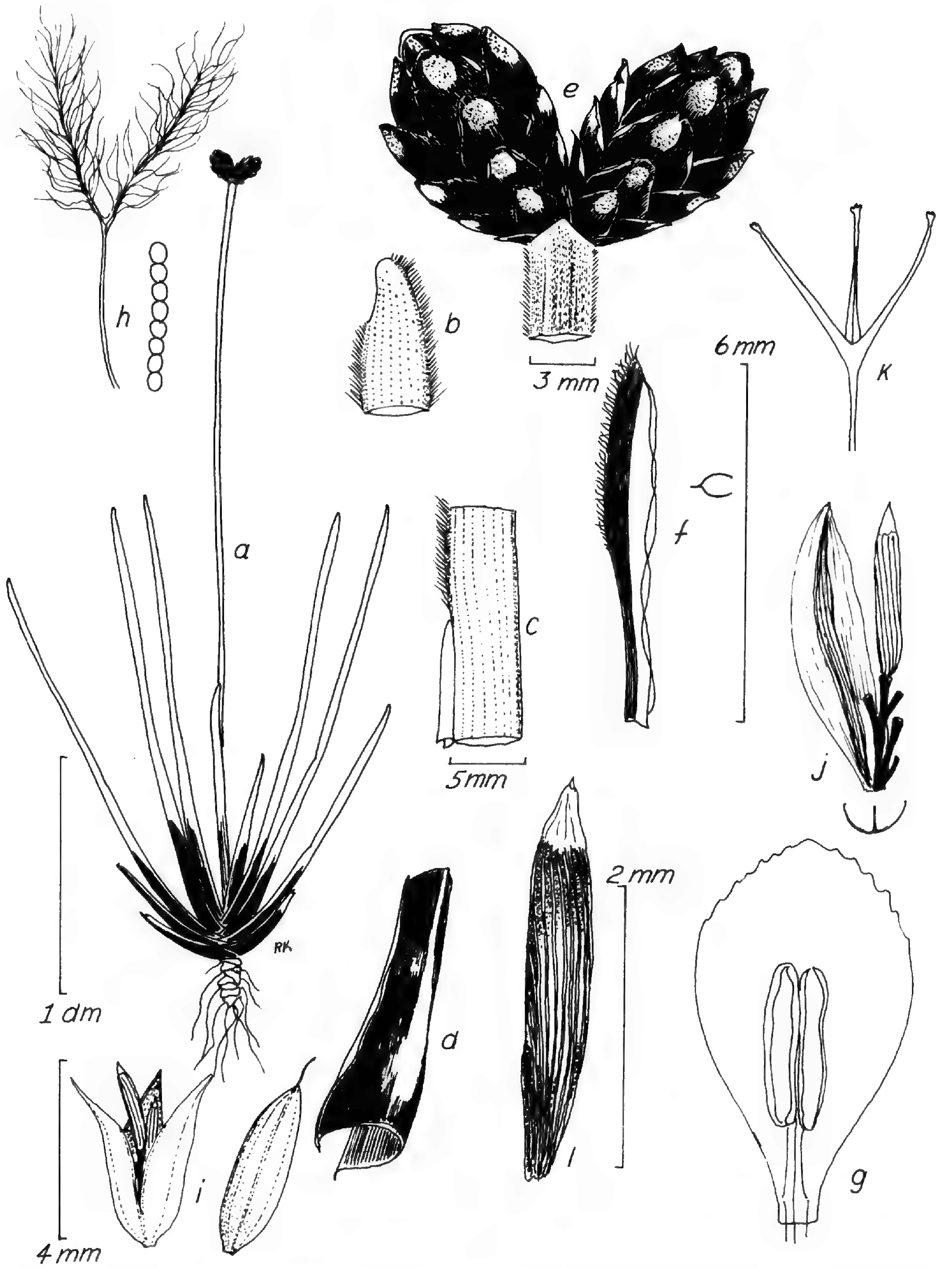


FIGURE 15. Xyris bicephala *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Leaf blade-sheath junction.—d. Leaf base.—e. Spikes.—f. Lateral sepal.—g. Petal blade, stamen.—h. Staminode, enlarged sector of hair.—i. Opening (left) and closed (right) capsule.—j. Capsule, showing one valve, placenta.—k. Style apex.—l. Seed.*

16. Xyris teinosperma Idrobo & Lyman B. Smith, Caldasia 6: 224. 1954. TYPE: Colombia. Vaupés: Yapoboda, 10 Dec. 1943, *P. M. Allen 3195* (holotype, COL; isotype, MO). Figure 16.

Sturdy solitary to densely cespitose perennial 5–8 dm high, the stems short and stocky. Leaves mostly spreading flabellately, 4–6 dm long; sheaths entire, in longer leaves less than ½ as long as blades, the dilated bases castaneous and lustrous, upwardly green or stramineous, keeled, tapering evenly to blades, there eligulate or with a narrow thin ligule to 3 mm long, the blades linear, flattened, straight and stiff, 4–10 mm wide, tapering slightly above middle then abruptly narrowed at apex to an incurved or erect, narrowly rounded or broadly acute, thickened tip; margins cartilaginous-thickened, pale, smooth; surfaces deep yellow-green, finely nerved, smooth. Scape sheaths much shorter than leaves, closed below, multicostate, distally keeled, open and with a stubby blade. Scapes distally ancipital, 3–4 mm wide, with 2 smooth costae making edges, surfaces yellow-green, striate, smooth. Spikes ovoid, 2–3 cm long, acute, of very many firm, tightly spirally imbricate bracts, these brown with conspicuous paler dorsal areas; sterile bracts many, the lowest much smaller than the fertile bracts, triangular-ovate, keeled, grading into fertile bracts, these oblong to obovate, ecarinate, 10–15 mm long, apically narrowly rounded and subentire. Lateral sepals free, subequilateral, linear-oblanceolate, 10–11 mm long, acute, the wide keel above middle finely lacerate and/or villosulous, aging subentire. Petal blades broadly oblong-elliptic, 1–1.2 cm long, yellow, the broadly rounded apex erose. Anthers oblong-linear, ca. 3.5 mm long, deeply bifid and sagittate, on filaments ca. 1.5 mm long. Staminodia multibrachiate, the slender branches densely plumose with long, penicillate hairs. Capsule narrowly ellipsoid, 8–10 mm long, the massive placenta basal, the valves dehiscing to reveal deep septa at base. Seeds several on short, bulbous funicles, linear, ca. 3 mm long, including an apical coma of pale, narrow, erect squamellae ca. 1 mm long, the narrow, pale brown seed body with a few strongly raised, pale, short-squamellate ribs.

Distribution. Wet, low savanna in SE Colombia, SW Venezuela, and contiguous Amazonas, Brazil.

This is one of the most distinctive species of *Xyris*, particularly noticeable in the low savannas along the upper Río Orinoco. Its slender, long-comose seeds are the longest known for the genus; its lovely pale yellow petal blades, unfolding in midday, form the largest known flower in *Xyris*.

17. Xyris lomatophylla C. Martius, Flora 24(2): 57. 1841. TYPE: Colombia. Amazonas: "In campis, Arara Coará, *Martius*" (lectotype, M; phototype, GH). Figure 17.

Robust, stiff, hard-based, solitary to cespitose perennial 5–7 dm high, the stems contracted. Leaves spreading flabellately, 0.5–3 dm long; sheaths eciliate, cartilaginous-keeled, fully the length of the blades, abruptly dilated at very base, dark brown or castaneous, shading distally to brown, narrowing gradually upward into blade, there with a short, narrowly triangular, erect ligule; blades flattened, twisted, ensiform, mostly 3–5 mm wide, narrowly acute or abruptly narrowly rounded, with a pale-cartilaginous-thickened, smooth or (frequently) ciliolate border, the surface smooth, finely nerved, dark green. Scape sheaths slightly shorter than leaves, twisted, proximally dark red-brown, keeled, with a cartilaginous costa, distally with a strong, short blade like that of leaves. Scape twisted, straight or flexuous, distally terete or oval in cross section, 1–1.5 mm wide, ecostate, smooth, longitudinally striate. Spikes dull brown, ovoid to cylindrical, 1–3 cm long, blunt, base attenuate or broadly rounded, with many spirally imbricate bracts with large, deep brown, apically broadened dorsal areas and broad, wooly-villous margins; sterile bracts many, the lowest much smaller than the fertile bracts,

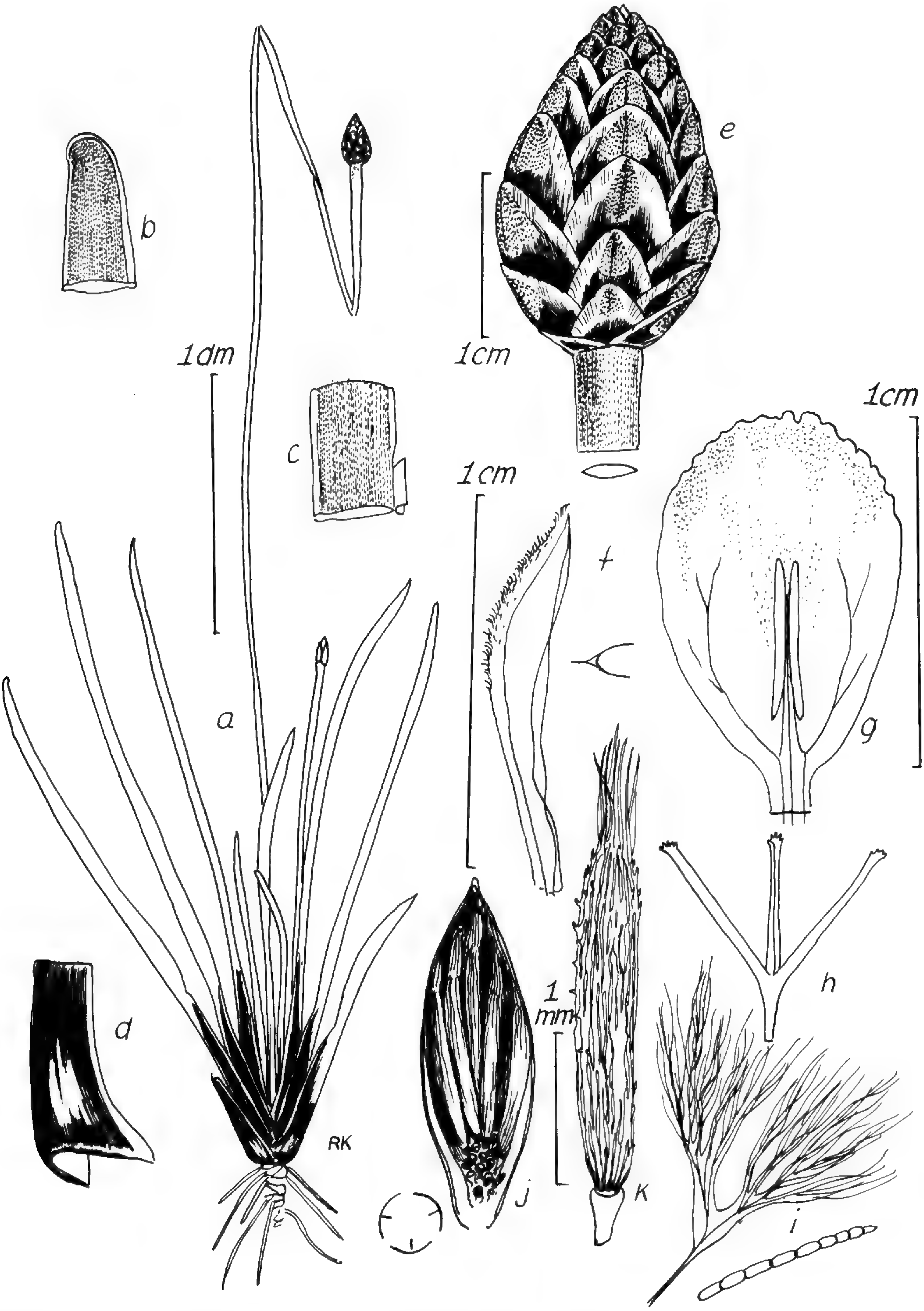


FIGURE 16. Xyris teinosperma (Kral & Huber 70708).—*a. Habit sketch.—b. Leaf tip.—c. Leaf blade-sheath junction.—d. Leaf base.—e. Spike.—f. Lateral sepal.—g. Petal blade, stamen.—h. Stylar apex.—i. Staminode, enlarged tip of beard hair.—j. Capsule, one valve removed to show placentation.—k. Seed.*

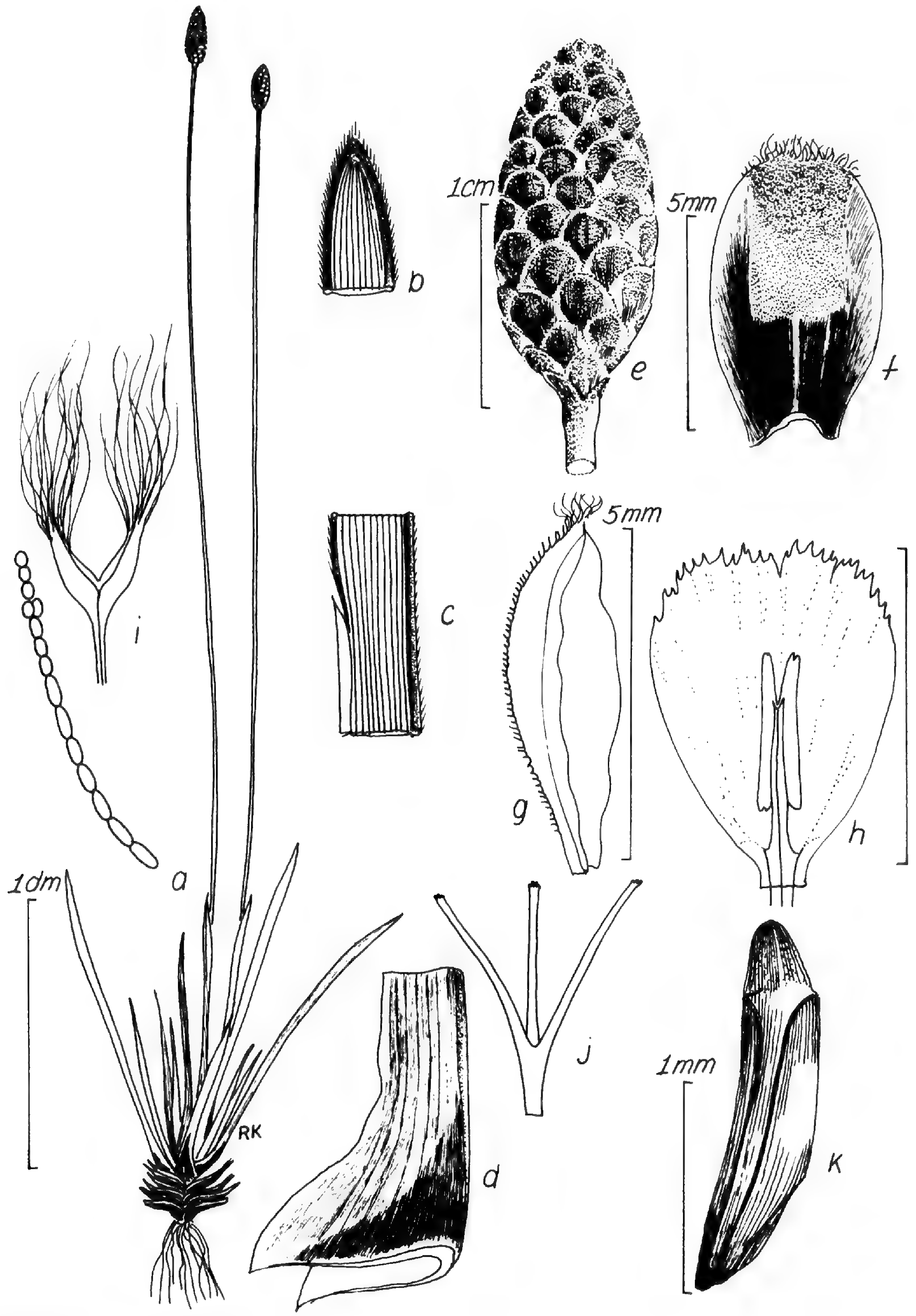


FIGURE 17. Xyris lomatophylla (Huber & Tillett 3058).—*a. Habit sketch.—b. Leaf apex.—c. Leaf sheath-blade junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode.—j. Stylar apex.—k. Seed.*

ovate, slightly keeled, grading gradually larger to fertile bracts, these obovate or broadly elliptic, 7–7.5 mm long, ecarinate. Lateral sepals free, very inequilateral, oblong-curvate, ca. 6 mm long, blunt, lustrous-brown, thin, the wide, firm keel increasingly densely brown-ciliate from near base to tip, there frequently villous-fimbriate. Petal blades broadly obovate, yellow, to nearly suborbicular, ca. 5 mm long, the broadly rounded apex lacerate. Staminodia bibrachiate, the flat, narrowly triangular branches tipped with a dense tuft of penicillate hairs. Anthers lance-oblong, ca. 2.5 mm long, deeply bifid and sagittate, on filaments 0.5 mm long. Capsule ellipsoid, planoconvex, ca. 3–4 mm long, the placentation basal, the valves without septa. Seeds few, cylindrical, 2–2.5 mm long including a white, conic apiculus ca. 0.5 mm long, pale amber, longitudinally finely lined, coarsely overlain by a few prominent dark ribs.

Distribution. Low, wet, sandy savanna, Amazonian southeastern Colombia through the savannas along the upper Río Orinoco and the Río Negro, T. F. Amazonas, Venezuela, southeastward into Pará, Brazil.

Additional specimens examined. BRAZIL. PARÁ: campo inundavel, Missão Velha, Rio Cururu, Alto Tapajós, 19 July 1959, *Egler & Raimundo 952* (US). "*Xyris lomatophylla* Mart. Brasilia prov. Río Negro, Legit *Martius*, Herbar. reg. Monacense Duplum 1864," attributed to Brazil but according to Dr. L. B. Smith, actually Colombian.

In spike character this species most resembles *X. globosa* but differs in its (usually) more elongate spikes; broader, flatter, cartilaginous-bordered leaves; and longer, narrower seeds. In the Venezuelan savanna along the upper Río Orinoco it may be the dominant species.

18. Xyris contracta Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 33. 1963. TYPE: Venezuela. T. F. Amazonas: Cerro de La Neblina, Río Yatua, summit, 1,200–1,300 m, flowers yellow; infrequent in stream bed, upper Cañon Grande, 1,900 m, 11 Dec. 1957, *B. Maguire, J. J. Wurdack & C. K. Maguire 42359* (holotype, NY; isotypes, US, VEN). Figure 18.

Cespitose, thick-based, smooth perennial 2–3(–5.5) dm high, the stem short, to ca. 3 cm long. Leaves ascending, 1–2(–3) dm long; sheaths entire, less than ½ as long as blades, lustrous at base, deep red-brown, dorsally rounded-convex, firm, narrowing gradually and keeled to blade and with a prominent, erect, broadly oblong, blunt ligule 2.5–3 mm long; blade narrowly linear, ca. 1(–3) mm wide, flat, acute at apex, the margins without border, entire, surfaces finely nerved, green. Scape sheath slightly to much shorter than leaves, proximally maroon or castaneous, opening distally, green, producing a strong blade. Scapes linear, straight, distally terete, ca. 1 mm thick, ecostate or with 1–2 very low, smooth costae, or flattened and 2-edged, to 2 mm wide. Spikes ellipsoid, ca. 1.5 cm long, acute, dull red-brown with numerous bracts in several subvertical ranks. Sterile bracts several, lowest keeled, slightly smaller than the fertile bracts and grading into them; fertile bracts oblong, 7–8 mm long, strongly rounded-folded, ecarinate, subentire, apically rounded-emarginate, when young frequently villose-ciliate apically, all with pale, subapical, somewhat indistinct, elliptic dorsal areas. Lateral sepals free, subequilateral, oblanceolate-linear, 7–8 mm long, straight, pale red-brown, the wide, thin keel ciliolate or papillate from middle to apex, or at apex also sparsely red-villosulous. Petal blades broadly obovate or reniform, ca. 7–8 mm long, yellow, the broadly rounded apex lacerate. Staminodia bibrachiate, the branches long-penicillate. Anthers ca. 2.5 mm long, oblong, on filaments ca. 1 mm long. Capsule ellipsoid, 4–4.5 mm long, septa lacking, the placentation basal. Seeds numerous, ellipsoid-fusiform, ca. 2 mm long, including a narrowly conic, pale apiculus ca. 0.4 mm long, the body dark, translucent, longitudinally prominently several-ribbed, with occasional cross-ribs.

Distribution. So far known only from the type area, re-collected there by Steyermark (*104018*, US, VEN) and on the Bra-

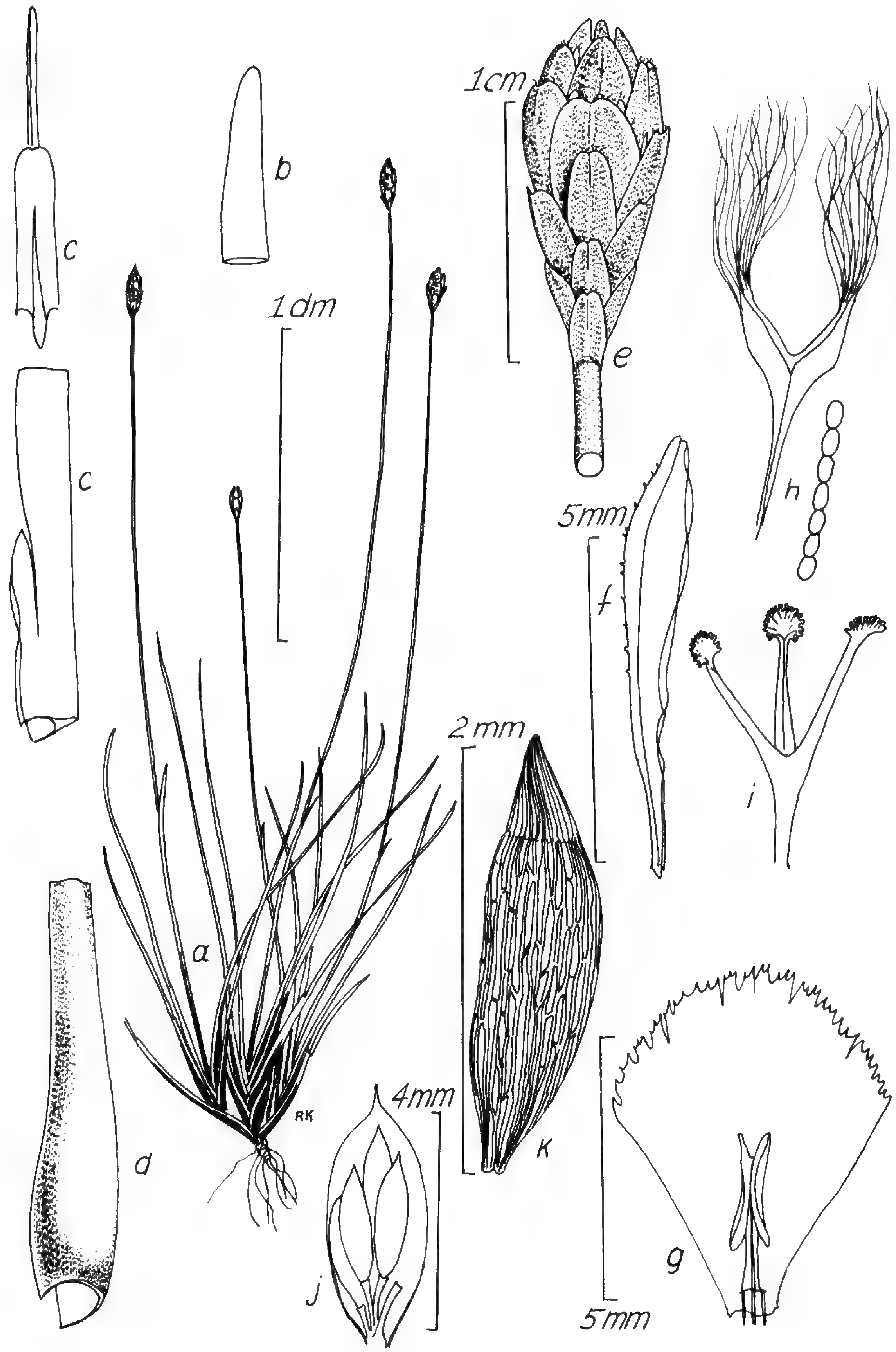


FIGURE 18. Xyris contracta *(from the type).—a. Habit sketch.—b. Leaf tip.—c. Adaxial (inside) view of leaf–sheath junction and side view of same.—d. Leaf base.—e. Spike.—f. Lateral sepal.—g. Petal blade, stamen.—h. Staminode, enlarged sector of beard hair.—i. Stylar apex.—j. Capsule, one valve removed.—k. Seed.*

zilian side of the Neblina crest (Rio Cauaburi, Brazil, *Maguire et al. 60483*, NY).

This rare plant is very distinctive in its combination of narrow, smooth leaves, dark, lustrous, ribless sheath bases, contracted leaf blade base, large ellipsoid spikes, and distinctive seeds. The only exceptional material is that collected by Steyermark which, while definitely this species, is a longer- and wider-leaved extreme with scapes distally flattened and 2-edged, much wider than in the type. I have not seen any further collections of this among many recent collections made by the Neblina workers.

19. Xyris seubertii Nilsson, Sv. Vet. Akad. Handl. 24(14): 51, pl. 4. 1892. TYPE: Guyana: "British Guiana, Rich. *Schomburgk n. 897*" (phototype, US). Figure 19.

X. calcarata Heimerl, Ann. Naturhist. Hofmus. Wien 21: 68, pl. 4, f. 1–3. 1906. TYPE: Brazil: *Tamberlik s.n.* (W—lost; phototype, F).

Slender, solitary to cespitose, hard-based, smooth and glaucous perennial 2–7 dm high, the stems contracted. Leaves spreading flabellately, 0.5–2.5 dm long; sheaths eciliate, at very base abruptly dilated, castaneous to dull, dark brown, above pink or pale purple, sharply keeled, narrowing gradually to blades, often ½ or more as long as blades, at apex producing a narrowly triangular, erect or spreading ligule or tapering directly into blade; blades linear-ensiform, flattened, straight or slightly twisted, 1.5–3.5 mm wide, narrowing above middle gradually into an incurved-acute or acuminate tip, the margins thin, entire to papillose, tuberculate, or scabridulous-ciliolate, the surfaces green, smooth, finely multinerved. Scape sheaths often as long as leaves, tubular and multicostate toward base, often rose or purple, ribbed, above open, keeled, with short, flat blades similar to those of leaves. Scapes straight or flexuous, twisted, subterete toward apex, 0.5–0.7 mm thick, ecostate or with 1 or more costae and striate, mostly smooth. Spikes ovoid, broadly ellipsoid or suborbicular, 0.8–1.2 cm long, pale brown, of many spirally imbricate bracts with distinct though narrow dorsal areas, the sterile bracts few, broadly rounded, slightly shorter and narrower than the fertile bracts but with 1 or 2 of the lowest often with dorsal areas prolonged as cusps or short blades equaling or exceeding spike; fertile bracts strongly convex-backed, obovate, 5–6 mm long, broadly rounded at apex, sometimes with apical, red-villosulous tuft. Lateral sepals ca. ⅕–⅓ connate, inequilateral, lanceolate, 6–6.5 mm long, blunt, slightly exserted, thin, the tan, firm keel above middle to apex increasingly densely reddish villous. Petal blades broadly obovate to reniform, ca. 6–7 mm long, yellow, the very broadly rounded apex wavy-erose. Staminodia bibrachiate, the branches long-penicillate. Anthers narrowly oblong, ca. 2 mm long, deeply bifid, deeply sagittate, on filaments ca. 1 mm long. Capsule obovoid, ca. 3 mm long, placentation free-central, the valves without septa. Seeds numerous, broadly ellipsoid to ovoid, ca. 0.3–0.4 mm long, apiculate, amber, finely striate-reticulate.

Distribution. Abundant and widespread from the Gran Sabana of Estado Bolívar, Venezuela, eastward into Guyana, increasingly abundant south of the Amazon Basin in the Brazilian planalto southward to São Paulo.

This species is distinctly weedy, often a pioneer in mechanically disturbed, eroded, or burned savanna. Its glaucous foliage and rather pale yellow flowers, which unfold in late morning, make it particularly handsome.

20. Xyris huberi Kral & Lyman B. Smith, nom. nov. TYPE: Venezuela. T. F. Amazonas: Cerro Yapacana, en la sabana grande entre el Caño Cotua y el pie del cerro, 3°45′N, 66°45′W, 125 m, 7 May 1970, *J. A. Steyermark & G. Bunting 103241* (holotype, US; isotype, VEN). Figure 20.

X. foveolata Kral & Lyman B. Smith, Phytologia 53: 435–436. 1983, non Irmscher.
X. yapacanensis Steyerm. & Lyman B. Smith, nom. nud.

Short-lived, cespitose, lustrous perennial from a short, thick, subvertical rhizome, the

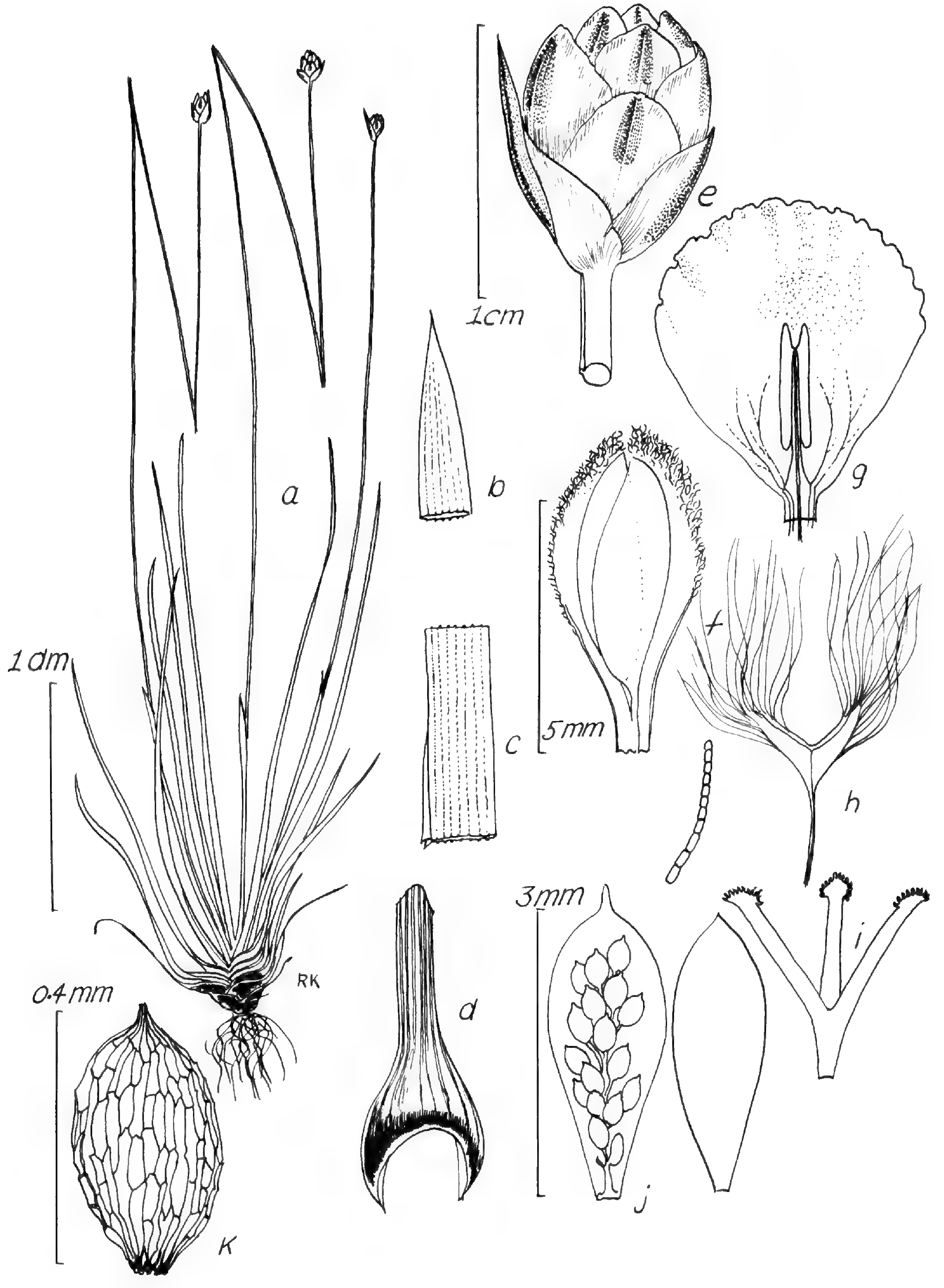


FIGURE 19. Xyris seubertii (Kral 70579).—*a. Habit sketch.—b. Leaf apex.—c. Leaf at blade–sheath junction.—d. Leaf base.—e. Spike.—f. Lateral sepal (pair, connate).—g. Petal blade, stamen.—h. Staminode, beard hair.—i. Stylar apex.—j. Capsule, placentation, one valve removed, one valve outline.—k. Seed.*

roots slender. Leaves ensiform-linear, (7–)8–15(–16) cm long, spreading flabellately, longer than the scape sheaths; sheaths entire, carinate, the carinae ciliate-scabrid, the sides deep brown, narrowing from the dilated, castaneous base gradually to the blade, there the edges converging to form a triangular, linear-acute, slightly spreading ligule 1.5–2 mm long; blades equal to or twice as long as sheaths, flat or somewhat twisted, strongly compressed, 1.5–2 mm wide, the surfaces green, tinged with brown or rusty brown, punctate (stomata depressed), longitudinally multinerved; apices narrowly acute, erect or incurved, slightly thickened; margins thickened, yellowish, densely pale ciliate with antrorse hairs. Sheaths of scapes multicostate, twisted, carinate, the carinae ciliate, the blades short, similar to leaf blades. Scapes 1.5–2.5 dm high, straight or somewhat flexuous, slightly twisted, distally 1–1.5 mm wide, punctate, bicostate, brownish, ancipital, the edges antrorsely long-ciliate. Spikes obovoid, 6–7 mm long, obtuse, few-flowered, bracts loosely imbricate, subdecussate, with scarious, reddish brown, revolute, ciliate borders and large, pale brown dorsal areas; sterile bracts 2–4, the lower pair oblong-triangular, 4–5 mm long, strongly carinate, the inner pair absent or ovate-triangular, ecarinate, the backs low-rounded, 1-nerved; fertile bracts narrowly ovate, narrowly rounded-folded, ca. 5 mm long, toward apex subcuculate, strongly papillose. Lateral sepals free, equilateral, somewhat curved toward base, lance-linear, ca. 4 mm long, narrowly rounded, acute or bidentate at apex; keel firm, entire toward base, ciliate from middle to apex. Petal blades obovate, ca. 5 mm long, pale yellow, the broadly rounded apex lacerate. Staminodia bibrachiate, the branches long-penicillate apically. Anthers linear-lanceolate, ca. 1.5 mm long, deeply bifid and sagittate on filaments ca. 1 mm long. Capsule narrowly obovoid, 2.5 mm long, the valves eseptate, the placentation basal. Seeds cylindric-fusiform, amber, 1.3–1.4 mm long, longitudinally spirally anastomosing-lined, with a few stronger, darker ribs.

Distribution. Confined to low-elevation savanna along the upper Río Orinoco and tributaries, T. F. Amazonas, Venezuela.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: Dept. Atabapo, Cerro Yapacana, 3 June 1978, *Huber 2030* (VEN); ca. 1 km a E del Caserio de Guarinuma, 23 Feb. 1979, *Huber 3356* (VEN); Cerro Yapacana, 28 Feb. 1980, *Huber 4815, 4829* (US, VEN); Dept. Casiquiare, 2–3 km al SE del bajo Guasacavi, 10 Mar. 1980, *Huber 5114* (US, VEN).

This species is distinguished by a combination of flattened, prominently thick-edged and ciliate leaves; ancipital and ciliate scapes; and hooded-tipped and reddish-margined, ciliate bracts. The margins of the leaf sheath, while thin, are firm and terminate in a long, narrow, sharp ligule. The large pale dorsal areas and surfaces of leaf blades and scapes are all strongly punctate.

21. **Xyris graniticola** Kral, sp. nov. TYPE: Venezuela: Amazonas. Dept. Atures, vegetación de laja (VL) sobre afloramiento granítico en raudal "pereza" en el Río Autana, 9 Nov. 1984, *F. Guánchez & E. Melgueiro 3425* (holotype, VEN; isotypes, TFAV, VDB). Figure 21.

Planta perennis, densicaespitosa, glabra; radices graciles. Caules breves vel usque ad 3 cm longis. Folia principalia erecta vel leviter flabellate expansa, 10–25 cm longa, scapos circa aequantes, vaginis scaporum longiora; vaginae integrae, carinatae, nitidae, pallide brunneolae, laminis 1–2-plo breviores, ad basin gradatim dilatatae, in laminas gradatim decrescentes, ad apicem ligulatae, ligula rigida, erecta, linearotriangulata, usque ad 1.5 mm longa; laminae anguste lineares, tortae, leviter complanatae, 0.5–0.7 mm latae, longitudine inconspicue paucinervatae, margine ad basin truncato-incrassatae, hispidulae, ferrugineae; apices peranguste conicae, ad apicem dorsaliter scabridae. Vaginae scaporum prope basin brunneolae, nitidae, apicem versus apertae, laminis brevis. Scapi leviter torti, teretes, vel in sectio transversali elliptici, ca. 0.5 mm lati, ecostati, olivacei. Spicae pauciflorae, anguste vel late turbinatae, ca. 4–5 mm longae; bracteae leviter expansae, integrae, decussatae, infimae 4 steriles, par inferiora lanceolata, ca. 4 mm longa, carinata, area dorsali lineari, par intima late triangulata, ca. 3.5 mm longa, area dorsali triangulata, leviter nervata; bracteae fertiles oblongae, 4–4.5 mm longae, anguste obtusae, subconduplicatae, anguste rotundatae, inconspicue unicostatae, dorsum ad basin castaneo, ad apicem area dorsali ovata, viridi. Sepala lateralia libera, aequilateralia, ca. 4 mm longa, obtusa, leviter curvata, ala carinali angusta, integra vel remote papillosa. Laminae petalorum obtriangulatae, luteolae, ca. 2–2.5 mm longae, apice subtruncatae, irregulariter dentatae. Staminodia bibrachiata, brachiis lon-

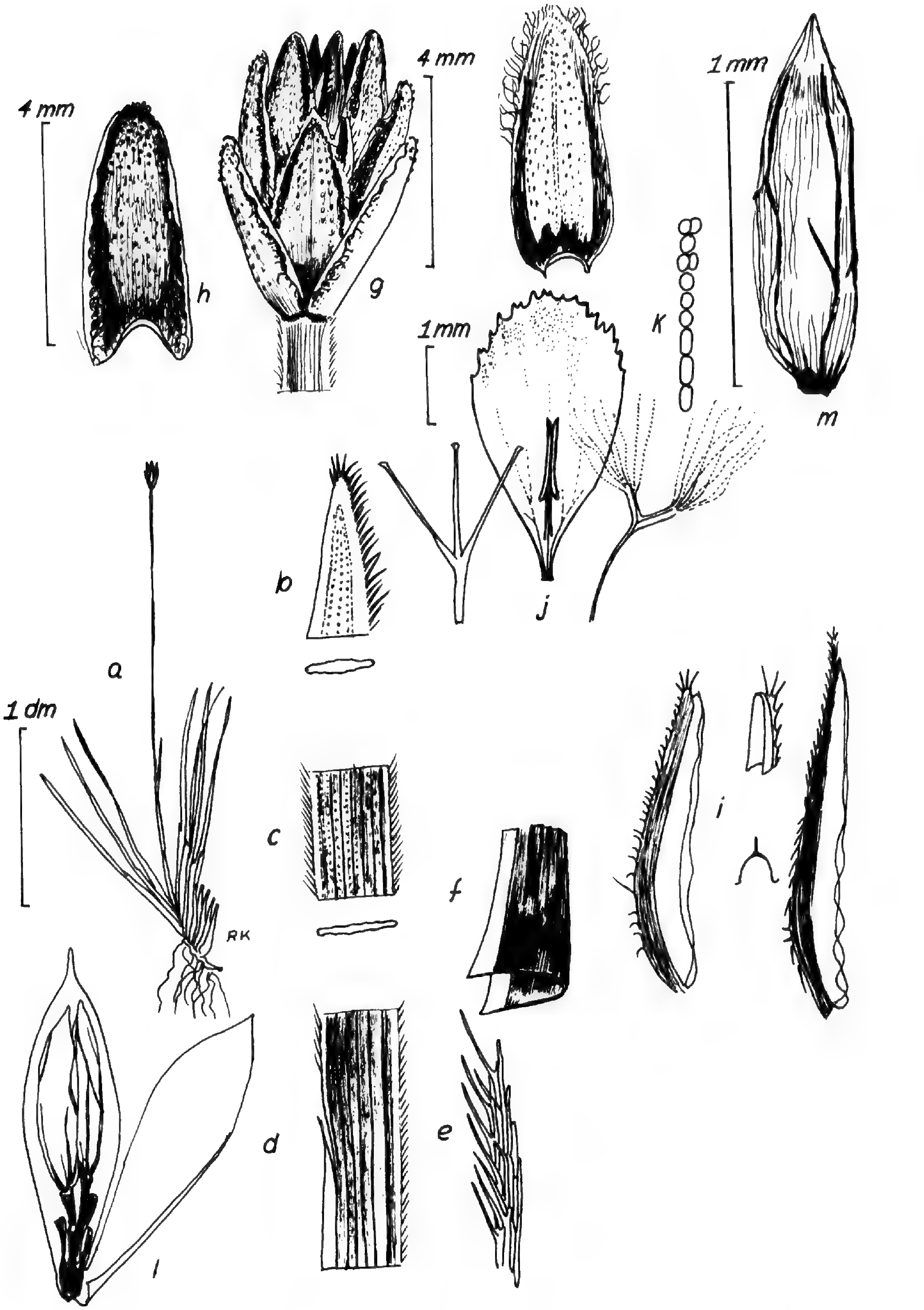


FIGURE 20. Xyris huberi (Huber 4815).—*a. Habit sketch.—b. Leaf apex.—c. Sector of leaf midblade.—d. Leaf–sheath junction.—e. Trichomes of leaf blade margin, enlarged.—f. Leaf base.—g. Spike.—h. Fertile bracts (left and right of spike).—i. Lateral sepals (extremes at left and right).—j. Petal blade and stamen; stylar apex on left, staminode on right.—k. Enlarged tip of beard hair.—l. Capsule, one valve removed, showing basal-central placentation.—m. Seed.*

gipenicillatis. Antherae oblongae, profunde bifidae et sagittatae, ca. 1 mm longae, filiis ca. 0.5 mm longis. Capsula matura ca. 3 mm longa, obovoidea; placenta basalis. Semina ovoidea, ca. 0.5 mm longa, translucentia, atroferruginea vel fusca, subtiliter longitudine multicostata.

The plant perennial, densely cespitose, smooth; the roots slender-fibrous. Stems short or up to 3 cm long. Principal leaves erect to slightly flabellately spreading, 10–25 cm long, about as long as the scapes, longer than the scape sheaths; sheaths entire, carinate, shining, pale brown, ½ or more the length of the blades, gradually dilated toward base, gradually narrowing into the blades, ligulate at apex, the ligule erect, rigid, linear-triangular, up to 1.5 mm long; blades narrowly linear, twisted, somewhat flattened, 0.5–0.7 mm wide, inconspicuously few-nerved, the margin toward the base beveled-incrassate, reddish, hispidulous; tips narrowly conic, dorsally scabrid at apex. Scape sheaths brownish toward base, shining, open, short-bladed toward apex. Scapes somewhat twisted, terete or elliptic in cross section, ca. 0.5 mm wide, ecostate, olivaceous. Spikes few-flowered, narrowly to broadly turbinate, ca. 4–5 mm long; bracts slightly spreading, entire, decussate, with conspicuous dorsal areas, the lowest 4 sterile, the lowermost pair lanceolate, ca. 4 mm long, carinate, the dorsal area linear, the inner pair broadly triangular, ca. 3.5 mm long, the dorsal area triangular, lightly nervose; fertile bracts oblong, 4–4.5 mm long, narrowly obtuse, subconduplicate, narrowly rounded, inconspicuously unicostate, the back castaneous toward base, with an ovate green dorsal area toward apex. Lateral sepals free, equilateral, ca. 4 mm long, oblong, obtuse, slightly curvate, the keel narrow, entire to remotely papillate. Petal blades obtriangular, yellow, ca. 2–2.5 mm long, the apex subtruncate, irregularly dentate. Staminodes bibrachiate, the branches long-penicillate. Anthers oblong, deeply bifid and sagittate, ca. 1 mm long, on filaments ca. 0.5 mm long. Mature capsule obovoid, ca. 3 mm long, the placenta basal. Seeds ovoid or ellipsoid, ca. 0.5 mm long, translucent, deep reddish brown or brown, finely longitudinally many-lined.

Distribution. A "laja" plant known only from the type locality.

This species comes, in treatments of Venezuelan *Xyris*, nearest those perennials with discernably leafy stems, distinct dorsal areas, and comparatively low stature, such as *X. frondosa* Mag. & Sm. However, the few-flowered spikes, in their turbinate outline and broad dorsal areas, are strikingly similar to those of *X. guianensis* Steud., here differing primarily in the nearly entire-keeled, less curvate lateral sepal. The latter plant is also shorter-stemmed, its leaves wiry-bordered.

22. Xyris frondosa Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 33, fig. 18A–E. 1963. TYPE: Venezuela. Bolívar: frequent in scrub forest near Summit Camp, 1,925 m, Central Section, Chimantá Massif, 2 Feb. 1955, *J. A. Steyermark & J. J. Wurdack 346* (holotype, NY; isotypes, F, US, VEN). Figure 22.

Moderately low, slender, densely cespitose perennial 2–3 dm high, the stems ascending, elongate, and forming frondlike plates of leaves. Leaves flabellately spreading, mostly 15–20 cm long; sheaths firm, entire, up to ½ as long as blades, deep reddish brown, papillate, tapering evenly to blade, often ciliate-carinate, at blade junction with an erect, narrowly triangular ligule to 1 mm long or eligulate; blades flat, often twisted, linear, 1.5–2.5 mm wide, tapering evenly to an acute-incurved, densely pale-ciliate apex, the margins ascending-ciliate with pale narrow hairs, submarginally with a deep reddish brown border, the surfaces green or maroon, finely multinerved, mostly smooth. Scape sheaths shorter than leaves, loosely carinate, keel ciliate, open at apex, short-bladed. Scapes slenderly linear, straight or slightly flexuous, slightly twisted, distally terete or slightly compressed, ecostate or low-bicostate, smooth. Spikes ellipsoid, 6–7 mm long, reddish brown, several-flowered, the bracts tightly spirally imbricate and with distinct reddish brown dorsal areas,

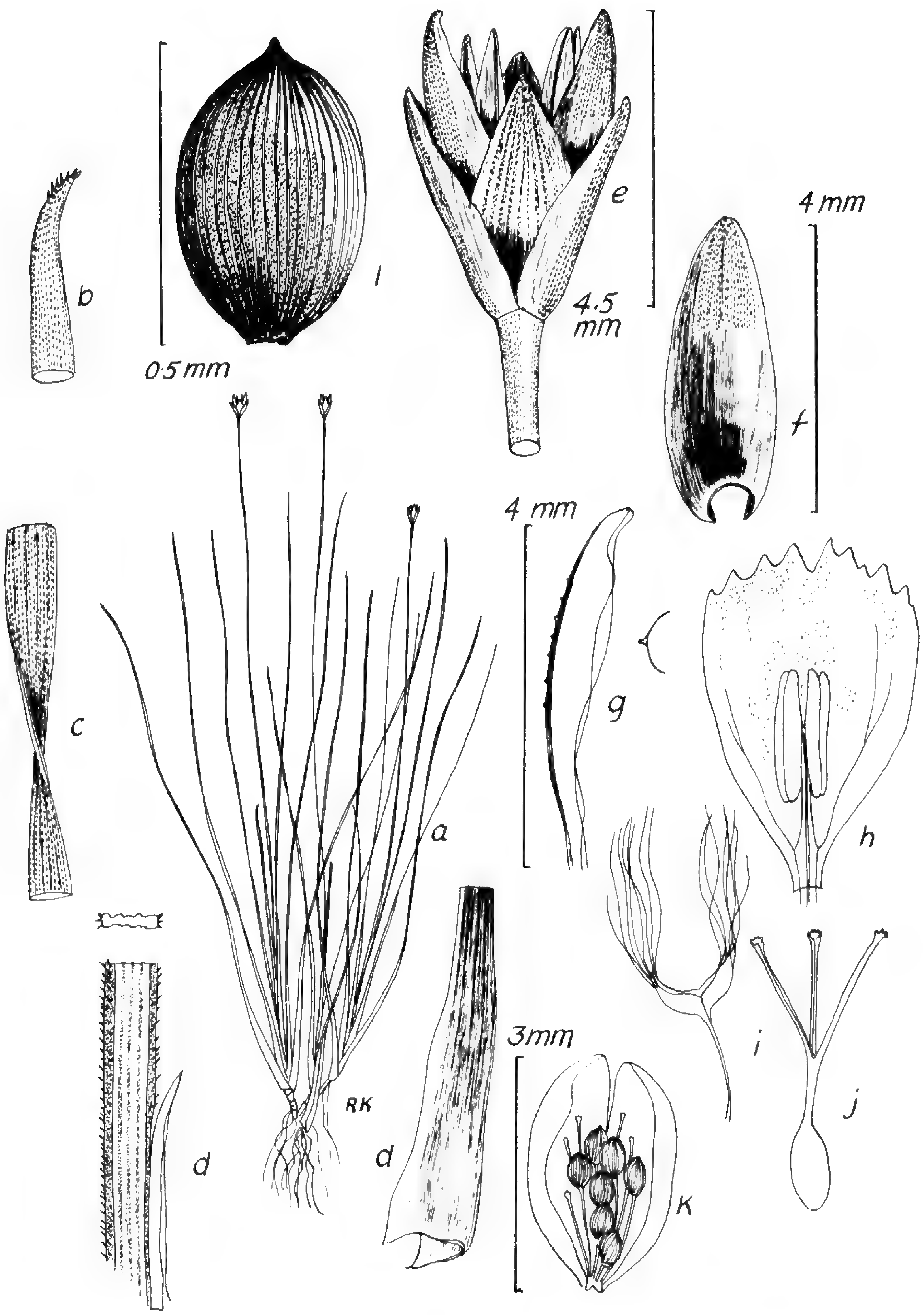


FIGURE 21. Xyris graniticola *(from the isotype)*.—*a. Habit sketch.—b. Leaf apex.—c. Sector of midblade.— d. Leaf sheath–blade junction (at left); leaf base (at right).—e. Spike.—f. Fertile bract.—g. Lateral sepal.— h. Petal blade, stamen.—i. Staminode.—j. Ovary, style branches.—k. Capsule, one valve removed.—l. Seed.*

apically often white-villosulous-ciliate; sterile bracts smallest, grading into the fertile bracts, triangular or ovate, acute, keeled, the fertile bracts obovate, ecarinate, 4.5–5 mm long, subentire, broadly rounded apically, backs convexly rounded, the dorsal areas bisected by a low but distinct rib. Lateral sepals oblong, curvate, free, inequilateral, ca. 4.5 mm long,

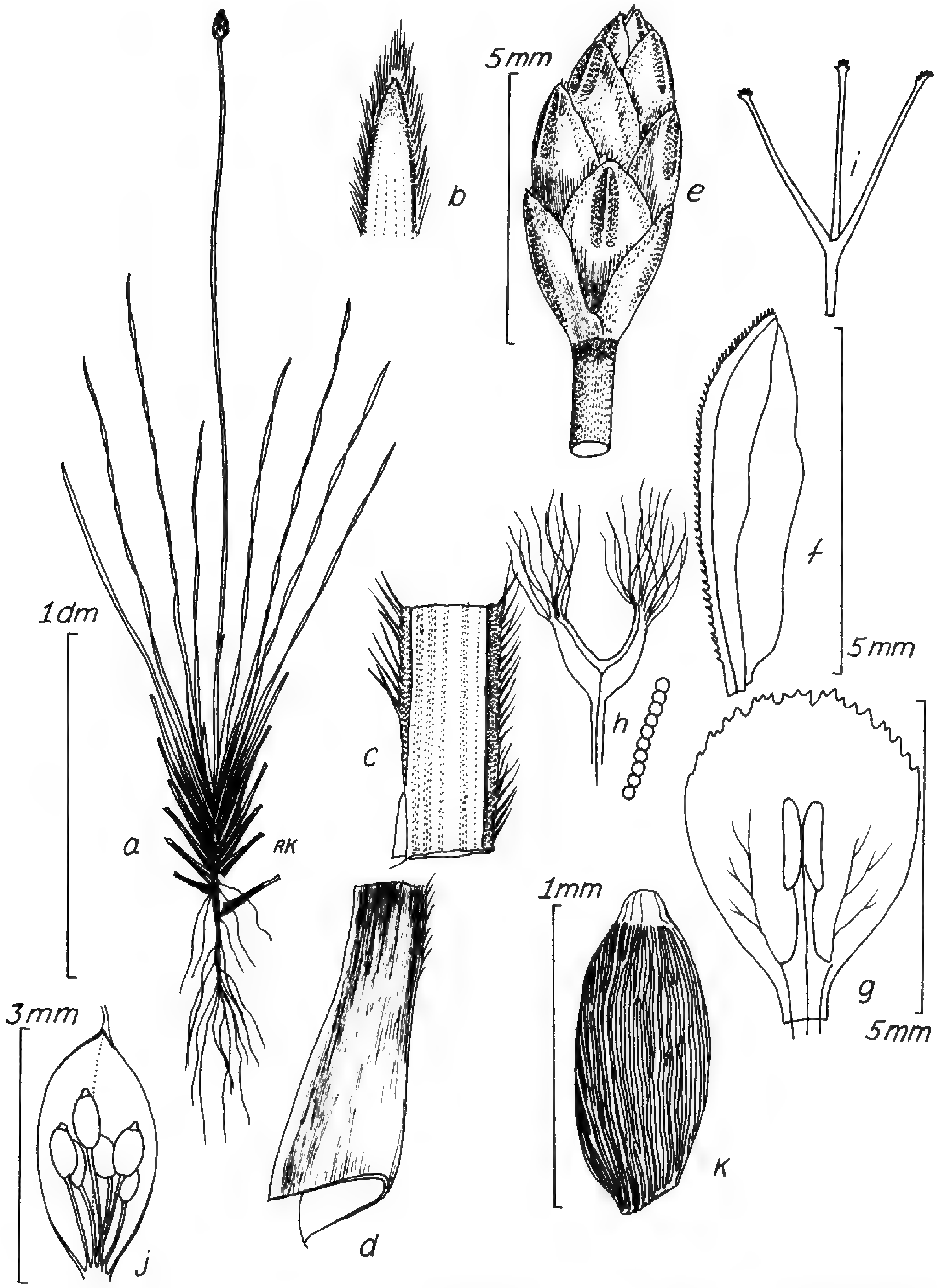


FIGURE 22. Xyris frondosa *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Leaf blade–sheath junction.—d. Leaf base.—e. Spike.—f. Lateral sepal.—g. Petal, stamen.—h. Staminode.—i. Stylar apex.—j. Capsule, one valve removed, showing basal placentation.—k. Seed.*

blunt, pale reddish brown with a dark, firm, irregularly tuberculate-ciliate or ciliolate keel from base to apex. Petal blades broadly obovate to suborbicular, yellow, ca. 5 mm long, the apical margin lacerate-dentate. Staminodia bibrachiate, the broad, flat branches densely penicillate at tip. Anthers oblong, ca. 1 mm long, bifid, auriculate, on flattened filaments ca. 1 mm long. Capsule ellipsoid or narrowly obovoid, ca. 3 mm long, the placentation basal, the valves without evident septa. Seeds several, on long funiculi, ellipsoid to oblong-cylindrical, ca. 1 mm long, translucently deep amber, pale apiculate, with fine, longitudinal, anastomosing ribs.

Distribution. Abundant in wet, high savanna, the Chimantá Massif and associated systems, usually above 1,500 meters, Estado Bolívar, Venezuela.

Additional collections examined (since those published by Maguire & Smith (1963)). VENEZUELA. BOLÍVAR: Macizo del Chimantá, *Huber & Steyermark 6907* (VDB, VEN); Chimantá, Apacará-tepui, *Huber & Steyermark 6961* (VDB, VEN); sección oriental del Chimantá-tepui, *Huber & Steyermark 7161* (VDB, VEN); Auyan-tepui, *Huber & Medina 8538* (NY, VEN); Apacará-tepui, *Huber & Colella 8727* (NY), *8736*, *8774* (NY, VDB, VEN); Churi-tepui, *Huber & Colella 9000* (NY, VDB, VEN); Acopan tepui, *Huber et al. 9069* (NY); ca. 25 km al SE de Canaima, *Huber 9730* (MYF, VDB); Murey-tepui, *Huber 11586* (MYF, VDB, VEN); Abacapá tepui, *Huber 11471* (MYF, VDB, VEN); Meseta de Jaua, Cerro Jaua, *Steyermark 98124* (MO, NY, VEN); Auyan-tepui, *Steyermark 93505* (NY, US, VEN), *93697* (F, NY, US, VEN), *93757* (NY, US, VDB, VEN), *93992* (L, NY, US, VEN); Cerro Jaua, *Steyermark 98055* (F, VEN), *109387* (NY, VEN); Cerro Guanacoco, *Steyermark et al. 109731* (US, VEN), *109734* (US, VEN); Cerro Jaua, *Steyermark 109426* (US, VDB, VEN), *109460* (K, MO, US, VEN), *109610* (US, VDB, VEN); Cerro Guaiquinima, *Steyermark & Dunsterville 113173* (F, US); Murey (Eruoda) tepui, *Steyermark et al. 115839* (F, MO, US, VEN).

This low-growing species with its long-stemmed fronds of rusty-bordered, ciliate leaves and small spikes with distinct dorsal areas, has no near morphological neighbor within its narrow range.

23. Xyris chimantae Kral & Lyman B. Smith, Phytologia 53: 432–433, fig. 1a–h. 1983. TYPE: Venezuela. Bolívar: Chimantá Massif, central section, swampy depression in wet savanna along east branch of headwaters of Río Tirica, 2,120 m, 12 Feb. 1955, *J. A. Steyermark & J. J. Wurdack 768* (holotype, VEN; isotypes, F, NY). Figure 23.

Cespitose perennial to 6 dm high, the stems either short or ascending through deep substrate and to 1 dm long, the bases mostly covered by scalelike old leaf bases. Roots slender, arising from lowermost nodes. Principal leaves stiff, spreading distichously, (1.8–)2–4(–4.8) dm long, longer than scape sheaths; blades narrowly linear, 3–4 times longer than the sheaths, slightly twisted, flattened, somewhat thickened and with thick margins, 2–2.5 mm wide, olivaceous to yellow-brown, finely papillose-rugulose; apices abruptly incurved-acute, thickened, entire to scabrociliate; margins slightly papillose to minutely scabro-ciliate; sheaths ecarinate, the broad bases firm, lustrous, castaneous to yellow-brown, entire, narrowing gradually into blades, eligulate. Scape sheaths proximally tubular, dark, multicostate, papillose, distally open, short-bladed. Scapes slenderly lineal, straight or slightly flexuous, slightly twisted, distally subterete to oval or elliptic in cross section, ecostate to narrowly bicostate, the costae papillose to scabrid. Spikes obovoid to obconic, ca. 1 cm long, many-flowered, the bracts loosely imbricate, subdecussate, ecarinate, without dorsal area, smooth, light to deep brown, strongly lacerate; sterile bracts several, ovate, shorter than the fertile bracts and grading into them; fertile bracts several, ovate, 7 mm long, narrowly rounded, reddish ciliate at apex when young, with the median nerve low but manifest. Lateral sepals free, subequilateral, oblanceolate, ca. 5.5 mm long, included to exserted at apex of spike, slightly curvate, acute; keel reddish fimbriociliate from middle to tip. Petal blades obovate-rhombic, ca. 6 mm long, yellow, apically narrowly rounded, erose. Staminodia bibrachiate, the branches long-penicillate. Anthers narrowly oblong, ca. 2 mm long, shallowly bifid, shallowly auriculate, on filaments ca. 1 mm long. Capsule cylindric-ellipsoid, ca. 5 mm long, the valves with septa from base to tip. Seeds narrowly ellipsoid-fusiform, ca. 2 mm long, including a terminal white, conic scale 0.6–0.7 mm long, the seed body reddish brown, translucent, conspicuously longitudinally multiribbed.

Distribution. Locally abundant in wet savanna at elevations over 1,900 meters, the

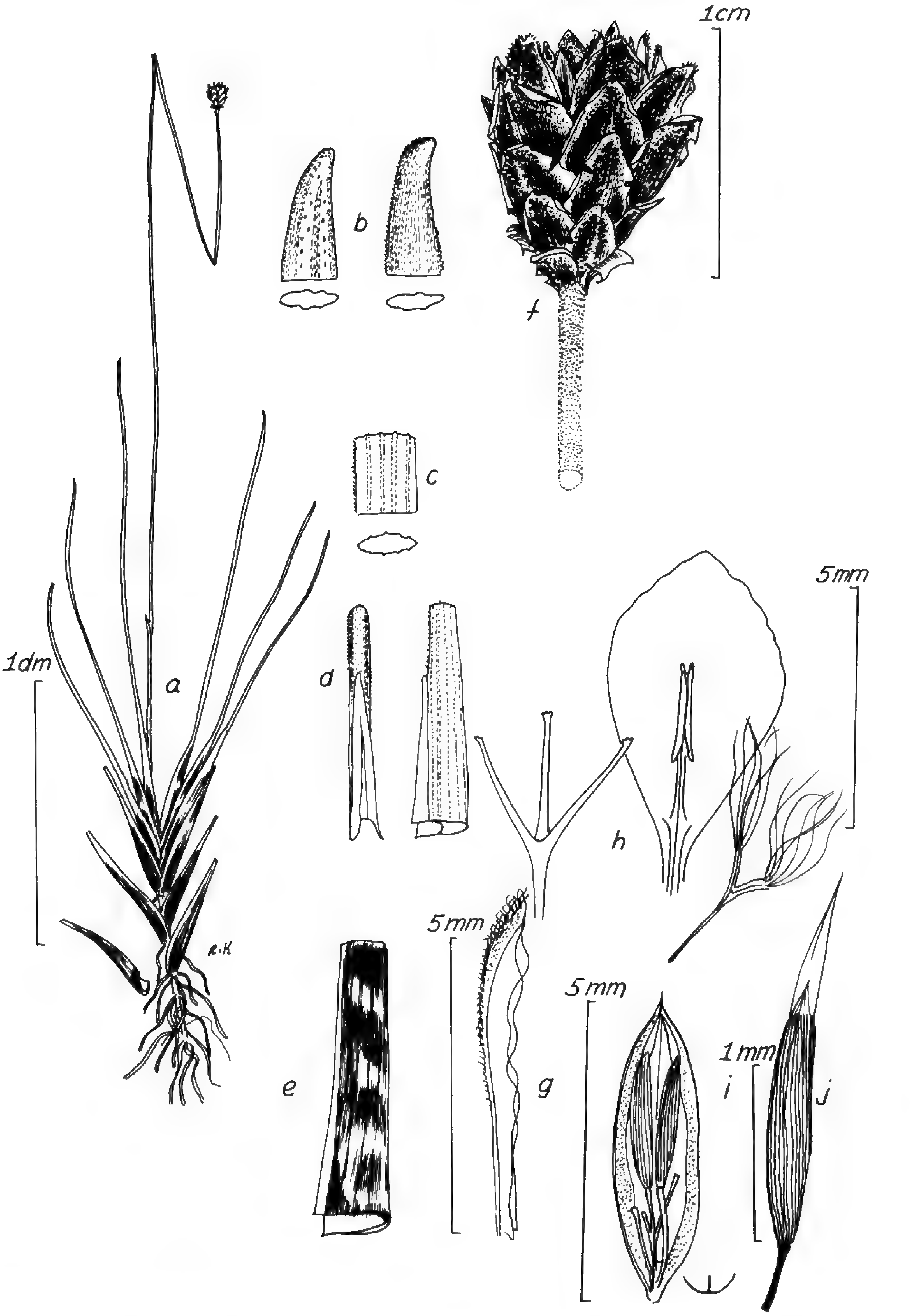


FIGURE 23. Xyris chimantae *(from the type).—a. Habit sketch.—b. Two leaf tips.—c. Leaf blade, sector at midblade.—d. Two views of leaf sheath–blade junction.—e. Leaf base.—f. Spike and upper scape.—g. Lateral sepal.—h. Petal blade, stamen, staminode, stylar apex.—i. Capsule, showing side views of two septa (stippled).—j. Seed.*

Chimantá Massif in Estado Bolívar, Venezuela.

Additional specimens examined. VENEZUELA. BOLÍVAR: *Huber & Dezzeo 8592* (NY); *Huber & Colella 8735* (NY, VDB, VEN); *Huber et al. 10181* (MYF, VDB); *Steyermark & Wurdack 486* (F, NY, US, VEN); *Steyermark & Wurdack 1010* (F, NY, VEN); *Steyermark 75870* (F, NY, VEN); *Steyermark et al. 115835* (US, VEN); *Steyermark et al. 115922* (MO, US, VDB); *Steyermark et al. 128375 & 128380* (VDB, VEN).

This species is most similar to *X. lugubris* Malme but is overall more slender and has spikes of narrower outline and longer seeds.

24. Xyris stenophylloides Malme, Bull. Torrey Bot. Club 58: 323. 1931. TYPE: Venezuela. T. F. Amazonas: gorge of Caño Negro, Savanna Hills, growing in tussocks, Cerro Duida, 4,000 ft., *G. H. H. Tate 808* (lectotype, NY; paratype, "Savanna Hills, summit of Cerro Duida, 2 Sept. 1944, *Steyermark 58211*," F, NY, US, VEN). Figure 24.

Slender, densely cespitose, hard-based, smooth perennial 3–4 dm high, the stems contracted. Leaves erect or ascending, to 2.5 dm long; sheaths entire, much less than ½ as long as blades, the bases lustrous pale brown shading upward through yellow-brown to green, tapering from a slightly dilated base gradually to blade, there abruptly narrowed and producing an oblong, rounded or acute ligule to 1 mm long; blades narrowly linear, pale green, proximally and medially somewhat flattened, ca. 1 mm wide, narrowing gradually above middle to a narrowed, bluntly conic or flattened, thickened apex, the margins thick and rounded, smooth, the surfaces green, strongly 1–2-nerved, sometimes sulcate. Scape sheaths shorter than leaves, proximally tubular, striate, lustrous brown at base, open toward apex, there producing a short, erect, cusplike blade. Scapes straight or flexuous, twisted, distally subterete, 0.5–0.7 mm thick, with broad, low costae and shallowly sulcate, striate. Spikes broadly turbinate, 7–8 mm high, red-brown, of several loosely subdecussate bracts without dorsal areas, the sterile ones several, the lowest much smaller, ovate, narrowly rounded, slightly convex-carinate, grading gradually to fertile bracts, these oblong, 5.5–6 mm long, apically truncate or broadly rounded, erose or lacerate, ecarinate, slightly folded, low-papillose. Lateral sepals free, equilateral, elliptic-linear, broadly acute, ca. 5 mm long, tan, the firm narrow keel entire. Petal blades broadly obovate, ca. 4 mm long, the broadly rounded apex erose. Staminodia bibrachiate, the slender branches long-penicillate-pubescent. Anthers lance-oblong, ca. 1.5 mm long, deeply bifid and sagittate, on filaments ca. 1 mm long. Capsule obovoid, ca. 3 mm long, the central axis extending ⅔ the fruit length, the placentation appearing axile at least at fruit base, the valves with broad, thin septa. Mature seeds fusiform, ca. 1.5 mm long, pale brown, translucent, longitudinally multiribbed.

Distribution. Known only from the Cerro Duida area in rocky "open" seeps above 1,000 meters, very seldom collected, the only records other than types being the following.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: Jan.–Feb. 1969, *M. Farinas, J. Velasquez & E. Medina 406* (NY, VEN); vertiente norte del Tepuy Duida, 16 Nov. 1982, *F. Guanchez 2342* (TFAV, VDB, VEN); between Brocchinia Hills and Savanna Hills, 1,050–1,600 m, 2 Sep. 1944, *Steyermark 58211* (F, NY, US, VEN); topotype, *S. S. Tillett et al. 751-67* (MYF, VEN).

This species is in several characters closest to *X. scabridula* Steyerm. from the same massif; however, *X. scabridula* is harsher in foliage, has the leaves more thickened, and the lateral sepals broader and ciliate.

25. Xyris columbiana Malme, Ark. Bot. 13(3): 40. 1913. TYPE: Venezuela. Merida: "Jaji" (fide L. B. Smith, Caldesia 6(29): 22. 1954). The original label information is "*Xyris tortilis* Kl. Columbian. Moritz," the location given as "Taji," and was therefore interpreted by Malme as in Colombia (*Moritz 1202*, Herb. Berol. & *415*, BM; isolectotype, L). I have seen only the isolectotype and must also assume that the original material at B is lost, while that at BM remains to be designated lectotype. Figure 25.

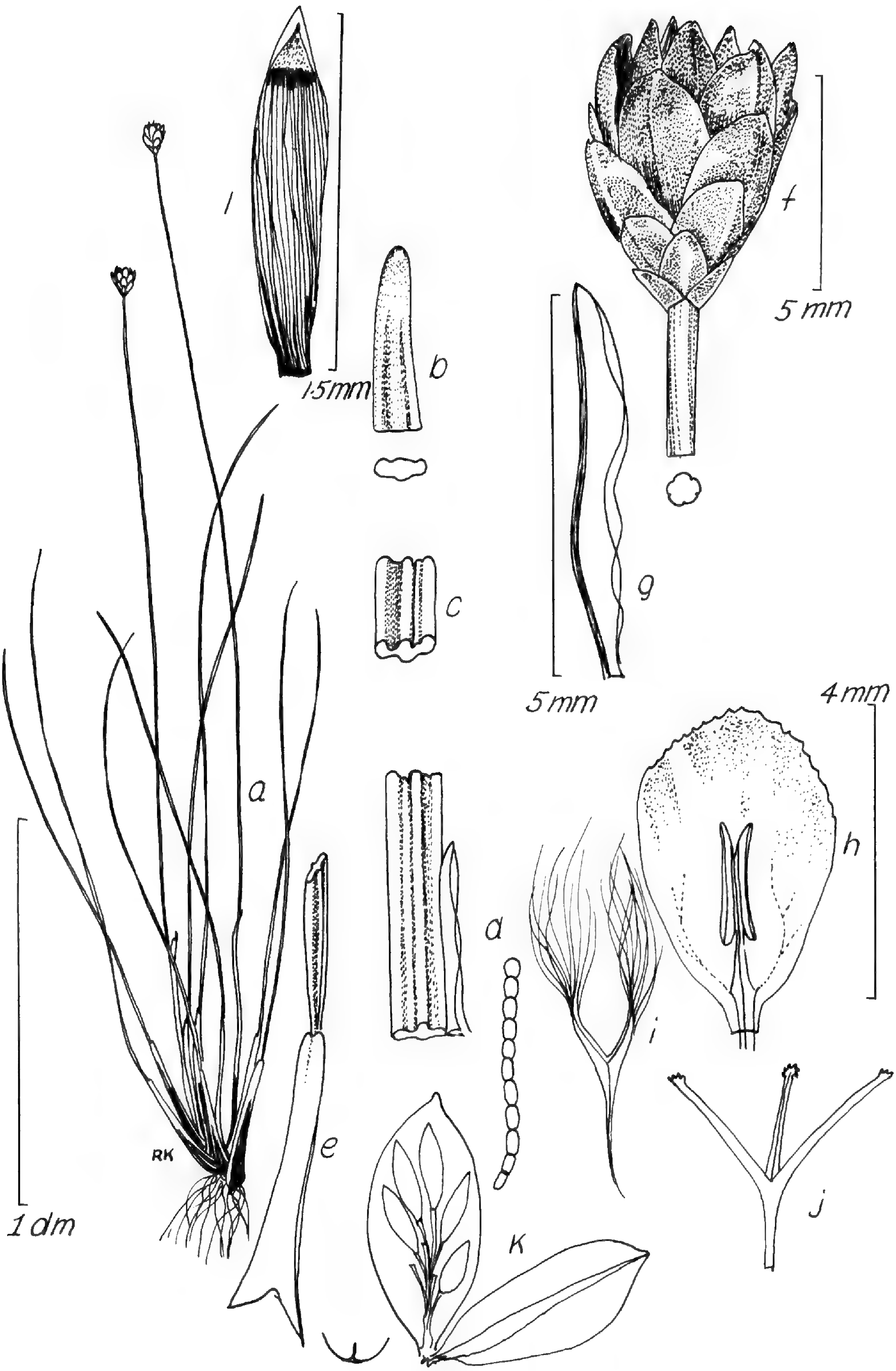


FIGURE 24. Xyris stenophylloides (Tate 808, Steyermark 58211).—*a. Habit sketch.—b. Leaf apex.—c. Sector from midblade.—d. Leaf at junction of sheath and blade.—e. Leaf base, inside view, showing orientation of blade base.—f. Spike and upper portion of scape.—g. Lateral sepal.—h. Petal blade.—i. Staminode.—j. Stylar apex.—k. Opened capsule showing two valves, placentation.—l. Seed.*

Cespitose, soft-based perennial to 6 dm high, the stems short. Leaves erect or ascending, mostly 2–3 dm long; sheaths entire, less than ½ as long as blades, narrowing gradually from the somewhat dilated, reddish green base to the blade, there producing a broadly oblong ligule 1–2 mm long; blades narrowly ensiform-linear, 0.5–1.5 mm wide, slightly twisted, flattened but round-edged, the apex narrowly acute, conic, the surfaces variously papillose-rugulose, dull green. Scape sheaths shorter than foliage leaves, the bases tubular, multicostate, the open apex producing a short, erect blade. Scapes straight or somewhat flexuous, narrowly lineal, terete or subterete distally, ca. 1 mm thick, unicostate, the costa low but strong, smooth or papillate. Spikes broadly obovoid to broadly ellipsoid or subglobose, 7–9 mm long, of several spirally imbricate, thin, castaneous bracts without dorsal areas, the sterile ones mostly 4–6, the lowest pair strongly keeled, ovate-triangular, 3.5–4 mm long, the inner slightly longer and broader, grading into the fertile bracts, these broadly obovate, ca. 5 mm long, broadly rounded apically, entire-margined, the backs slightly convex, ecarinate. Lateral sepals free, inequilateral, 5–6 mm long, strongly curvate, oblanceolate, pale brown with deep brown, firm keels, these ciliolate to villosulous-ciliate from ca. middle to apex. Petal blades ca. 6 mm long, elliptic, the broadly acute apex erose. Staminodia bibrachiate, the branches densely long-penicillate. Anthers oblong, ca. 2 mm long, the apex deeply bifid, the base sagittate, on filaments ca. 1 mm long. Capsule ellipsoid, 4–5 mm long; placentation free-central, the axis tending to separate into 3 branches distally, the ovules very numerous. Seeds ellipsoid, ca. 0.7 mm long, translucent, finely ribbed longitudinally.

Distribution. Andean paramos, apparently rare, Colombia and Venezuela.

Additional specimens examined. COLOMBIA. BOYACA: saturated sphagnum overlying sand, La Cumbre, valley of Río Pomera, 8,000 ft., 20 Aug. 1944, *N. C. Fassett 25631* (US); Cordillera Oriental, al NE de Arcabuco, linea divioria entre Boyaca y Santander del Sur, 2,600 m, 7 May 1972, *H. García-Barriga & R. Jaramillo M. 20267* (GH). ANTIOQUIA: a 1 km al sur de Hoyo Rico, ca. 2,600 m, 26 Sep. 1948, *F. A. Barkley 18A. 150* (US). VENEZUELA. MERIDA: Hoya del Río Capaz, bosque de San Eusebio: La Pinuela, bosque y pantamo, 2,600 m, 22 Oct. 1969, *J. Cuatrecasas et al. 28152* (US).

This has definite affinities with *X. subulata* Ruíz Lopez & Pavón but differs in having somewhat larger habit, larger, broader spikes which produce more florets, and more conspicuous indumentum of the lateral sepal keels.

26. Xyris subulata Ruíz Lopez & Pavón, Fl. Peruv. I: 46, pl. 71. 1798. TYPE: Peru. Huanuco: Pachitea, Pillao, 1787, *Ruíz Lopez & Pavón* (lectotype, MA; isolectotype, presumably at F).

Schizmaxon distichioides Steud., Bot. Zeitung (Berlin) 14: 391. 1856.

Densely cespitose, dwarf or to 5 dm high, the stems abbreviated to quite elongate and frondlike, to 1 dm long, the leaves erect to spreading flabellately, shorter than scapes or surpassing them, the sheaths entire or ciliate, mostly firm and lustrous, equaling blades in length or less than ½ as long, the blades mostly narrowly linear, the tips incurved-acute to blunt, the margins thin or incrassate, entire to papillate-scabrid or ciliolate, the surfaces usually dark green, smooth to (toward base) papillose-rugulose. Scape sheaths tubular proximally, open and carinate distally, the blades short to much elongated as in leaves. Scapes straight or flexuous, twisted, narrowly lineal to filiform, terete to somewhat compressed toward apex, ecostate to bicostate, smooth or papillate or ciliolate-scabrid along costae. Spikes mostly narrowly oblong to ovoid, mostly blunt, 0.5–1 cm long, the bracts decussate, thin, carinate to ecarinate, entire, deep olive brown, reddish brown or (mostly) near black, the sterile bracts usually 4, the lowest pair keeled, ca. ½ length of spike or less, the inner pair broader, slightly longer and ecostate, the fertile bracts mostly 2–4, broadly ovate, apically narrowly or broadly rounded, the backs papillose to smooth, folded-rounded. Lateral sepals mostly oblong-linear, free, subequilateral, mostly navicular, 3.5–6 mm long, narrowly to broadly acute,

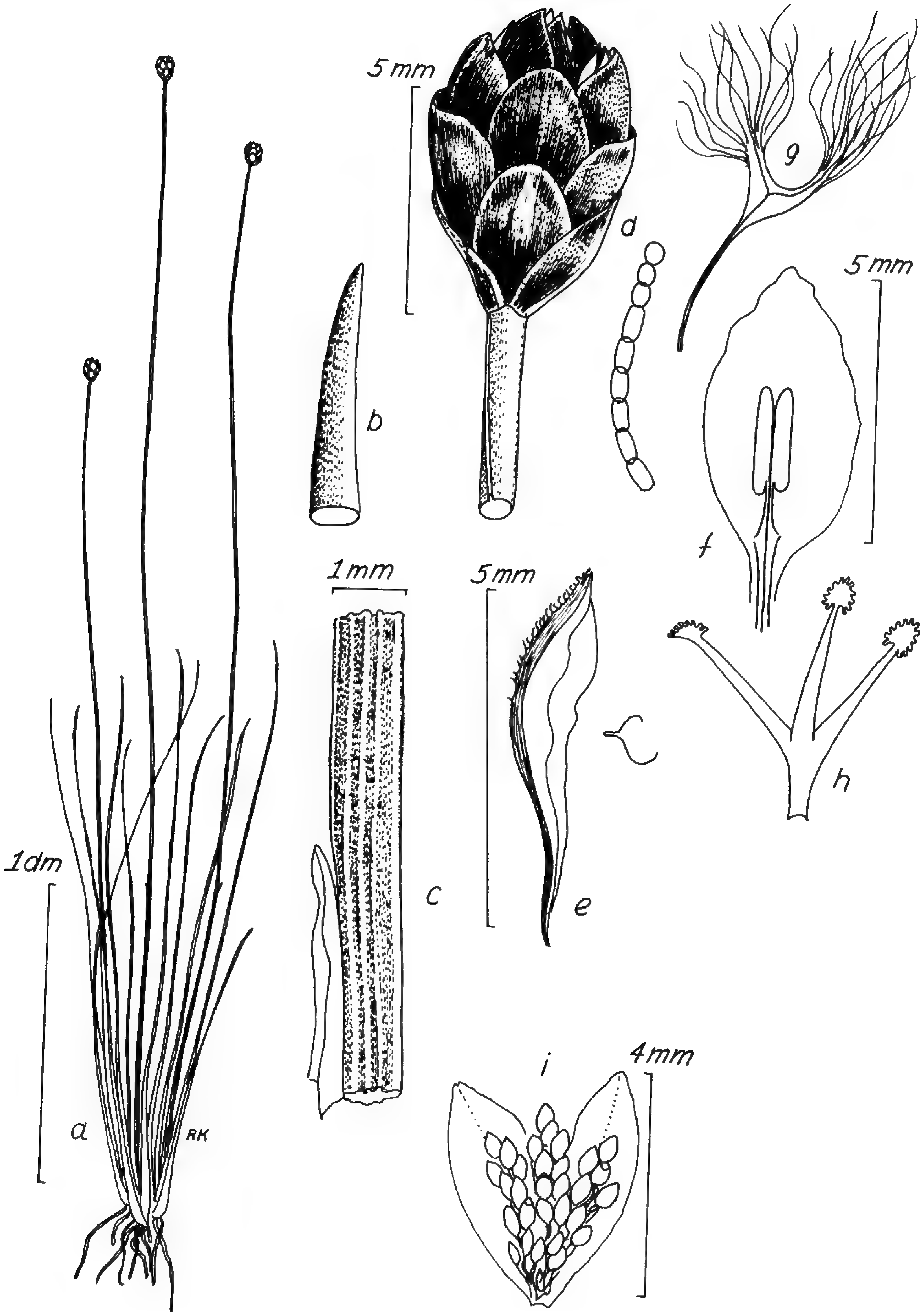


FIGURE 25. Xyris columbiana (Cuatrecasas et al. 28152).—*a. Habit sketch.—b. Leaf apex.—c. Leaf blade at junction with sheath.—d. Spike.—e. Lateral sepal.—f. Petal blade, stamen.—g. Staminode, enlarged sector of beard hair.—h. Stylar apex.—i. Capsule, one valve removed.*

with or without keel, entire to ciliolate or papillate along the crest or back medially. Petal blades broadly ovate to nearly orbicular, yellow, 3.5–5 mm long the broadly rounded apex erose or entire. Staminodia bibrachiate, branches long-penicillate. Anthers oblong, 0.6–2 mm long, the connective broad, on filaments 1–2 mm long. Capsule firm-valved, ellipsoid, 2–4 mm long, the placentation basal-central, the funicles elongate, the valves without septa or producing these at very base. Seeds ovoid to fusiform-cylindric, 0.5–1 mm long, prominently longitudinally ribbed or alveolate-reticulate.

This species has at least five marked varieties, the complex ranging widely along the "young" western cordilleras, from Costa Rica south to Chile, always in the high, cool to cold, "páramo." Only two of the varieties are known definitely to occur in the area of this treatment, but the key below includes the type variety which may yet be found there.

KEY TO SUBSPECIES OF *XYRIS SUBULATA*

1a. Edges of leaf sheaths variously ciliate; stems usually elongate.
    2a. The plants with leaves much shorter than scapes; seeds ca. 1 mm long; lateral sepals ca. 5 mm long .... 26A. *X. subulata* var. *subulata*
    2b. The plants dwarf, with leaves mostly equaling or exceeding scapes; seeds ca. 0.5 mm long; lateral sepals 3.5–4 mm long .... 26B. *X. subulata* var. *breviscapa*
1b. Edges of leaf sheaths entire; stems mostly contracted .... 26C. *X. subulata* var. *acutifolia*

26A. **Xyris subulata** Ruíz Lopez & Pavón var. **subulata.** Figure 26A.

Plants 10–30 cm high, the stems often elongate, with overlapping leaves forming fronds. Leaves flabellately ascending, loosely imbricate, ⅓–⅔ as long as scapes, the lustrous, pale red-brown sheaths ½ as long as the darker blades or longer, spreading arachnoid-ciliate, tapering gradually from the broad, clasping bases into blades, eligulate, the blades narrowly linear to filiform, mostly 0.5–1 mm wide, pale to deep green or red-green, compressed, flat to somewhat thickened, often terete toward apex, the tips terete, narrowly conic but blunt, the ventral edge a broad, papillose-rugulose band, the dorsal edge smooth or papillose, the surfaces papillose or smooth. Scape sheaths shorter than or slightly overtopping principal leaves, with strong, incurved-tipped blades similar to leaves. Scapes filiform, straight or flexuous, slightly twisted, terete below, subterete toward apex, or slightly compressed and bicostate, 0.3–0.5 mm wide, the surfaces mostly olive, smooth or (more often) tuberculate-papillose at least on costae. Spikes mostly ovoid to lance-ovoid, 2–4-flowered, 5–7 mm long, pale brown to near black, the bracts thin, loosely imbricate, decussate, entire or erose, without dorsal areas, the sterile pairs 2, the lowest pair shortest, ovate, carinate, the inner pair mostly broader, slightly longer, less carinate, the lowest pair of fertile bracts ecarinate but folded, much longer than the sterile bracts, ca. 4–5 mm long, entire, aging lacerate, dull or lustrous. Lateral sepals free, very thin, subequilateral, ca. 5 mm long, navicular, the midzone nearly without keel, entire. Petal blades broadly obovate to nearly suborbicular, ca. 5 mm long, yellow, broadly rounded, subentire. Anthers ca. 1 mm long, oblong, deeply bifid at apex, the filaments ca. 1.5 mm long. Staminodia bibrachiate, the flattened, narrow branches elongate, long-penicillate. Capsule firm-valved, brown, ellipsoid, ca. 3 mm long, placentation basal, funiculi elongate. Seeds fusiform-cylindric, ca. 1 mm long, caudate, red-brown, translucent, longitudinally irregularly multiribbed.

Distribution. South America, Andean paramos, rare in Colombia, increasingly frequent, Ecuador south through Peru. For Colombia I have only one certain record.

Additional specimen examined. COLOMBIA. ANTIOQUIA: Páramo Frontino Cerro de Campanas, *Espeletia* paramo, 3,650–4,290 m, clumps of ca. 20 plants, 28 Oct. 1976, *J. D. Boeke & J. B. McElroy 287* (U).

The long "stems" of this and related taxa may in part be a result of the deep humus deposits in which dense clumps of this sort of

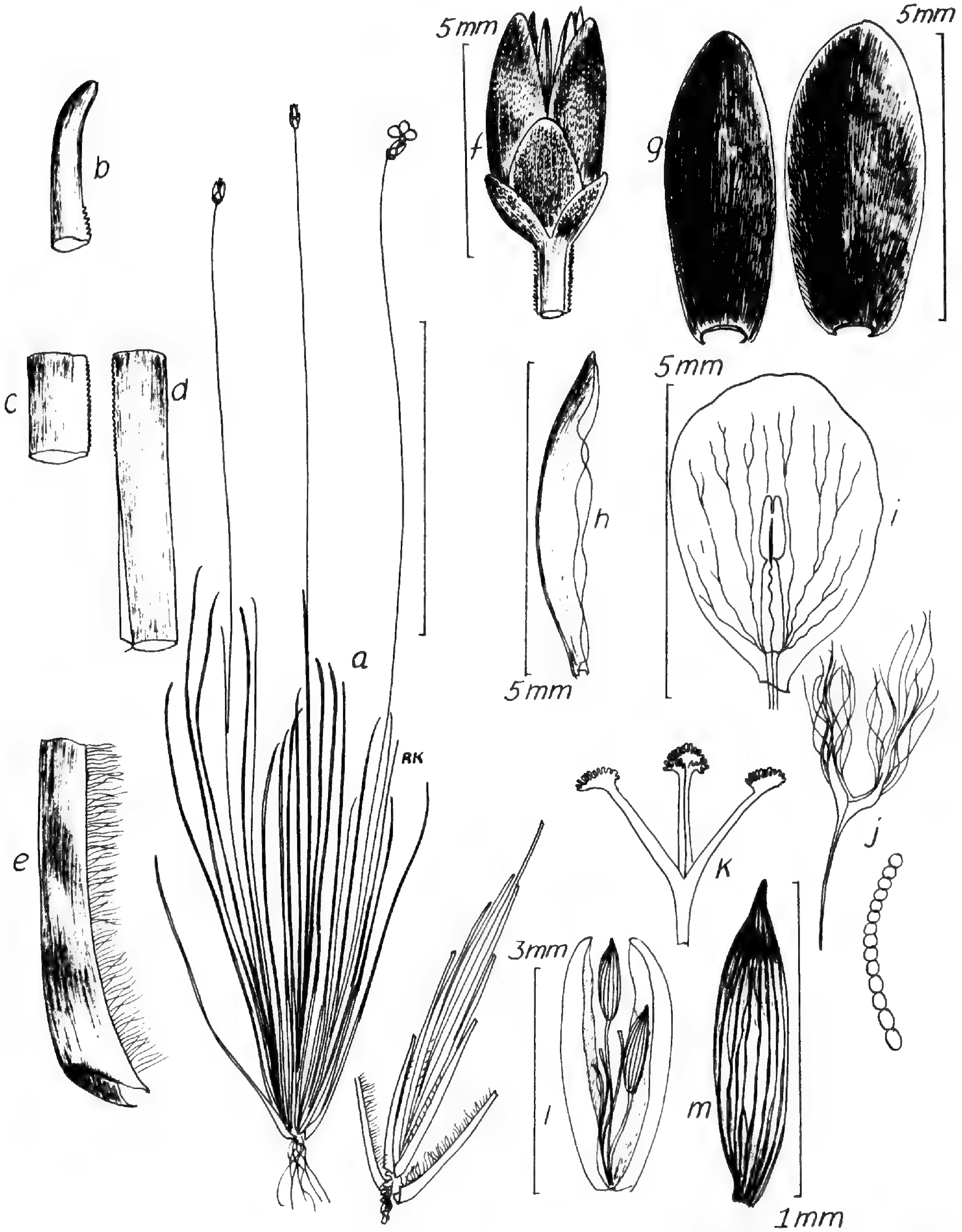


FIGURE 26A. Xyris subulata *var.* subulata *(drawn from several Peruvian examples)*.—*a. Habit sketch.*—*b. Leaf apex.*—*c. Short sector of leaf blade.*—*d. Leaf sheath–blade junction.*—*e. Leaf base.*—*f. Spike.*—*g. Back (abaxial) view, two fertile bracts.*—*h. Lateral sepal.*—*i. Petal blade, stamen.*—*j. Staminode.*—*k. Stylar apex.*—*l. Capsule.*—*m. Seed.*

plant are rooted, this "burying" resulting in significant elongation of internodes comparable to that in *X. witsenioides* Oliv. and related species.

26B. Xyris subulata var. **breviscapa** Idrobo & Lyman B. Smith, Caldasia 6: 220, fig. 16. 1954. TYPE: Colombia. Putumayo: alta cuenca del Río Putumayo, filo de la Cordillera entre El Encano y Sibundoy, paramo de San Antonio de Bordencillo, 3,250 m, 4 Jan. 1941, *J. Cuatrecasas 11744* (holotype, US; isotype, COL). Figure 26B.

Densely cespitose perennial, tufted as in moss, to 1 dm high, usually much lower, the stems ascending from fascicled rhizomes, forming frondlike plates of leaves and leaf bases. Leaves 2.5–10 cm long, loosely imbricate, ascending-flabellate, the sheaths as long as blades or slightly longer, lustrous pale brown, smooth-keeled, low-costate, tapering gradually from broad, clasping bases into the blades, eligulate, the blades filiform to narrowly linear, flattened, ca. 0.5 mm wide, the apex subterete, slender-incurved, smooth, the ventral margin slightly thickened, pale, papillose-rugulose, the surface olive, with a few low nerves, usually smooth. Scape sheaths slightly longer than or slightly shorter than principal leaves, with elongate, incurved blades as in leaves. Scapes to 1 dm high, overtopping leaves or overtopped by leaves, filiform, 0.3–0.4 mm thick distally, there terete or slightly flattened, usually bicostate, the costae scabridulous, the surfaces olivaceous, usually papillate. Spikes narrowly to broadly ovoid, pale brown to dark brown, 4–7 mm long, the bracts decussately arranged, loosely imbricate, thin, the sterile of 2 pairs, the lowest pair broadly ovate-triangular, keeled, ca. 2 mm long, the inner pair ovate, carinate only toward the apex, ca. 3 mm long, the fertile bracts 2(–4), oblong-ovate, 3.5–4 mm long, the apex entire or erose, scarious, folded or carinate. Lateral sepals free, subequilateral, oblong, 3.5–4 mm long, the apex obtuse, nearly without keel, this a darker thickening medially, entire. Petal blades broadly elliptic to broadly obovate, yellow, 3.5–4 mm long, subentire, apiculate, erose. Anthers oblong, 0.6–0.7 mm long, deeply bifid, on filaments ca. 1 mm long. Staminodia bibrachiate, long-penicillate. Capsule broadly ellipsoid or obovoid, brown, ca. 2 mm long, the placentation basal, the funiculi elongate. Seeds ca. 0.5 mm long, ovoid, short-apiculate, rather coarsely ridged and cross-ridged, this irregularly reticulate.

Distribution. High grassy paramos of the Andes, Colombia south into Peru and Bolivia.

Additional specimens examined. BOLIVIA: Cordillera Real, Cocopunco, 10,000 ft., 24–29 Mar. 1926, *G. H. H. Tate 321* (NY); Tolapampa, 25 Sep. 1902, 10,000 ft., *R. S. Williams 1638* (NY—a putative isotype of *X. cryptocarpum* Rusby, which appears to be a nom. nud.). COLOMBIA. ANTIOQUIA: Páramo Frontino, near Llano Grande, *Espeletia* páramo, 3,450 m, *Boeke & McElroy 262* (NY, U). AZUAY. Cordillera Oriental, alrededores del Páramo de Patococha entre Gualaceo y Limón, 6–7 Aug. 1969, 3,400–3,450 m, *Barclay & Juajibioy 8626* (NY). CAUCA: Macizo Colombiano, Valle de Las Papas, alrededores de Valencia, ca. 3 km from Casa, Los Andes, Sta. 10, ca. 3,150 m, 4 Oct. 1958, *Barclay & Juajibioy 5915* (NY); Cordillera Central, cabeceras del Río Palo, altos páramos entre Quebrada de San Paulino y Quebrada del Lopez: Lagunilla de Las Casitas, 3,700 m, 3 Dec. 1944, *Cuatrecasas 19006* (GH). HUILA-CAUCA: Macizo Colombiano, Páramo de Las Papas, El Boquerón, paramo abierto y bosque Filo de La Cuchilla que sierra por el sur La Laguna de La Magdalena, 3,450 m, 5 Sep. 1958, *Idrobo et al. 2967* (VEN). LOJA: Muletrack Amaluza–Palanda, western slope near pass (at Laguna Areviatadas Pilares), 3,350–3,450 m, 22 Sep. 1976, *Ollgaard & Balslev 9680, 9707* (NY). PERU. CUSCO: Paso de Tres Cruces, Cerro de Cusilluyoc, 3,800–3,900 m, 3 May 1925, *Pennell 13886* (F, NY).

This variety is distinguished from the others primarily by its low habit, seeding spikes often overtopped by leaves, and distinctly shorter, coarsely reticulate seeds.

26C. **Xyris subulata** var. **acutifolia** Heimerl, Ann. k. k. Naturh. Hofmus. Wien 21: 63. 1906. *X. acutifolia* (Heimerl) Malme, Ark. Bot. 13(3): 40. 1913. TYPE: Colombia: Depto. Cundimarca, "Bogotá, Goudot" (presumably at W). Figure 26C.

Cespitose glabrous perennial, the stems contracted to slightly elongated. Leaves erect or slightly spreading, to 2 dm long; sheaths mostly ½ as long as blades or less, the bases shining, pale brown to brown or tan, mostly narrowing gradually into blades, eligulate or with narrow, scarious ligules to 2 mm long, entire; blades filiform to narrowly linear, 0.5–2 mm wide, slightly to very flattened, often twisted, narrowly acute apically, incurved, the margins smooth to papillate-scaberulous or

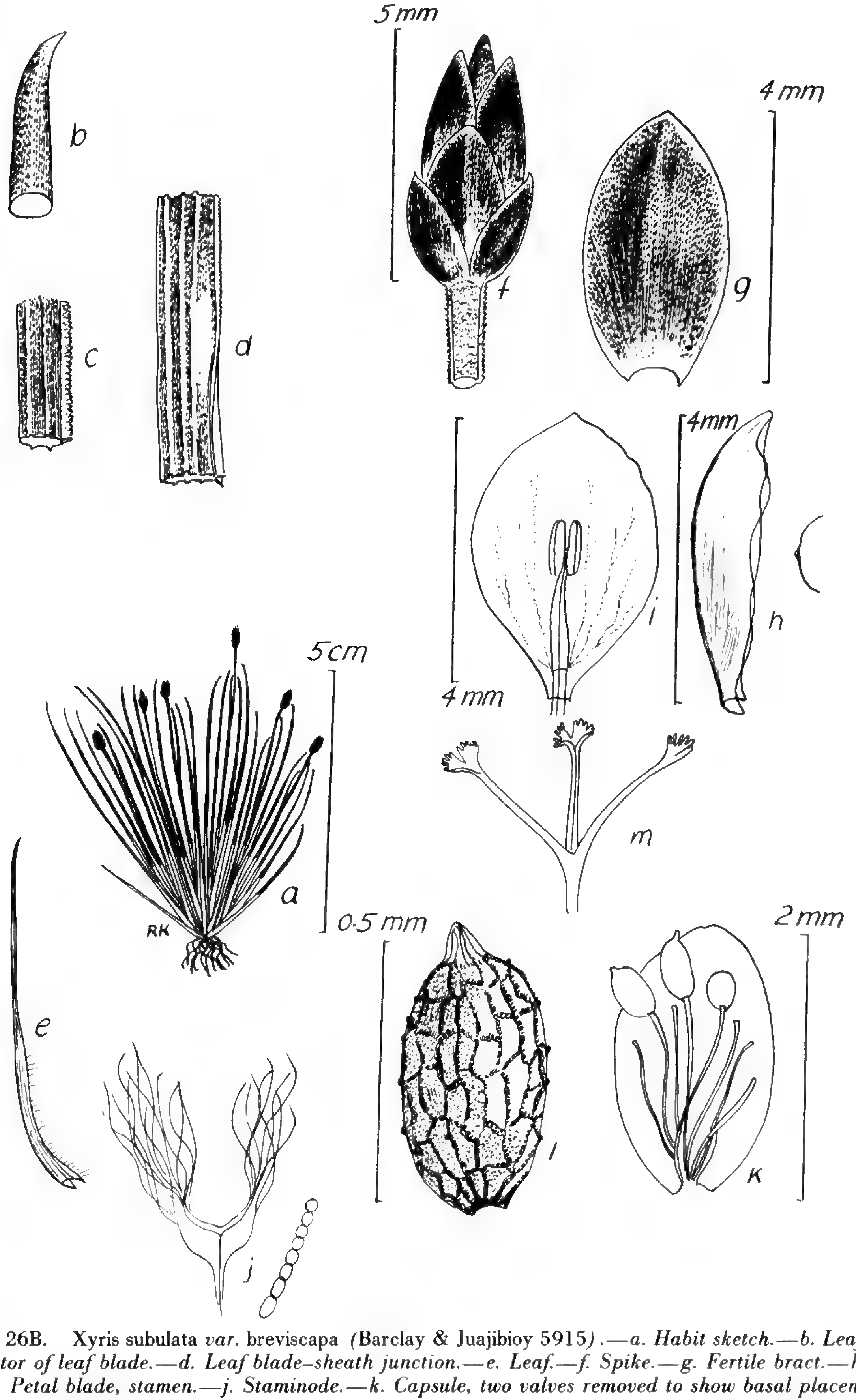


FIGURE 26B. Xyris subulata *var.* breviscapa *(*Barclay & Juajibioy 5915*).—a. Habit sketch.—b. Leaf apex.—c. Midsector of leaf blade.—d. Leaf blade–sheath junction.—e. Leaf.—f. Spike.—g. Fertile bract.—h. Lateral sepal.—i. Petal blade, stamen.—j. Staminode.—k. Capsule, two valves removed to show basal placentation.—l. Seed.—m. Stylar apex.*

pale-ciliolate, the surfaces deep green, strongly or weakly nerved, smooth to papillose-rugulose, the latter particularly toward base. Scapes to 3 dm high, straight or flexuous, twisted, narrowly lineal, 0.5–1 mm thick, distally terete or oval, ecostate to commonly bicostate, the surfaces smooth to papillose-rugulose, the costae smooth to scabrid. Scape sheaths shorter than leaves, with short, erect blades. Spikes narrowly oblong to ovoid, mostly blunt, 0.5–1 cm long, the bracts decussate, thin, mostly ecostate, entire, deep olive brown, reddish brown or (mostly) near black, the sterile bracts usually 4, the lowest pair strongly keeled, ca. ½ spike length or less, the inner pair broader, slightly longer and ecostate, the fertile bracts 2–4, broadly ovate, narrowly or broadly rounded apically, the backs papillose to smooth, folded-rounded. Lateral sepals oblong-linear to elliptic-linear, free, subequilateral, mostly navicular, 4–6 mm long, narrowly to broadly acute, with or without keel, entire to ciliolate or papillate along the crest or back medially. Petal blades mostly ovate, 4–5 mm long, pale yellow, narrowly rounded apically, coarsely erose. Staminodia bibrachiate, with broad, flat branches apically multipenicillate. Anthers oblong, ca. 2 mm long, blunt, widely separated by broad connective on filaments ca. 2 mm long. Fruit ellipsoid, ca. 3–4 mm long, the placentation basal-central, the funicles elongate; capsule valves without septa or with septa only at base. Seeds ellipsoid-fusiform, ca. 0.7–1 mm long, deep amber, strongly longitudinally multiribbed.

Distribution. Páramos, high mountain bogs, western cordilleras, mostly over 2,000 meters high, Costa Rica south through the Andean chains to Peru, locally abundant.

Selected additional specimens examined. COLOMBIA. ANTIOQUIA: Páramo Frontino, Cerro de Campanas, *Boeke & McElroy 287* (NY). BOYACÁ: Sierra Nevada del Cocuy, Páramo Cóncavo, *Cleef 10004* (COL, U, US, VDB). CAUCA: Valle de Las Papas, near Valencia, *Core 999* (GH, NY); Cundimarca, páramo entre Cógua y San Cayetano, Laguna Verde y alrededores, 500 m al NW de La Laguna Verde, *Cleef 6240* (COL, U, VDB). META: Páramo de Sumapaz, Hoya de La Quebrada Sitiales, Vallecito Pantanoso 0.5 km SW de La Laguna La Primavera, *Cleef 1050* (U, US, VDB). HUILA: "Balsillas" on Río Balsillas, *Rusby & Pennell 775* (GH, NY); Norte de Santander, Páramo del Hatico, en route from Toledo to Pamplona, *Killip & Smith 20620* (GH, PH, NY). COSTA RICA. CARTAGO: bog in cloud forest along Pan Am. Highway near Cerro Las Vueltas, *Holm & Iltis 444* (F, GH, MO, NY, U, US). LIMÓN: Cordillera de Talamanca, Valle de Silencio, along Río Terbi 1.5 airline km W of Costa Rican–Panamanian border, 2,300 m, *Davidse et al. 28575* (MO, VDB, VEN). SAN JOSÉ: cloud forest area N of Cerro de La Muerte, Cordillera de Talamanca, *L. O. Williams et al. 24146* (F, NY, US). PERU. AMAZONAS: Chachapoyas, Jalca zone 3–6 km W of Molinopampa, *Wurdack 1405* (GH, NY, US). PASCO: Oxapampa, trail to summit of Cordillera Yanachaga via Río San Daniel, *D. N. Smith 7714* (MO, VDB). VENEZUELA. ANZOATEGUI: Cerro Peonia above Sta. Cruz, headwaters of Río Manantiales, E of Bergantin, *Steyermark 61697* (F, NY, US, VEN). LARA: trail from Hunocaro to Buenas Aires (Caserio) below Páramo Las Rosas, *Liesner et al. 8118* (MO, VDB). MERIDA: Páramo de Sto. Domingo, *A. Jahn 1102* (GH, MO, NY, US, VEN); San Raphael, *E. Reed 854* (US). SUCRE: Cerro Turumuquire, *Steyermark 62624* (F, MO, NY, US, VEN). TACHIRA: Páramo de Tama, cerca de la frontera Colombo–Venezolana, *Steyermark & Dunsterville 98625* (F, NY, US, VEN). TRUJILLO: Su-Oaramo y páramo de Guaramacal, *F. Ortega 2654* (MO, PORT, NY, VDB).

This is the most abundant variety, therefore the most collected, and is usually distinguished from the others by its generally shorter stems, paler brown sheaths, and particularly its entire (vs. long-ciliate) leaf-sheath margins.

27. Xyris valdeapiculata Kral, sp. nov. TYPE: Venezuela. T. F. Amazonas: Dpto. Río Negro, Valle de Titirico N of Pico Phelps in Cerro Neblina, ca. 0°56′N, 65°58′W, ca. 2,200 m; peat bog interspersed with shrub and low, rocky but wet ridges, 1 Dec. 1984, fls. open in A.M., *R. Kral 71919* (holotype, VEN; isotypes, F, MO, NY, US, VDB). Figure 27.

Planta perennis, caespitosa, glabra, gracilis. Radices graciles. Caules breves. Folia principalia leviter expansa vel flabellate expansa, 8–14 cm longa, vaginis scaporum longiora; vaginae integrae, basin versus ecarinatae, pallide brunneolae, nitidae, leviter dilatatae, multicostatae, in laminas gradatim decrescentes et carinatae, ad apicem breviligulatae; laminae anguste linearia, 2–3-plo vagines longiores, 1–2.5 mm latae, compressae, olivaceae, longitudine leviter multinervosae; apices incurvato-acuta, leviter incrassata; margine tenuis, retrorse scabrociliatae, pallidae. Scapi leviter torti vel recti, 20–35 cm alti, ca. 1 mm lati, ad apicem subteretes sed prominente bicostatae, costis dense pallide scabrociliatis. Spicae pauciflorae, brunneolae, anguste turbinatae (demum late turbinatae) ca. 10 mm longae; bracteae sine area dorsali, laxe

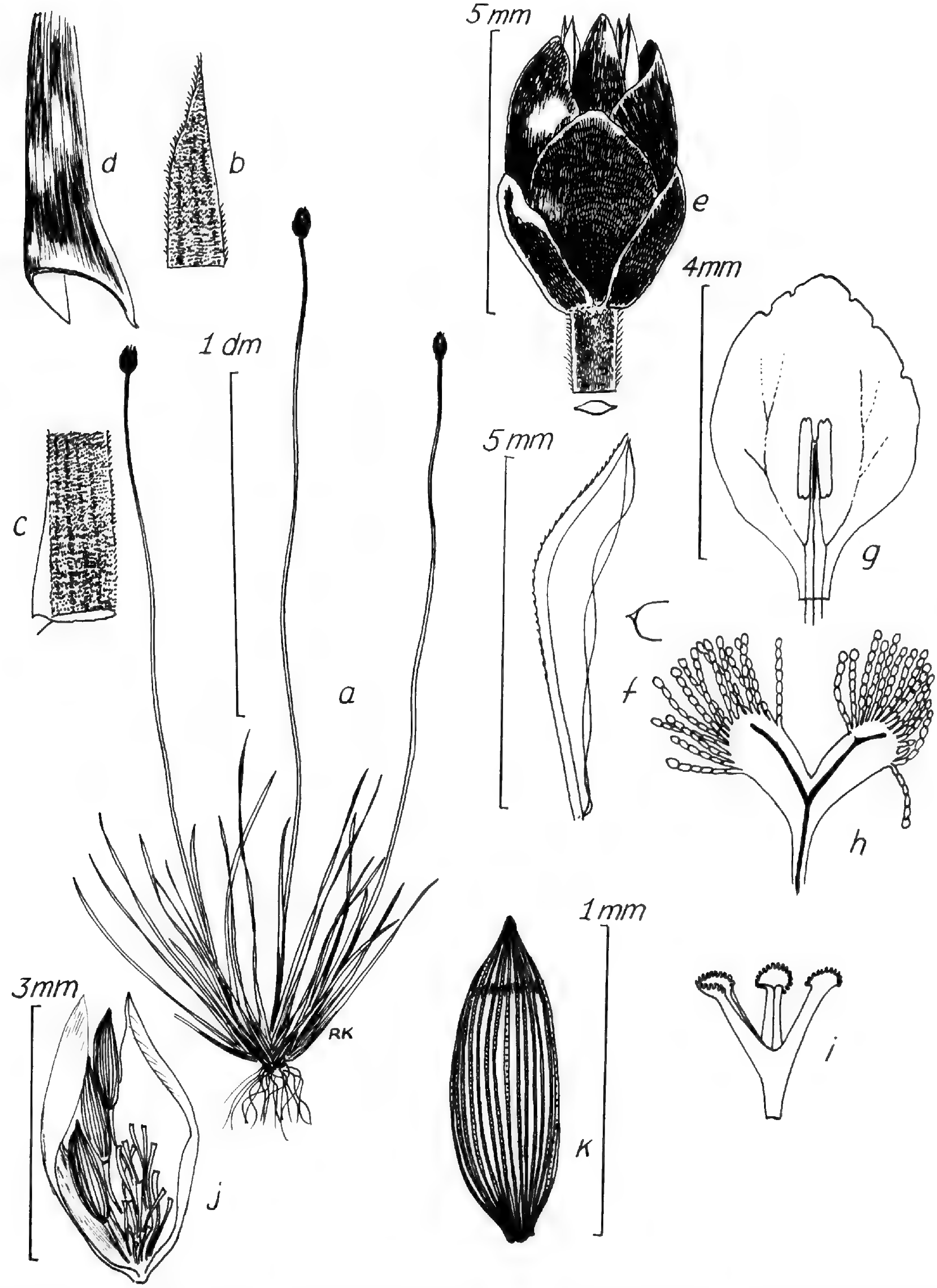


FIGURE 26C. Xyris subulata *var.* acutifolia *(*Steyermark & Dunsterville 101199*).—a. Habit sketch.—b. Leaf apex.—c. Leaf blade–sheath junction.—d. Leaf base.—e. Spike and upper scape.—f. Lateral sepal.—g. Petal blade, stamen.—h. Staminode.—i. Stylar apex.—j. Capsule, showing basal–central placentation.—k. Seed.*

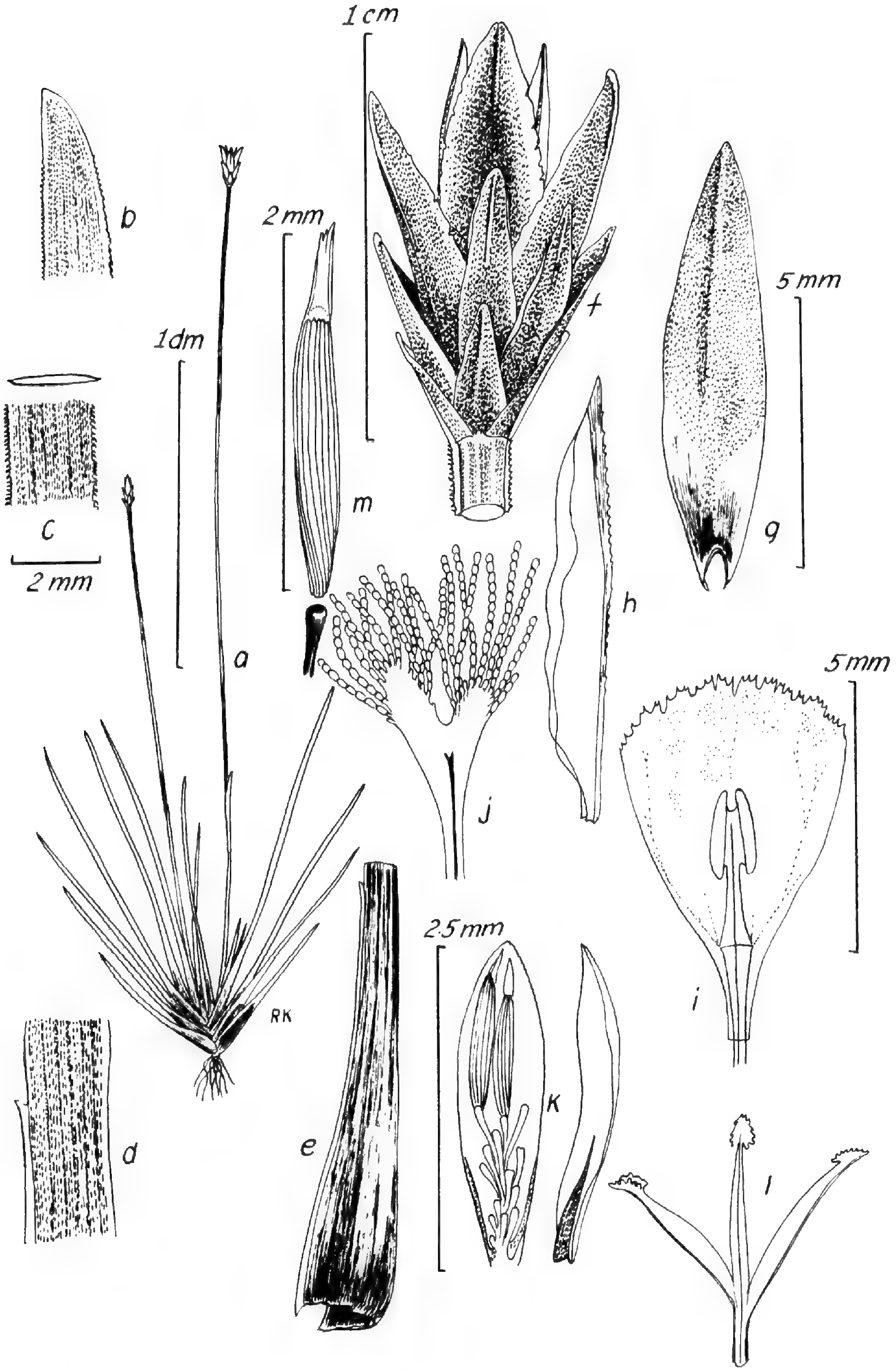


FIGURE 27. Xyris valdeapiculata (Kral 71919).—*a. Habit sketch.—b. Leaf tip.—c. Leaf blade, midsector.—d. Leaf blade-sheath junction.—e. Leaf base.—f. Spike.—g. Fertile bract.—h. Lateral sepal.—i. Petal blade, stamen.—j. Staminode.—k. Capsule outline, free-central placenta imposed; oblique view of valve.—l. Stylar apex.—m. Seed.*

spiraliter imbricatae, leviter expansae, integrae, infimae 5–6 steriles, par inferior anguste triangulata, ca. 4 mm longa, valde carinata, scabrociliata, 2–3-plo fertiles breviores, intimae leviter longiores, lanceolatae, carinatae, usque ad 5 mm longae, in fertiles abrupte transientes; bracteae fertiles late lanceolatae, usque ad 8 mm longae, a medio ad apicem valde carinatae, integrae (demum laceratae). Sepala lateralia libera, subaequilateralia, 7–8 mm longa, acuminata, leviter curvata, ala carinali angusta, incrassata, integra vel leviter scabrida. Laminae petalorum obtriangulatae, luteolae, ca. 5 mm longae, apice laceratae. Staminodia bibrachiata, brachiis disparibus, oblongis, penicillatis. Antherae oblongae, profunde bifidae et sagittatae, ca. 1 mm longae, filiis ca. 1 mm longis. Capsula matura anguste ellipsoidea, 4.5 mm longa, acuta, valvis basin versus septo habens; placenta centralis, funiculis crassis. Semina cylindrica (cum apicula) 2 mm longa, pallide brunneola, opaca, longitudine spiraliter multicostata, apiculo albosquamoso, ca. 0.5 mm longo.

Plants perennial, cespitose, smooth, slender, the roots slender-fibrous. Stems short. Leaves slightly to flabellately spreading, 8–14 cm long, longer than the scape sheaths; sheaths entire, ecarinate toward base, lustrous pale brown, slightly dilated, multicostate, gradually narrowing, carinate into the leaf blades, at apex short-ligulate; blades narrowly linear, 2–3 times longer than the sheaths, 1–2.5 mm wide, flat, olivaceous, finely multinerved; tips incurved-acute, slightly thickened; edges thin, retrorsely scabrociliolate, pale. Scapes slightly twisted or straight, 20–35 cm high, ca. 1 mm wide, subterete toward apex but prominently bicostate, the costae densely pale scabrociliate. Spikes few-flowered, brownish, narrowly turbinate, becoming broadly turbinate, ca. 10 mm long; bracts without dorsal area, laxly spirally imbricate, slightly spreading, entire, the lowest 5–6 sterile, the lowest pair narrowly triangular, ca. 4 mm long, strongly carinate, scabrociliate, 2–3 times shorter than the fertile bracts, the inner bracts slightly longer, lanceolate, carinate, up to 5 mm long, grading abruptly into the fertile bracts; these broadly lanceolate, up to 8 mm long, strongly carinate from middle to tip, entire (aging lacerate). Lateral sepals free, subequilateral, 7–8 mm long, acuminate, slightly curvate, the keel narrow, thick, entire to slightly scabrid. Petal blades obtriangular, yellow, ca. 5 mm long, apically lacerate. Staminodia bibranched, the branches unequal, oblong, penicillate at tips. Anthers oblong, deeply bifid and sagittate, ca. 1 mm long, on filaments ca. 1 mm long. Mature fruit narrowly ellipsoid, 4.5 mm long, acute, the valves with septa toward base; placenta free-central, with thickened funicles. Seed cylindric, 2 mm long including apiculus, pale brown, opaque, longitudinally spirally ribbed, the apiculus a pale scale ca. 0.5 mm long.

Distribution. Known only from the type locality.

In general dimensions and in strongly two-edged, ciliate scape, the new species resembles *X. bicostata* Maguire & Lyman B. Smith but lacks a dorsal area. Also, the lustrous brown leaf sheaths are entire rather than long-ciliate. In the locale, it is associated with an abundance of *X. xiphophylla* Maguire & Lyman B. Smith, *X. bicostata* Maguire & Lyman B. Smith, and *X. atriceps* Malme. Its petals unfold in late morning. As in several of the high-tepui endemics of the Guayana Highland, *X. valdeapiculata* has an elongated (2 mm) seed, the name for the species chosen to reflect the long, pale, thin apiculus.

28. Xyris tatei Malme, Bull. Torrey Bot. Club 58: 324, pl. 24, fig. 1A. 1931. TYPE: Venezuela. T. F. Amazonas: moist slopes of the Savanna Hills, summit of Mount Duida, 4,400 ft., *G. H. H. Tate 835* (lectotype, NY; phototypes, F, NY). Figure 28.

Robust, cespitose, hard-based perennial 6–9 dm high, the stem stout, contracted, or up to 9 cm long. Leaves spreading flabellately or ascending, 2.4–6 dm long; sheaths eciliate, usually ½ as long as blades, or shorter, broad at very base, lustrous deep red-brown or castaneous, thence upward shading to pale green, narrowing gradually to blade, there with an erect, pale, triangular ligule 1–2 mm long; blades linear, flattened, 3–7 mm wide, narrowing gradually above middle, abruptly narrowed at apex, incurved-acute, the tip somewhat incrassate; margins slightly to very thickened, pale, smooth or papillose; surfaces green, multinerved, smooth. Scape sheaths

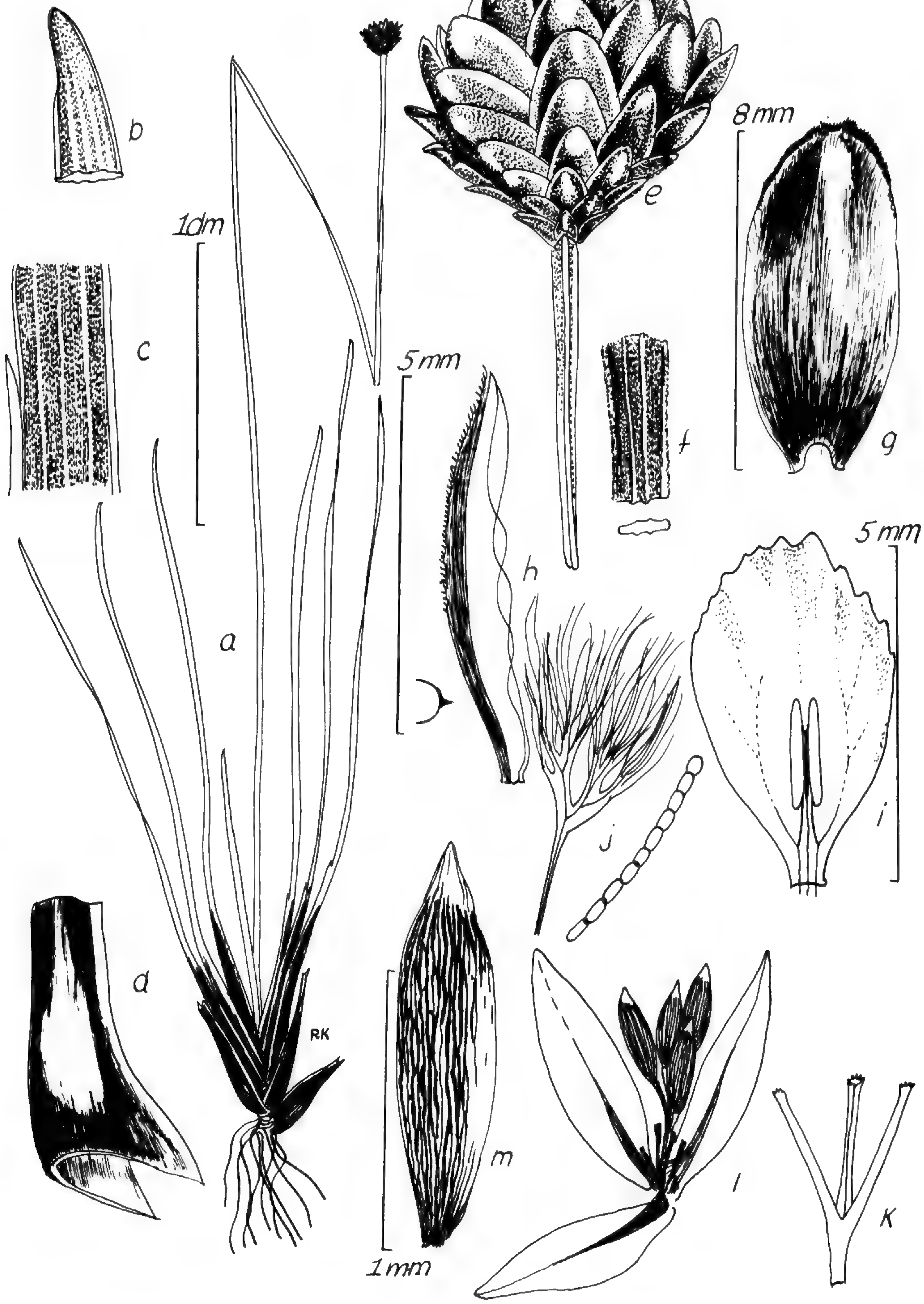


FIGURE 28. Xyris tatei (Tate 835).—*a. Habit sketch.—b. Leaf apex.—c. Leaf at blade-sheath junction.—d. Leaf base.—e. Spike.—f. Sector of upper part of scape.—g. Fertile bract.—h. Lateral sepal.—i. Petal blade, stamen.—j. Staminode, enlarged tip of beard hair.—k. Stylar apex.—l. Capsule, spread at maturity to show basal-central orientation of placenta, septa of valve bases.—m. Seed.*

shorter than leaves, tubular and costate at base, keeled, open toward apex, producing a short, erect blade. Scapes flattened distally, 2–3 mm wide, the edges comprising 2 densely papillate pale costae, the sides sometimes with 1–2 more lower costae. Spikes globose to hemispherical or broadly turbinate, 1–1.5 cm high, the base attenuate, with many firm, lustrous brown, imbricate bracts in nearly vertical rows and without dorsal areas; fertile bracts numerous, the lowest bracts much smaller than the fertile bracts, ovate-triangular, carinate, grading into the fertile bracts, these broadly oblong to obovate, 6–8 mm long, broadly rounded at apex, with reddish scarious (rarely also reddish ciliolate) borders or subentire, the backs low-convex with a low, pale median nerve toward apex. Lateral sepals free, equilateral, narrowly oblong-elliptic, ca. 6–6.5 mm long, acute, reddish brown, the firm keel red-ciliolate from middle to apex. Petal blades obovate, ca. 5–5.5 mm long, the narrowly rounded apex and margins erose. Anthers oblong-lineal, 2–2.2 mm long, deeply bifid and shallowly auriculate, on erect filaments ca. 1 mm long. Staminodia with branches rebranched, the flattened ultimate branchlets long-penicillate. Capsule narrowly ellipsoid, acuminate, ca. 4–5 mm long, the placentation appearing basal-central, but each valve with a strong septum at base. Seeds few, cylindrical-fusiform, ca. 1.5–2 mm long, dark amber with apex conic and pale, the body finely and prominently longitudinally multiribbed.

Distribution. Known only from high, wet, rocky savanna, Cerro Duida, at elevations over 1,000 meters.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: Cerro Duida (all specimens): Río Cunucunuma, occasional in moist places in open scrub, basin of Caño Negro at 2,000 m, *Maguire, Cowan & Wurdack 29694* (NY); open places near summit of Culebra Peak, 1,800 m, *Maguire 29155* (NY, VEN); Río Cunucunuma, to 1 m high, occasional along Culebra Creek at 1,100 m, *Maguire, Cowan & Wurdack 29511* (NY); moist slopes of Savanna Hills, summit of Mt. Duida, 4,400 ft., *Tate 778* (NY).

This taxon resembles *X. albescens* Steyerm. superficially, but that species has its leaf-blade edges and its scape edges prominently ciliate with pale hairs, while its seeds are longer and much narrower.

29. Xyris melanovaginata Kral & Lyman B. Smith, sp. nov. TYPE: Venezuela. Bolívar: Dist. Piar, Macizo del Chimantá. Sección oriental del Chimantá-tepui, cabeceras del afluente derecho superior del Río Tirica ("Caño del Grillo"), 5°18′N, 62°3′W, ca. 2,450 m, 7–9 Feb. 1983, *O. Huber & J. A. Steyermark 7136* (holotype, VEN; isotype, VDB). Figure 29.

Planta robusta, perennis, caespitosa, 5–10 dm alta, basibus firmis, per bases persistentes veternas foliorum obtectis. Caules incrassati, varie elongati (basibus in substratio profunde elongati). Folia principalia rigida, disticha, flabellate expansa, 2–3 dm longa; vaginis scaporum longiora; vaginae integrae, vulgo laminis aut dimedio breviorae vel minus, lamprocastaneae, sursum in laminas gradatim contractae, ad apicem ligulatae, ligula anguste triangulata, ca. 2 mm longa; laminae planae, ensiformilineares, 4–6 mm latae, apices incurvati-acuti, incrassati; margines integri vel ciliolati aut pallide ciliatopilosi; paginae atrovirides, leviter multinervosae, glabrae. Vaginae scaporum foliis breviore, laxae, a basin castaneae, tubulosae, ad apicem carinatae et apertae, laminis brevibus, laminis foliorum similibus. Scapi recti vel aliquantum curvati, valde complanatae, ad apicem ancipiti, 2–4 mm lati, margine glabri vel varie pallide vel albociliatae. Spicae ovoideae vel ellipsoideae aut cylindricae, 1–3 cm longae, obtusae, atroporphyreae vel olivaceicastaneae, attenuatae, multiflorae; bracteae arcte spiraliter imbricatae, steriles multae, fertilibus breviores, latae ovatae vel obovatae, ecarinatae vel ad apicem leviter carinatae, fertiles gradatim profluentes, haec oblongae vel late obovatae, 5.5–7 mm longae, late rotundatae, integrae vel erosae, ecarinatae, leviter convexae, sine area dorsali. Sepala lateralia libera, subaequilatera, oblongo-linearia, ca. 5 mm longa, obtusa, vel acuta, pallide brunneola; ala carinali firma, super mediam ciliolata vel piloso ciliata. Laminae petalorum obovatae, ca. 6 mm longae, luteolae. Staminodia bibrachiata, brachiis longipenicillatis. Antherae latae oblongae, ca. 1 mm longae, filiis ca. 0.5 mm longis. Capsula anguste ellipsoidea vel obovoidea, 4–5 mm longa; placentae axiales. Semina pauca, ellipsoidea, apiculata, 1.3–1.5 mm longa, porphyrea, translucida, longitudine leviter multicostata.

Robust, cespitose perennial 5–10 dm high, the stems stout, contracted or elongated to 2 dm, producing frondlike plates of leaves. Leaves spreading flabellately, 2–3 dm long, sheaths entire, mostly ½ as long as blades or shorter, firm, castaneous, lustrous, tapering gradually from broad bases into blades, there

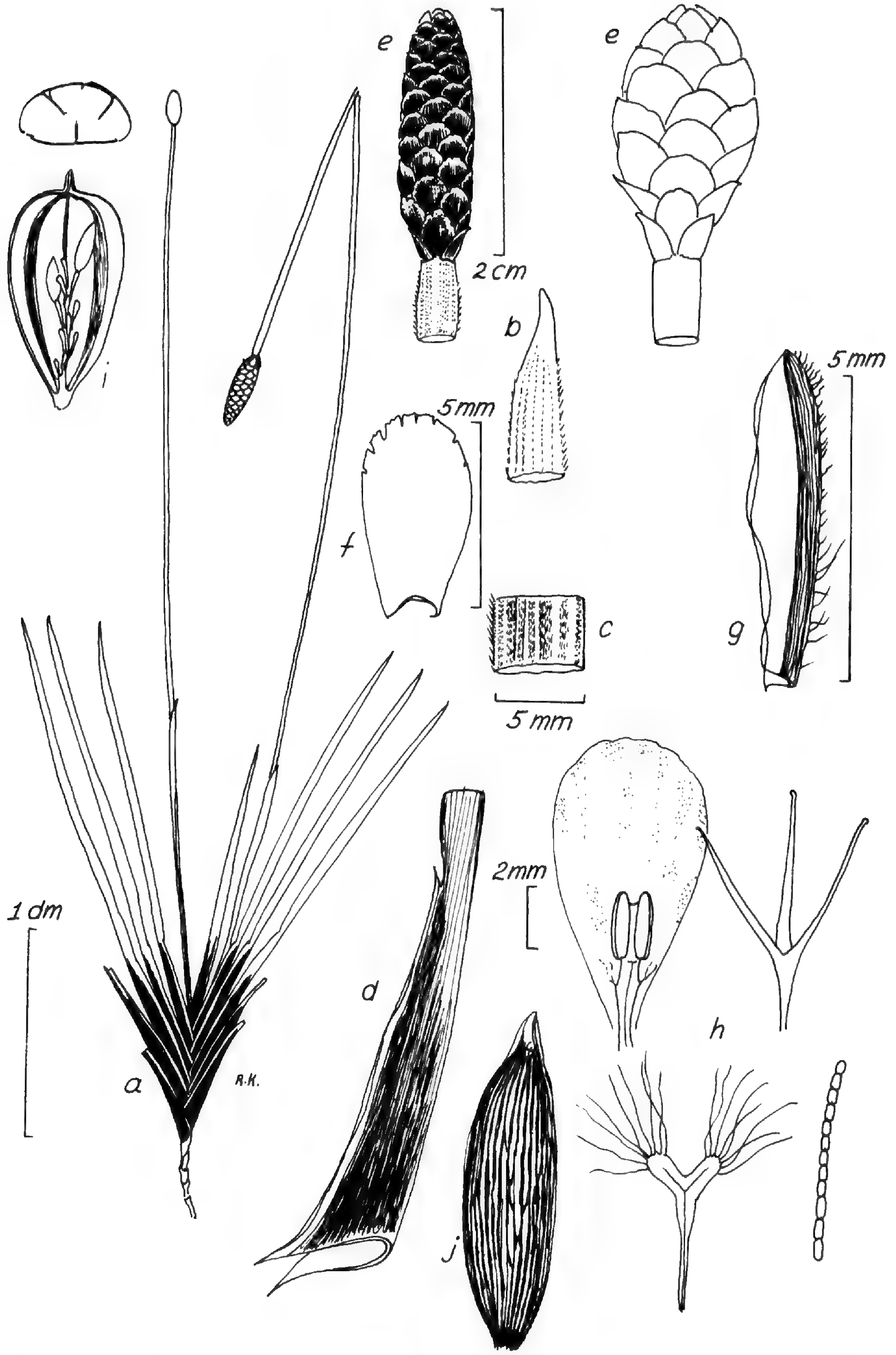


FIGURE 29. Xyris melanovaginata *(from the type)*.—*a. Habit sketch.—b. Leaf apex.—c. Leaf at ca. mid-blade.—d. Leaf base.—e. Two spikes.—f. Fertile bract.—g. Lateral sepal.—h. Clockwise—petal blade and stamen, stylar apex, enlarged sketch of beard hair, staminode.—i. Capsule: above, cross section showing disposition of septa; below, longitudinal view showing placentation, septa shaded.—j. Seed.*

producing a scarious, narrowly triangular ligule ca. 2 mm long; blades flat, gladiate-linear, 4–6 mm wide, the apex incurved-acute, incrassate, the margins usually with submarginal narrow red-brown bands, the edges cartilaginous, smooth or ciliolate or pale-pilose-ciliate, the surfaces deep green, finely multinerved, smooth. Scape sheaths shorter than leaves, proximally castaneous and tubular, keeled and open above, producing a short, flat blade. Scapes strongly flattened, distally ancipital, 2–4 mm wide, the edges smooth to variously pale-ciliate. Spikes ovoid to ellipsoid or cylindric, 1–3 cm long, blunt, dark red-brown or olivaceous-castaneous, attenuate, of many spirally imbricate bracts, the sterile bracts many, broadly ovate to obovate, ecarinate or distally carinate, grading gradually larger into fertile bracts, these oblong to broadly obovate, 5.5–7 mm long, broadly rounded, entire or erose (lacerate in age), ecarinate and but slightly convex-backed, without dorsal area. Lateral sepals free, subequilateral, oblong-linear, blunt or acute, pale brown with firm ciliolate or pilose-ciliate keel. Petals with blades obovate, ca. 6 mm long, yellow, the broadly rounded apex erose. Staminodia bibrachiate, the branches at apex long-penicillate. Anthers broadly oblong, ca. 1 mm long, the connective broad, the filaments ca. 0.5 mm long. Capsule narrowly ellipsoid to obovoid, dorsiventrally compressed, 4–5 mm long, the placentae axile, the valves with prominent septa. Seeds ellipsoid, apiculate, 1.3–1.5 mm long, reddish brown, translucent, longitudinally finely anastomosing-ribbed.

Distribution. So far known only from the Chimantá Massif, there much collected in recent years.

Additional specimens examined. VENEZUELA. BOLÍVAR: sector centro-noreste, 26–29 Jan. 1983, *Huber & Steyermark 6950* (VDB, VEN); en ladera del Río Chimantá Superior, 1 Feb. 1983, *Huber & Steyermark 6983* (VDB, VEN); sector W del Acopan-tepui, 7–9 Feb. 1983, *Huber & Steyermark 7081* (MYF, VEN, VDB); sección oriental del Chimantá-tepui, *Huber & Steyermark 7136* (MYF, VDB); central section near Summit Camp, *Steyermark & Wurdack 347* (NY, US, VEN); island in Río Tirica above Middle Fall below Summit Camp, *Steyermark & Wurdack 487* (NY, US); upper shoulder of Apacará-tepui, SE facing upper shoulder, *Steyermark 75759* (F, NY, VEN); W part of Abacapá-tepui, 13 Apr. 1953, *Steyermark 74851* (F, NY, VEN); sector septentrional, Murey-tepui, 24 Feb. 1978, *Steyermark et al. 115769* (US, VEN), *115836* (MO, US, VEN); cumbre del Cerro Apacará, 8 June 1946, *F. Cardona 1586* (VEN); centro noreste sector, 26–29 Jan. 1983, *Steyermark et al. 128024, 128083, 128131, 128224* (VDB, VEN); Amuri-tepui, 2–5 Feb. 1983, *Steyermark et al. 128459*; same locality, 6 Feb. 1983, *Steyermark 128775* (VDB, VEN); sección oriental, 9 Feb. 1983, *Steyermark et al. 128883* (VDB, VEN); altiplanicie suroriental del Acopan-tepui, 14–16 Feb. 1984, *Steyermark et al. 129866* (MYF, VEN, VDB); Churi-tepui, 3 Feb. 1953, *Wurdack 34307* (NY, US).

This species, obviously abundant on the summits of the Chimantá Massif, and which has been in collections for many years, has been identified variously as *X. decussata* Gl., *X. albescens* Steyerm., *X. tatei* Malme, and otherwise. It is often very long-stemmed and is frequently a "plate" former like *X. witseniodes*, *X. ptariana*, *X. frondosa*, and other species. While it has ancipital scapes that are often ciliate as in *X. decussata*, it lacks the dense, continuous bands of reddish hairs of that species. Its elongate spikes are distinctive. While its scape and leaves are often pale-ciliate, its leaf blades are much longer than its leaf sheaths, its spikes are longer than in *X. albescens*, and its lateral sepals and seeds are shorter. Thus, more by a combination of characters held in part by different species, it is unique.

30. Xyris culmenicola Steyerm., Fieldiana, Bot. 28(1): 1951. TYPE: Venezuela. T. F. Amazonas: Brocchinia Hills, 1,700–1,980 m, Cerro Duida, 1 Sep. 1944, *J. Steyermark 58198* (holotype, F; isotypes, GH, NY, US). Figure 30.

Cespitose, robust, hard-based perennial 5–7 dm high, the stems contracted. Leaves erect to somewhat spreading, 2–3.5 dm long; sheaths entire, less than ½ as long as blades, deep, lustrous, reddish brown or castaneous at base, tapering gradually and keeled from broad base to blade, there essentially eligulate, the blades flat, linear, 2.4–5 mm wide, tapering very gradually from ca. midblade or

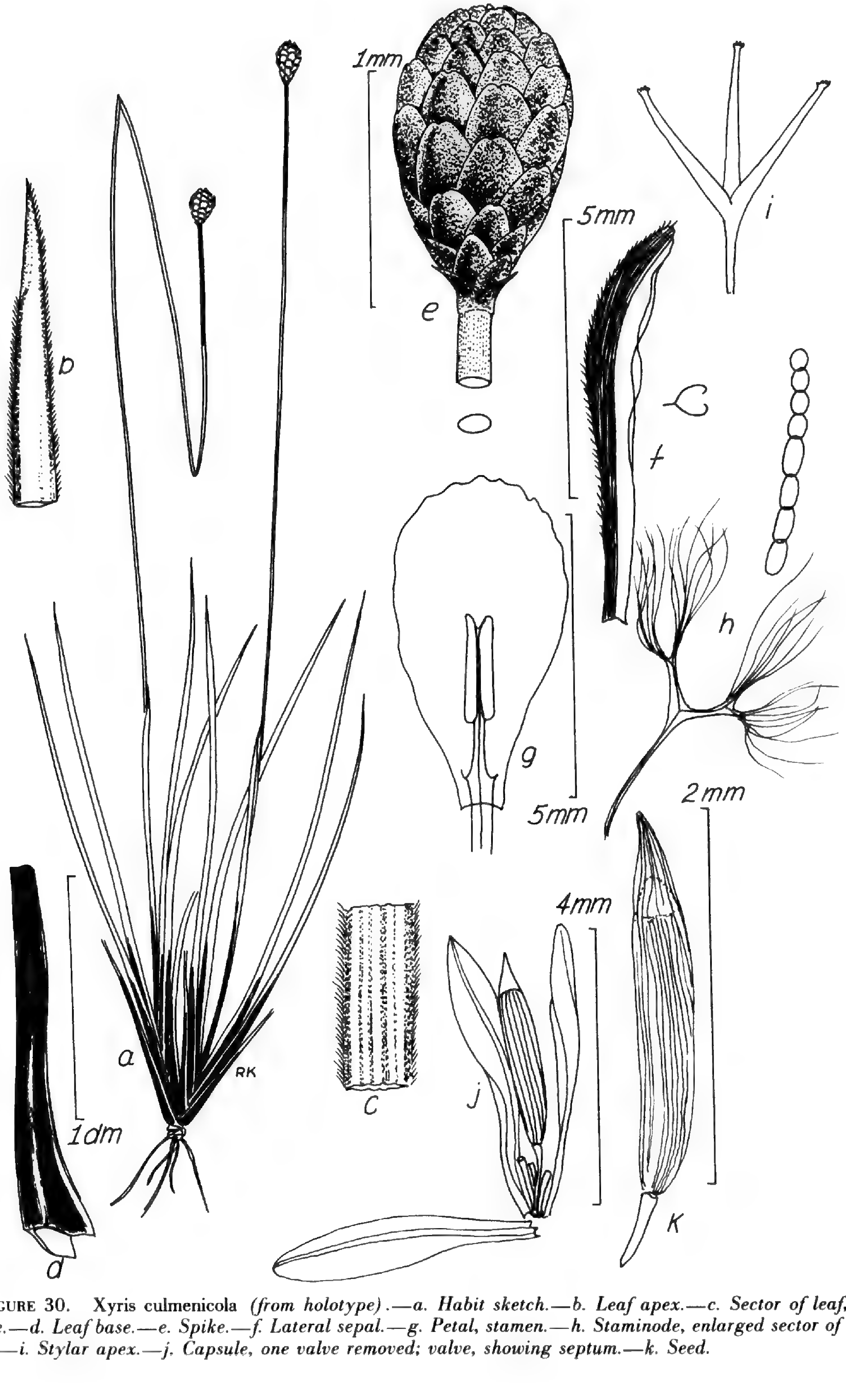


FIGURE 30. Xyris culmenicola *(from holotype)*.—*a. Habit sketch.—b. Leaf apex.—c. Sector of leaf, mid-blade.—d. Leaf base.—e. Spike.—f. Lateral sepal.—g. Petal, stamen.—h. Staminode, enlarged sector of beard hair.—i. Stylar apex.—j. Capsule, one valve removed; valve, showing septum.—k. Seed.*

below to a narrowly acute, erect or curvate apex, the tip slightly callused, the margins pilosulous-ciliate, the surface prominently multinerved, smooth, often with alternating broad, red-brown bands, 2 of these making submarginal borders. Scape sheaths much shorter than leaves, loosely tubular and castaneous below, open above, green, carinate and ciliate-keeled, with a short, erect, ciliate, blade. Scapes straight, slightly twisted, distally slightly compressed but in cross section oval or oblong, smooth, low-ribbed. Spikes dark brown, ovoid to broadly ellipsoid or broadly obovoid, 1.5–2 cm long, blunt, attenuate-based, of many firm, spirally imbricate, entire bracts without dorsal areas. Sterile bracts many, the lowest by far the smallest, keeled, ovate-triangular, grading gradually to fertile bracts, the fertile bracts obovate to oblong, 7–8 mm long, entire (becoming somewhat lacerate), often emarginate, the apex broadly to narrowly rounded, the backs ecarinate, slightly convex, not folded. Lateral sepals free, subequilateral, linear-oblanceolate, ca. 7–7.5 mm long, broadly acute, pale brown, curvate, the strong, dark keel rusty-ciliate from middle to apex. Petal blades broadly obovate, ca. 6 mm long, yellow, the broadly rounded apex erose. Staminodia quadribrachiate, the branches long-penicillate. Anthers oblong, ca. 1.5 mm long, short-bifid, auriculate, on filaments ca. 1 mm long. Capsule cylindric, ca. 4 mm long, the placentation apparently basal but with 3 strong septa intruding except at ovary apex. Seeds few on long funiculi, narrowly cylindric-fusiform, ca. 2 mm long, pale brown, translucent, including a translucent, pale, conic appendage ca. 0.5 mm long (outer integument), the body longitudinally multiribbed with a few coarser ribs produced by the outer integument.

Distribution. Grassy, rocky, wet savanna, summit elevations along Cerro Duida and Cerro Marahuaca, T. F. Amazonas, Venezuela.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: gallery forest and open area on Plateau of Huachamacari, 1 Mar. 1985, *Liesner 18121A* (MO, VDB, VEN); Cerro Huachamacari, Río Cunucunuma, near E escarpment at 1,900 m, *Maguire et al. 30123* (NY, US); summit of Cerro Duida, Brocchinia Hills, above Vegas Falls, 1 Sep. 1944, *Steyermark 58141* (F, K, NY, VEN, US); summit of Cerro Duida, Savanna Hills, 1,025–1,200 m, 2 Sep. 1944, *Steyermark 58233* (F, NY, US—a cotype); Cerro Marahuaca, cumbre, sección noroccidental, 2,500 m, 16 Feb. 1981, *Steyermark et al. 124426* (MO, VEN); Cerro Marahuaca, cumbre altiplanicie no arbolada, 2,580 m, 31 Jan. 1982, *Steyermark et al. 125892* (VEN, VDB); Cerro Marahuaca, parte aislada al Sur-Oeste del Cerro, 2,480 m, 9–10 Feb. 1982, *Steyermark et al. 126290* (VDB, VEN); Cerro Huachamacari, cumbre, 1,800 m, 10 Feb. 1982, *Steyermark et al. 126451*; Cerro Marahuaca, cumbre, parte central de la Meseta Sur-Este, 2,560 m, 10–12 Oct. 1983, *Steyermark 129444* (VDB, VEN); Cerro Duida, 29 Jan.–11 Feb., 1975, *S. S. Tillett et al. 751-74* (topotype, MYF, NY, VEN).

This falls in treatments next to *X. lugubris*, *X. tatei*, and *X. albescens* but is distinct in its longer spike, duller bracts, and more uniformly tapered, distinctively pigmented leaf blades, these sharper at apex.

31. Xyris lugubris Malme, Bull. Torrey Bot. Club 58: 324, pl. 24, fig. 1A. 1931. TYPE: Venezuela. T. F. Amazonas: summit of Mount Duida, 7,100 ft., Peak No. 7, *G. H. H. Tate 639* (Tyler–Duida Expedition Aug. 1928–Apr. 1929) (holotype, NY; phototype, NY). Figure 31.

Cespitose, hard-based perennial 3–10 dm high, the stems mostly contracted. Leaves erect or ascending, 2–5.5 dm long, the sheaths entire, less than ½ as long as blades, deep lustrous red-brown, smooth or papillate, keeled, gradually narrowed to blade, there eligulate or with an erect, narrowly triangular ligule to 4 mm long, the blades flattened, ensiform, 3–5 mm wide, gradually narrowed above middle to a narrowly acute, straight or incurved, thickened tip, the margins blunt or sharp-edged, smooth to papillose or tuberculate-scabrid, the surfaces dull green or green with long bands of brown or red-brown, multiribbed, smooth or papillate. Scape sheaths shorter than leaves, strongly costate, sharply keeled, with short, cusplike blades. Scapes straight or flexuous, distally subterete or slightly compressed, elliptic or oval in cross section, ca. 2 mm wide, smooth or sometimes striate, often punctate. Spikes broadly ob-

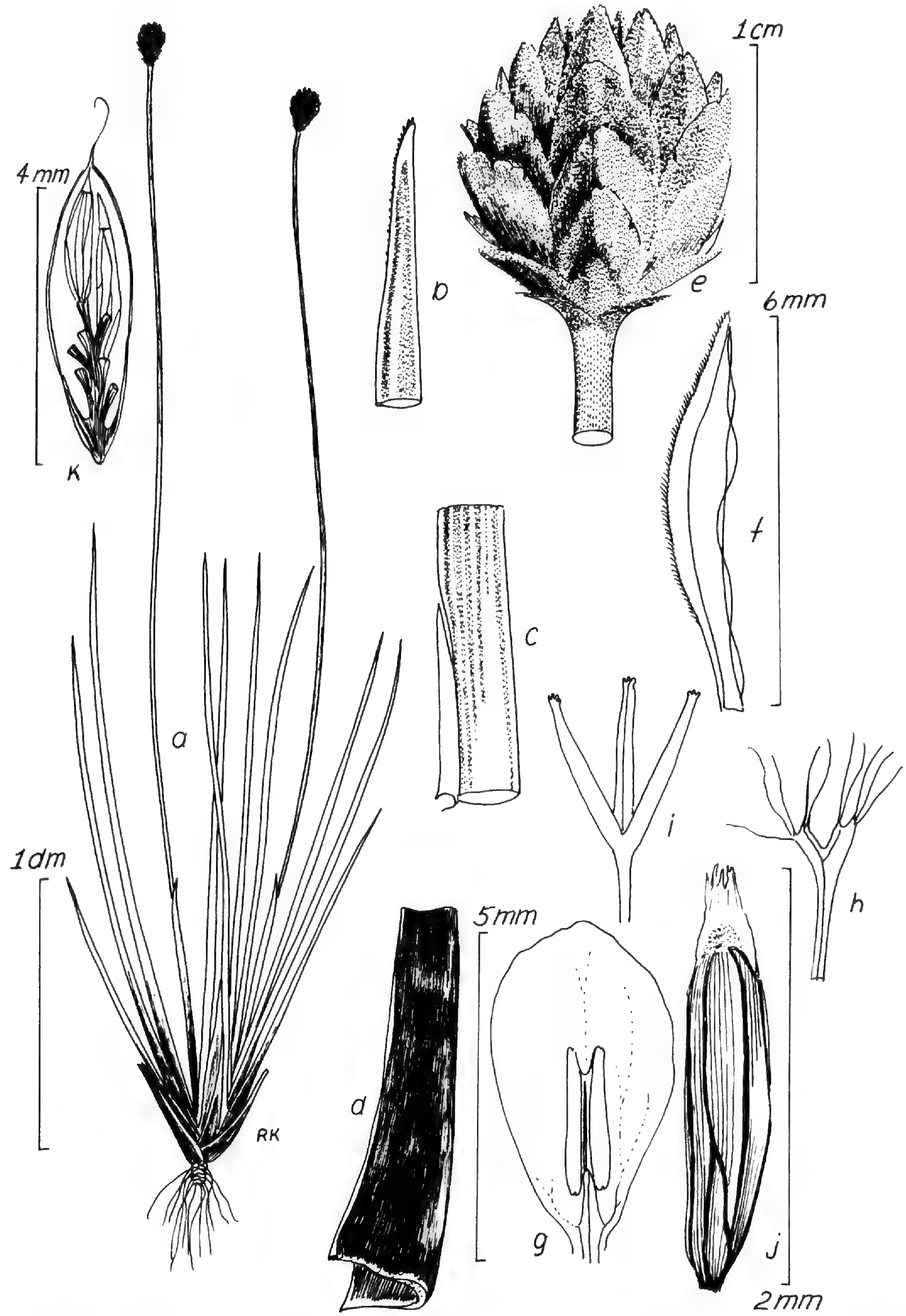


FIGURE 31. Xyris lugubris *(from the holotype)*.—*a. Habit sketch.*—*b. Leaf tip.*—*c. Leaf sheath-blade junction.*—*d. Leaf base.*—*e. Spike.*—*f. Lateral sepal.*—*g. Petal blade, stamen.*—*h. Staminode.*—*i. Stylar apex.*—*j. Seed.*—*k. Fruit, two valves removed to show central-basal placentation.*

ovoid to subglobose or hemispherical, ca. 1 cm long, blunt, of many dull, dark brown bracts in nearly vertical ranks of 5 or more; sterile bracts several, the lowest much smaller than fertile bracts, grading into them, the fertile bracts broadly oblong, 6–8 mm long, rounded and slightly folded, the apex narrowly rounded, the margins entire or lacerate, the backs folded-convex, often low-carinate toward apex. Lateral sepals equaling bracts, 6.5–8 mm long, linear-elliptic, dark red-brown, apically acute or narrow but blunt, the keel ciliolate from near base to apex. Petal blades obovate, 5–7 mm long, yellow, the apex narrowly rounded, the margins subentire. Staminodia bibrachiate, the broad, flattened branches sparsely penicillate. Anthers lance-oblong, ca. 2 mm long, deeply bifid and sagittate, on filaments ca. 0.5 mm long. Capsule ellipsoid, 4–6 mm long, the placentation central, the valves septate only near base. Seeds rather few, cylindrical, ca. 2 mm long, including a pale, squamiform apex ca. 0.5 mm long, coarsely longitudinally few-ribbed and finely lined.

Distribution. Wet, rocky savanna at or near summits, cerros Sipapo, Duida, and Neblina, T. F. Amazonas, Venezuela, infrequent.

Additional specimens examined. VENEZUELA, T. F. AMAZONAS: Camp Savanna, Campo Grande, 1,500 m, Cerro Sipapo, 10 Dec. 1948, *Maguire & Politi 27582* (GH, NY, US, VEN); Duida near summit of Culebra Peak, 1,800 m, 22 Apr. 1949, *Maguire 29155* (GH); Neblina, Río Yatua, west headland, open cumbre savanna 5 km W of Cumbre Camp, 2,000 m, 6 Jan. 1954, *Maguire et al. 37121* (F, K, NY, US, VEN); Neblina, W escarpment savanna 4–8 km S of Cumbre Camp, 1,850–1,900 m, 15 Jan. 1954, *Maguire et al. 37299* (NY); Neblina, en la cumbre del brazo nor-occidental, al norte del campamento base a lo largo del Río Mawarinuma, afluente del Río Baria, 1,880 m, 7–8 Feb. 1984, *Luteyn & Steyermark 9453* (NY, VDB, VEN); *Steyermark & Luteyn 129818* (MO, NY, VDB, VEN).

32. Xyris thysanolepis Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 17, fig. 3A–F. 1963. TYPE: Venezuela. Bolívar: rare around moist depressions and swales bordering river, scrub forest near Summit Camp, 1,925 m, central section Chimantá Massif, 2 Feb. 1955, *J. A. Steyermark & J. J. Wurdack 356* (holotype, NY; isotypes, MO, NY, US, VEN). Figure 32A–C.

A study of Venezuelan *Xyris* done in a way to reveal complexes has brought *Xyris thysanolepis*, *X. jauana*, and *X. sipapoa* into close alignment. In preparing descriptions and illustrations from type material of the three, and in studying materials collected later by myself and other collectors, I was forced to reassess taxonomic rank. *Xyris thysanolepis* and *X. sipapoa* were published in the same work and at that time were considered spatially isolated. *Xyris jauana* was considered well marked primarily on account of its connate lateral sepals, otherwise overlapping morphologically with *X. thysanolepis*. Ordinarily sepal connation, particularly high connation, is a very good character within complexes, but in this complex the character breaks down. A check of the structure shows that while lateral sepals of *X. thysanolepis* may be connate, those of *X. jauana* may be free. A check of type material of *X. sipapoa* shows that sepals range even in a single spike from connate to free. If this usually significant character difference is removed, a complex of three former species becomes a single species of two varieties, as below:

KEY TO THE VARIETIES OF *XYRIS THYSANOLEPIS*

1a. Leaf sheath bases bright to dull brown, eciliate to sparsely ciliate; apices of fertile bracts broadly rounded, the lacerate-scarious borders distinctly red; edges of leaf blades entire or inconspicuously ciliolate .... *X. thysanolepis* var. *thysanolepis* (including *X. jauana*)

1b. Leaf sheath bases lustrous deep brown or pale brown, mostly evidently ciliolate; apices of fertile bracts narrowed, somewhat keeled, the scarious borders pale or pale red-brown; edges of leaf blades densely ciliolate with fine, white hairs .... *X. thysanolepis* var. *sipapoa*

What then seems to emerge is a complex of medium- to high-elevation bog plants with scabrid, mostly unicostate scapes and lacerate-bordered, scarious-edged bracts, habitally similar, and showing a morphological affinity to *X. confusa* Smith & Downs of the Andes, possibly also to the Andean *X. andina* Malme.

Variety *thysanolepis* includes what was treated as *X. jauana*, which varies in regard to sepal connation and which (contrary to the type description) bears no evident dorsal area, only a low, short, apical carina. Variety *thysanolepis* is mostly in high areas of the Gran Sabana, Estado Bolívar, with one known outlier in Territorio Federal Amazonas (Cerro Yavi). The more slender var. *sipapoa* is apparently not rare on Cerro Sipapo, and plants answering to the type description have also been collected in Estado Bolívar (bog by rd. to Salto Aponguayo in rocky, sandy seeps, ca. 11 km SE of jct. with rd. to Kavanayen, 27 July 1983, *Kral & Gonzales 70524*, VDB, VEN).

32A. Xyris thysanolepis var. thysanolepis. Figure 32A, B.

X. jauana Lyman B. Smith & Steyerm., Bol. Soc. Venez. Ci. Nat. 132–133: 277, fig. 2a–g. 1976. TYPE: Venezuela. Bolívar: Meseta del Jaua, Cerro Jaua, selva de galeria al borde del tributario del Río Marajano, cumbre, 4°48′50″N, 64°34′10″W, 1,750–1,800 m, 22–28 Feb. 1974, *J. A. Steyermark, V. C. Espinosa & C. Brewer-Carias 109390* (holotype, VEN; isotypes, NY, US). Figure 32B.

Slender, solitary to cespitose, soft to firm-based perennial 2–10 dm high, the stem short or elongated to 6 cm, thick, the roots slender-fibrous. Leaves erect to spreading flabellately, 1–3 dm long; sheaths mostly ½ or more as long as blades, the slightly to very (orbicular) dilated base ciliate or not, tan to castaneous, shading above to pink, pale brown or stramineous, narrowing gradually into blade, keeled, the keel ciliolate or entire, the apex eligulate; blades linear, 2–5 mm wide, strongly flattened, the apex narrowly incurved-acute or acuminate, the margins usually thin, entire or ciliolate; surfaces pale green or yellow-green flecked with red, finely nerved, otherwise smooth. Scape sheaths shorter than to nearly as long as leaves, below terete and multicostate, above open, producing a short, erect, incurved-tipped, flat blade. Scapes straight or slightly flexuous, slightly twisted, subterete or oval in cross section toward apex, 1–2 mm wide, with 1, 2, (or more) costae, with 1 costa strong often making 1 edge, ciliate to densely ciliolate-scabridulous, the surfaces otherwise smooth, pale green, striate. Spikes pale red-brown, broadly ellipsoid, drying broadly obovoid, turbinate or globose, 0.7–1.3 cm long, of several spirally imbricate, firm, papillate or rarely smooth bracts with broad, scarious-lacerate, reddish or pale reddish brown borders or at least scarious-tipped; sterile bracts few, the lowest pair much smaller and narrower than the fertile bracts, keeled; fertile bracts broadly oblong to obovate, 6–8 mm long, the backs rounded or somewhat folded (inner ones increasingly folded-carinate), the apices narrowly or broadly rounded, the thin, colored borders variously lacerate and erect to squarrose. Lateral sepals free or up to ⅓ connate, subequilateral, thin, pale, lustrous reddish brown, 6–7 mm long, the apex acute, the narrow, curvate keel rusty-ciliolate to low-serrulate-lacerate from at least middle to apex. Petal blades elliptic to obovate, 4–5 mm long, yellow, the broadly to narrowly rounded apex erose. Staminodia bibrachiate, the narrow branches densely penicillate-ciliate. Anthers narrowly lance-oblong to linear-oblong, 1.5–2 mm long, deeply bifid and sagittate, on filaments ca. 1 mm long. Capsule planoconvex, broadly ellipsoid to narrowly obovoid, 3.5–4 mm long, the placentation basal, the valves without septa. Seeds numerous on elongate funicles, cylindric-fusiform, ca. 1 mm long, deep to pale amber, coarsely longitudinally anastomosing-ribbed.

Distribution. Locally abundant along streams through wet, rocky, medium- to high-elevation savanna, in Territorio Federal Amazonas and (more often) Estado Bolívar, Venezuela.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: depression on summit, Cerro Yavi, 2,200 m, 1–3 Mar. 1947, *Phelps & Hitchcock 38* (NY, VEN). BOLÍVAR: norte de la Cumbre del Cerro Roraima, 2,810 m, 27 Mar. 1982, *Aymard & Luteyn 2479* (NY, PORT); hacia Salto Aponwao (north part of Gran Sabana), 1,200 m, 7 Mar. 1983, *Huber & Entralgo 7405* (MYF); cumbre del Sororopán-tepui al N de Kavanayen, 2,040 m, 28 June 1983, *Huber & Alarcon 7741* (MYF); small stream

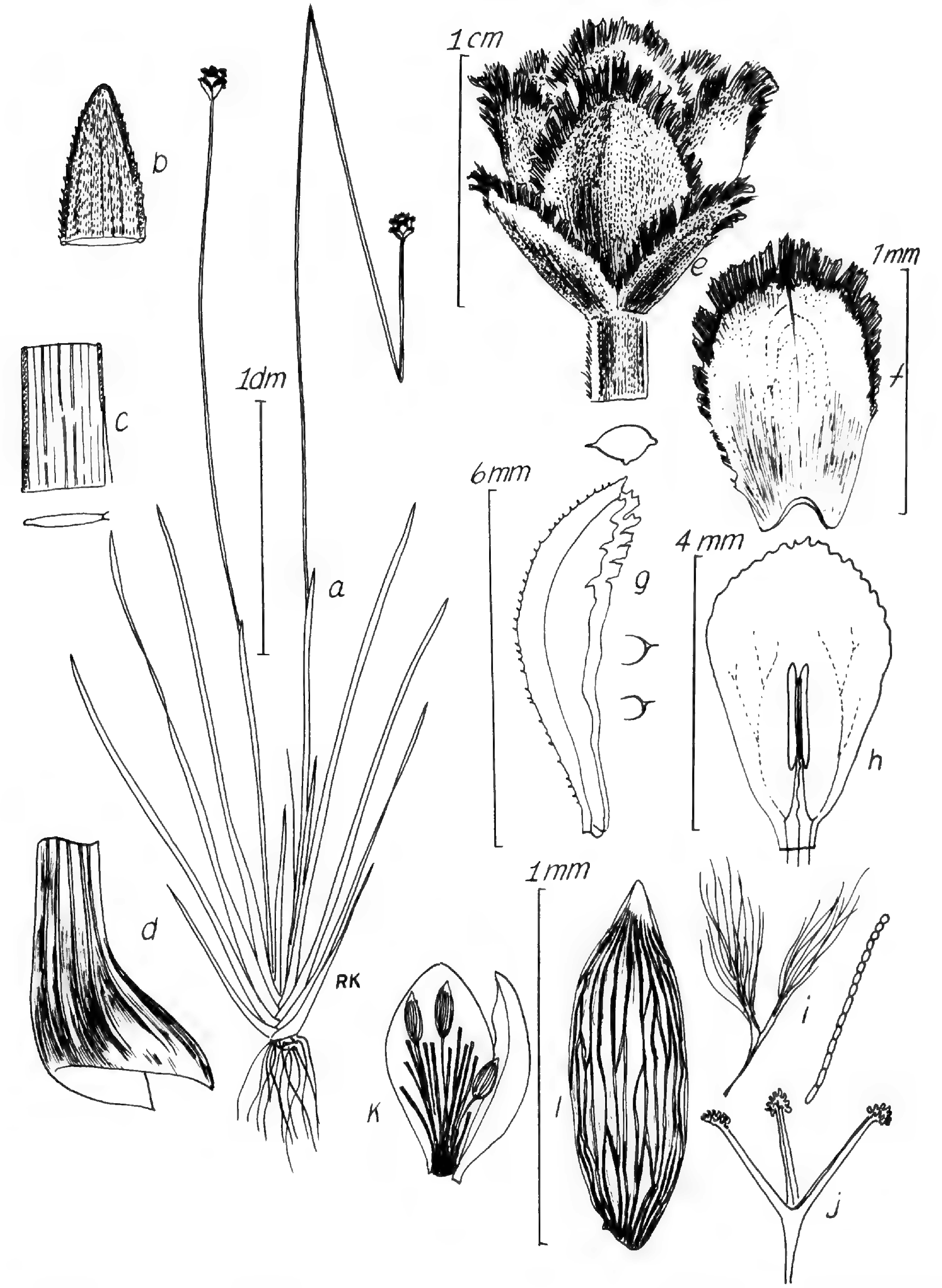


FIGURE 32A. Xyris thysanolepis (Kral 70446).—*a. Habit sketch.*—*b. Leaf apex.*—*c. Leaf blade–sheath junction.*—*d. Leaf base.*—*e. Spike.*—*f. Fertile bract.*—*g. Lateral sepal.*—*h. Petal blade, stamen.*—*i. Staminode, enlarged beard hair apex.*—*j. Stylar apex.*—*k. Dehisced capsule, showing basal placentation.*—*l. Seed.*

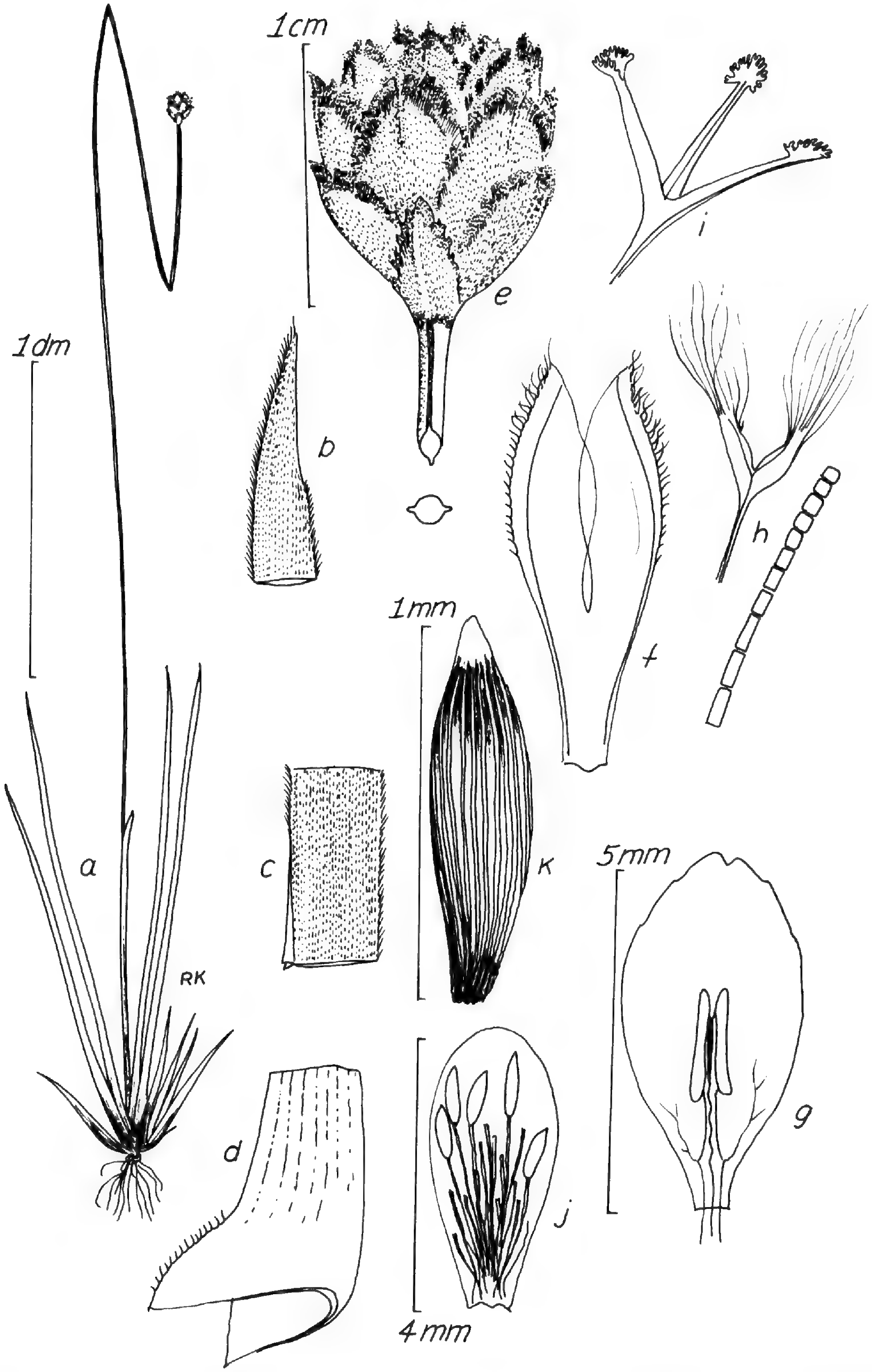


FIGURE 32B. Xyris thysanolepis *(type of* X. jauana*).—a. Habit sketch.—b. Leaf tip.—c. Leaf blade-sheath junction.—d. Leaf base.—e. Spike, upper scape.—f. Lateral sepals.—g. Petal blade, stamen.—h. Staminode, enlarged beard hair apex.—i. Stylar apex.—j. Capsule outline, placentation.—k. Seed.*

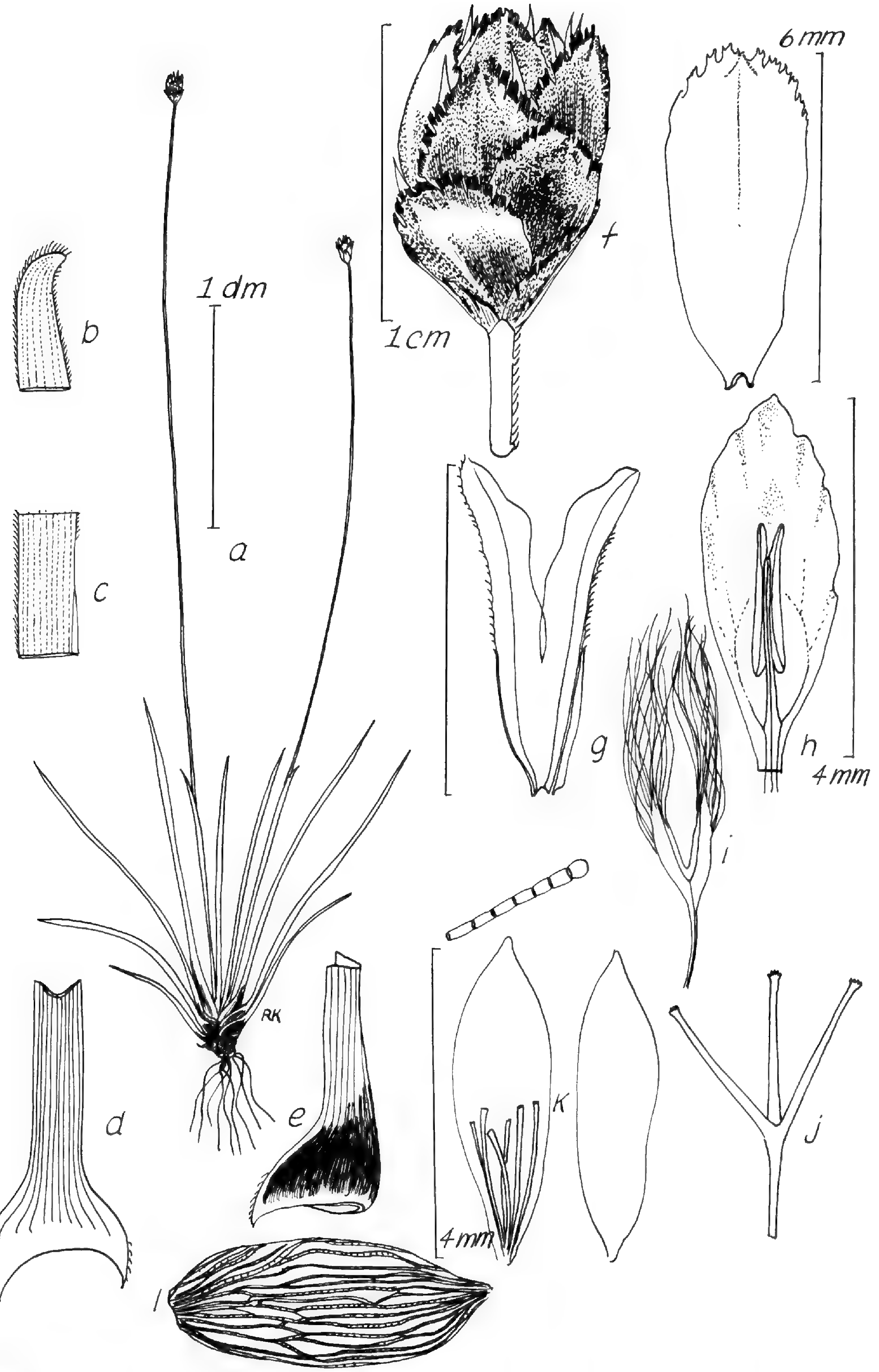


FIGURE 32C. Xyris thysanolepis *var.* sipapoa *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Leaf blade–sheath junction.—d. Leaf base.—e. Leaf base, side view.—f. Spike.—g. Lateral sepal.—h. Petal blade, stamen (just above, a fertile bract).—i. Staminode, to left an enlarged view of tip of beard hair.—j. Stylar apex.—k. Outlines of capsule with placenta, to right a valve outline.—l. Seed.*

at ravine base in bog ca. 1 km E of Kavanayen, 26 July 1983, *Kral 70446* (F, K, MO, NY, SP, U, US, VDB, VEN); 1.5 km E of Kavanayen, rocky seeps, S side of rd., 27 July 1983, *Kral 70535* (F, K, MO, NY, SP, U, US, VDB, VEN); Macizo del Chimantá, Apacara-tepui, sector Norte del Macizo, ca. 2,200 m, 30 Jan.–1 Feb. 1983, *Steyermark, Huber & Carreno E. 128407* (VDB, VEN).

32B. Xyris thysanolepis var. **sipapoa** (Maguire & Lyman B. Smith) Kral & Lyman B. Smith, stat. nov. *X. sipapoa* Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 18, fig. 4A–F. 1963. TYPE: Venezuela. T. F. Amazonas: frequent, banks of lower Caño Negro along open savannas, alt. 1,400 m, Cerro Sipapo, 25 Dec. 1948, *B. Maguire & L. Politi 27911* (holotype, NY; isotypes, GH, NY, US).

As in the rest of the species but usually somewhat lower in stature, the leaves strongly spreading flabellately, the bases abruptly orbicular-dilated and lustrous, mostly ciliolate, the blades with a fine marginal dusting of white hairs. Spikes mostly ovoid or ellipsoid, drying obovoid, the bracts carinate toward apex, the apex narrowed and folded, the margins pale-lacerate-scarious. Lateral sepals, sometimes in same spike, free to ⅓ connate.

Distribution. Wet to rather dry, medium- to high-elevation rocky savanna, Cerro Sipapo and environs, Territorio Federal Amazonas, Venezuela, and Gran Sabana, Estado Bolívar, Venezuela.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: Cerro Sipapo: frequent in bog-savanna, terraces S of Caño Negro at 1,600 m, 6 Jan. 1949, *Maguire & Politi 28194* (NY, US); frequent in savanna vic. Campo Grande, 1,500 m, 15 Dec. 1948, *Maguire & Politi 27684* (F, GH, NY, US); bog by rd. to Salto Aponguayo in rocky, sandy seeps, ca. 11 km SE of jct. with rd. to Kavanayen, 27 July 1983, *Kral 70524* (VDB, VEN, and to be distributed); savanna, ca. 1,200 m, Torom-meru, NW of Parupa, 14 Dec. 1984, *Kral 72063* (MYF, VDB, VEN, and to be distributed).

33. Xyris concinna N. E. Br., Trans. Linn. Soc. London, Bot. II(6): 68. 1901. TYPE: Venezuela. Bolívar: summit, Mt. Roraima, 8,600 ft., *McConnell & Quelch 496* (lectotype, K). Figure 33.

Hard-based, densely cespitose perennial 0.8–2 dm high, the stem contracted, to 1.5 cm long. Leaves spreading flabellately, 5–10 cm long; sheaths about as long as blades, entire (rarely with a few brown cilia at base), cochleariform toward base, thence contracted abruptly, ciliate-keeled, gradually narrowing to blade, eligulate; blades flat, narrowly linear, 1.5–2.5 mm wide, gradually tapering distally to an attenuate, terete, or narrowly acute, flattened apex, the tip with a tuft or short fringe of stiff, pale hairs, the margins minutely scabrociliate or papillose, the surface finely nerved, green or maroon, smooth. Scape sheath slightly shorter than leaves, loose, scabrid-keeled, short-bladed. Scapes slenderly linear, stiff, ca. 1 mm thick, oval or terete in cross section, unicostate, also finely fluted, the costa smooth, papillose or scabrociliolate. Spikes ovoid, 5–7 mm long, obovoid in fruit, reddish brown, of several spirally imbricate bracts without dorsal area and with broad, pale laceroscarious borders; sterile bracts 2–4, ovate, keeled, grading larger into fertile bracts, these few, lance-ovate or oblong, acute to acuminate, slightly to very keeled, 6–7 mm long, the backs papillose. Lateral sepals free, narrowly oblanceolate, equilateral, ca. 6 mm long, narrowly acute, the sides dull, pale brown, the keel narrow, firm, dark brown, entire or (usually) ciliate from middle to apex. Petal blades ca. 5 mm long, yellow, elliptic, subacute, wavy-margined. Staminodia bibrachiate, the branches flattened, the hairs penicillate but often multiseriate in narrow sheets. Anthers oblong, ca. 2 mm long, apically short-bifid, basally auriculate, on filaments ca. 1 mm long. Capsule oblong-ellipsoid, ca. 3 mm long, the valves eseptate, the placentation basal, funicles long. Seeds fusiform, ca. 1 mm long, red-brown, translucent, finely longitudinally ribbed.

Distribution. Infrequent in wet, high, sandstone savanna, the higher tepuis of the Gran Sabana, Estado Bolívar, Venezuela.

Additional specimens examined. VENEZUELA. BOLÍVAR: Matahui-tepui, 2,700–3,000 m, 22 Aug. 1982, *A. Castillo 2282* (UCV, VDB); Kukenán-tepui, sector mas septentrional, algo separado del macizo principal,

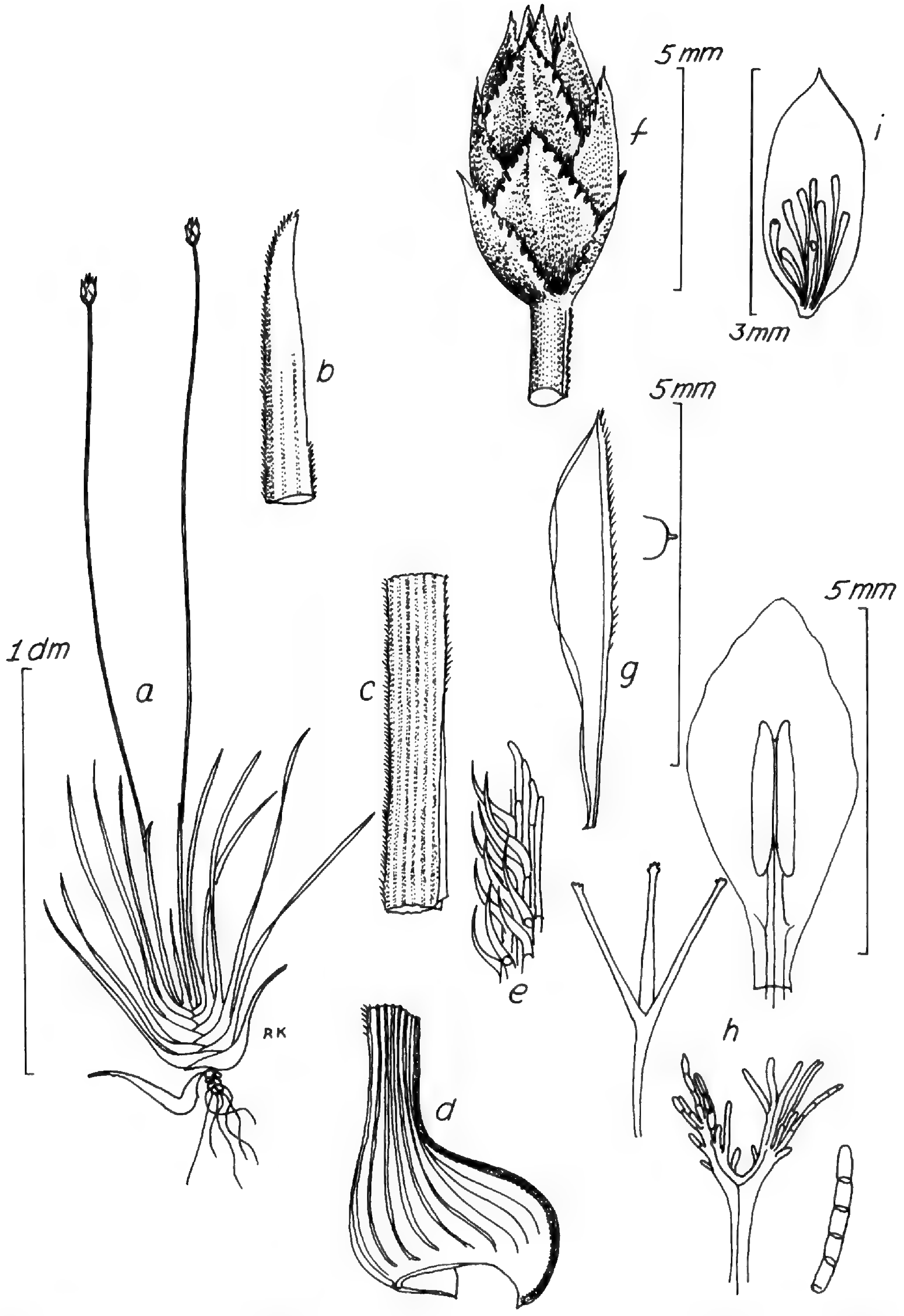


FIGURE 33. Xyris concinna (Steyermark 112658).—*a. Habit sketch.—b. Leaf apex.—c. Leaf blade–sheath junction.—d. Leaf base.—e. Small sector of leaf edge enlarged to show hairs.—f. Spike.—g. Lateral sepal.—h. Petal blade, stamen, staminode, enlarged part of beard hair, stylar apex.—i. Capsule, two valves removed to show placentation.*

2,500 m, 28 Apr. 1984, *Huber 9449* (MYF, VDB); Cumbre del Ilú-tepui, sector centro-meridional, 2,630 m, 29 Apr. 1984, *Huber 9498* (MYF, VDB); cumbre sur-occidental del Ilú-tepui, 2,700 m, 18 June 1985, *Huber & Alarcon 10602* (MYF, VDB); altiplanicie del Uei-tepui (Cerro del Sol), sector occidental por encima del valle del Río Arabopo, 2,150 m, 22 Jan. 1985, *Huber 10022* (MYF, VDB); Cerro Roraima: cumbre, parte noreste de

Venezuela inmediata al sur del hito que marca los limites con Guyana, Brasil y Venezuela, 2,750–2,800 m, 26 Aug.–2 Sep. 1976, *Steyermark et al. 112566* (MO, NY, US, VEN), *112648* (K, MO, NY, US, VEN).

The affinities of this low plant of high-altitude tepuis are definitely with *X. hymenachne* C. Martius, which is frequent in the surrounding lower-elevation savannas of the Gran Sabana. However, the leaves are harder, their bases more orbicularly dilated; the spike bracts are more folded and more acuminate; and the seeds are somewhat longer.

34. Xyris hymenachne C. Martius, Flora 24(2): 55. 1841. TYPE: Brazil: "Prov. Minarum, Mart. Hb. 872" (lectotype, BR; isolectotypes, L, M; phototypes, F, NY). Figure 34.

X. arescens Kunth, Enum. Pl. 4: 3. 1843.
X. submontana Gleason, Bull. Torrey Bot. Club 56: 393. 1929. TYPE: Brazil. Río Branco: Mt. Roraima, Philipp Swamp, 5,100–5,200 ft., 11 Nov. 1927, *G. H. H. Tate 334* (K).

Solitary or cespitose, often bulbous-based, slender perennial mostly 2–6 dm high, the stems contracted. Principal leaves ascending or spreading flabellately, 0.5–2 dm long; sheaths entire or sparsely brown ciliate at dilated base, dull brown or stramineous, at very base sometimes castaneous and abruptly orbicular-dilated, ½ or more as long as blades, tapering above gradually to blade, usually eligulate, the blades flat, straight or twisted, strongly compressed, 1.5–4 mm wide, acute to long-acuminate, the margins with edges thin or slightly thickened, smooth, papillate or ciliolate, the surface smooth to papillose-rugulose, finely nerved, dull green. Scape sheaths slightly to much shorter than leaves, tubular and sharply costate below, above open, strongly keeled, short-bladed. Scapes narrowly lineal, twisted, sometimes flexuous, distally subterete, 0.6–0.7 mm thick, mostly unicostate (sometimes multicostate), the costae low but distinct, smooth to papillate or ciliolate. Spikes obovoid to subglobose, 5–8 mm long, attenuate, dull pale red-brown, of several loosely spirally imbricate bracts, these rounded-convex, often medially low-ribbed, without distinct dorsal area, with erect, broad, pale, scarious-lacerate borders; sterile bracts slightly smaller than fertile bracts but lowest over ½ as long as spike, ecarinate, the inner sterile and lower fertile bracts obovate or broadly oblong, 7–8 mm long, the backs often papillate. Lateral sepals free, very inequilateral, oblong-curvate, 4–6 mm long, obtuse, the darker keel fimbriociliate or ciliate at least from middle to apex. Petal blades obovate, ca. 5 mm long, the apex narrowly rounded, the margins wavy. Staminodia bibrachiate, the broad, thin branches each tipped by a few penicillate hairs. Anthers lanceolaate, ca. 1.5 mm long, deeply bifid and sagittate, on filaments ca. 0.5 mm long. Capsule ellipsoid to broadly obovoid, ca. 4 mm long, the valves without septa, the placentation basal. Seeds cylindric-fusiform or narrowly ellipsoid, on long funicles, 0.6–0.7 mm long, apiculate, amber, longitudinally conspicuously multiribbed.

Distribution. Moist to wet, medium- to high-elevation savanna, South America east of the Andes, in northern South America, Colombia east into Guyana.

Selected Venezuelan specimens. T. F. AMAZONAS: Dto. Río Negro, seeps along Río Mawarinuma, just above Neblina expedition base camp, 26 Nov. 1984, *Kral 71823* (VEN, and to be distributed); same area, 2 km above Neblina base camp, 3 Dec. 1984, *Kral 71937* (VEN, and to be distributed); Neblina, rocky places along Caño Grande at 1,100 m, 24 Nov. 1957, *Maguire & Wurdack 42200A* (NY, US). BOLÍVAR: carretera El Dorado–La Gran Sabana, alrededores de km 132, ca. 1,200 m, 21 Feb. 1968, *Bunting 3050*, identified as *X. submontana* Gl. (US); hacia el Salto Aponwao, 1,200 m, 7 Mar. 1983, *Huber & Entralgo 7408* (MYF, VDB, VEN); several numbers by *Kral* along El Dorado–Sta. Elena Highway (Ven. 10) through the Gran Sabana (numbers *70305, 70326, 70367, 70392, 70413, 70447, 70467, 70515, 70559, 70591, 70620, 70628*, collected 22–29 July 1983, and with general distribution to include F, K, MO, NY, SP, U, US, VEN, VDB, etc.), subsequently *72004, 72061*, from the same area on 13 & 14 Dec. 1984 (MYF, VEN, and to be distributed); 17 km E of El Pauji, 64 km W of Sta. Elena, Río Las Ahallas, 30 Oct. 1985, *Liesner 19164* (MO, VDB, VEN); en selvas a orillas del Río Uairen, alto Caronia, 25 Apr. 1946, *Lasser 1712* (NY); Uiapan-tepui, 1,900 m, 1–15 Feb. 1948, *Phelps & Hitchcock 376* (NY); headwaters of Río Cuyuni, NE of Luepa, 1,300 m, 23 Apr. 1960, *Steyermark & Nilsson 492* (NY, VEN); dripping rocks at base of Ptari-tepui, 4 Nov. 1944, *Steyermark 59841* (F, US, VEN); Auyan-tepui, div. occidental del cerro, vic. "Rio Lomita Camp,"

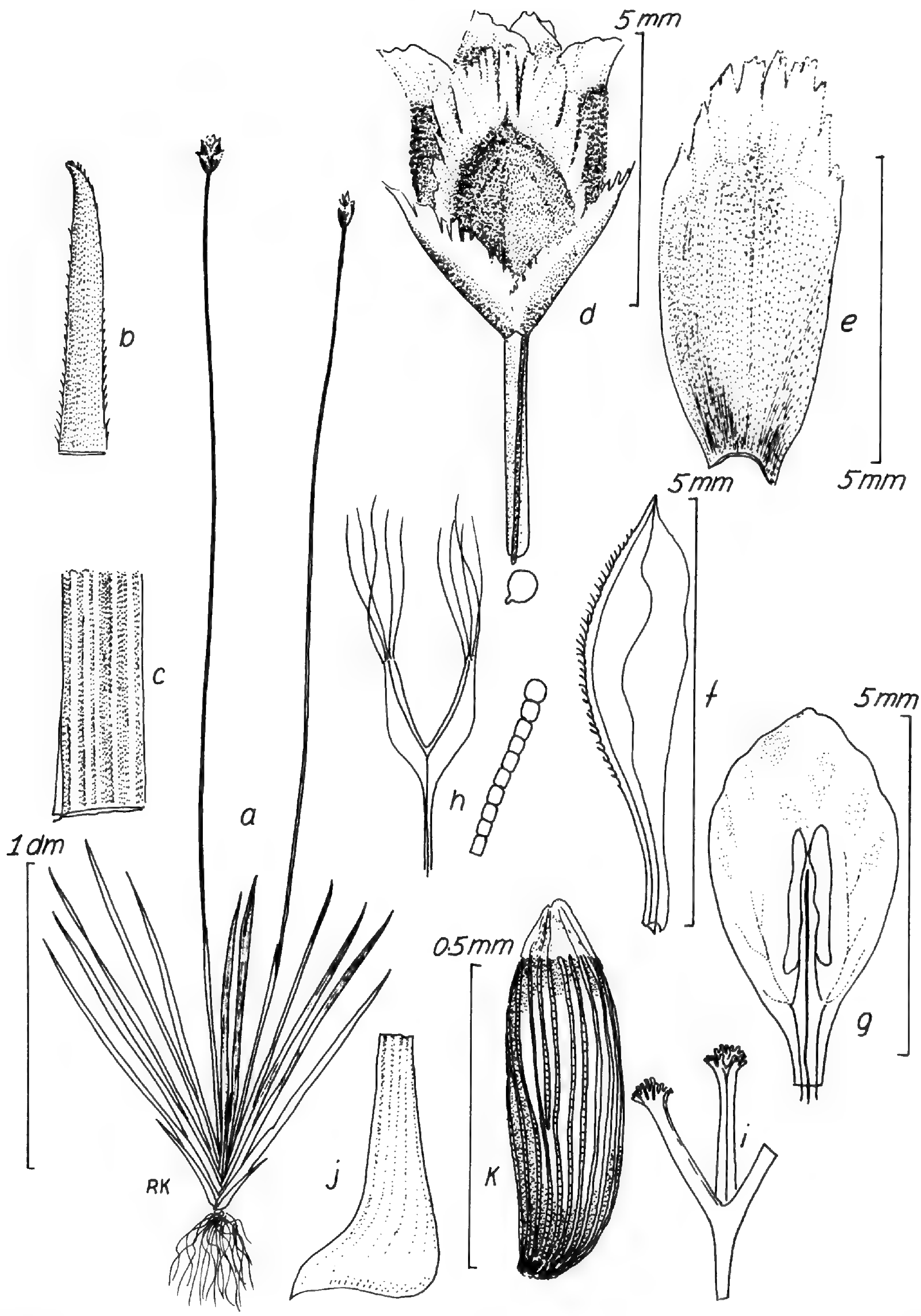


FIGURE 34. Xyris hymenachne (Steyermark 93465, Kral 70326).—*a. Habit sketch.*—*b. Leaf tip.*—*c. Leaf sheath–blade junction.*—*d. Spike.*—*e. Fertile bract.*—*f. Lateral sepal.*—*g. Petal blade, stamen.*—*h. Staminode.*—*i. Stylar apex.*—*j. Leaf base.*—*k. Seed.*

1,800 m, 7 May 1964, *Steyermark 93465* (K, NY, VDB, US).

This species, while very highly variable in stature and leaf, is distinguished primarily by the very broad, pale, scarious bract borders and the absence of a dorsal area. The leaf bases range from strongly dilated to indistinctly so, and the numbers of flowers and bracts in a spike vary widely. A perfect range of intermediates connects this to *X. submontana* Gleason, a not uncommon morphology in the Gran Sabana of Estado Bolívar, Venezuela. This last was supposed to be distinguishable on a basis of its comparative smoothness, the depressed-globose spikes, and the granular-papillose spike bracts. The species unfolds its blooms in morning. It is one of the weedier species, often coming in abundantly on moist to wet, nearly totally mineral substrates.

35. Xyris decussata Gleason, Bull. Torrey Bot. Club 56: 392. 1929. TYPE: Venezuela. Bolívar: Mt. Roraima, summit, 26 Nov. 1927, *G. H. H. Tate 427* (lectotype, NY). Figure 35.

Robust but low, cespitose, thick-based perennial 1.5–4.3 dm high, the stems stout and contracted or to 5(–15) cm long, ascending. Leaves rigid, spreading flabellately, 1–2 dm long; sheaths firm, entire, about as long as blades, castaneous, tapering gradually from broad base, apically with a short, often salient, small, narrowly triangular ligule; blades broadly linear, flat, 3–5 mm wide, abruptly broadly rounded at apex, the margin completely and densely rusty ciliate with hairs arising from a dark brown, incrassate border, the surfaces green, finely nerved, smooth. Scape sheaths shorter than leaves, tubular-carinate, the keel ciliate, alate, terminating in a very short, blunt, ciliate blade. Scapes straight, slightly twisted, distally flattened, 2–3 mm wide, bicostate, the costae densely rusty ciliate. Spikes subglobose or depressed-globose to obovoid, ca. 1 cm long, dark brown, of many, firm but loosely appressed bracts without distinct dorsal areas, usually in nearly vertical ranks; sterile bracts several, the lower ones triangular, much shorter than the fertile bracts and grading gradually into them, the fertile bracts ovate or broadly oblong, ca. 6 mm long, apically broadly to narrowly rounded and subentire, the backs ecarinate, slightly convex-rounded. Lateral sepals free, subequilateral, ca. 6 mm long, linear-oblanceolate, obtuse or broadly acute, dark brown, the firm dark keel entire or ciliate or ciliato-lacerate toward apex. Petal blades elliptic, ca. 5 mm long, yellow, the apex broadly and bluntly acute or narrowly rounded, the margin wavy. Staminodia 4-brachiate, the branches long-penicillate. Anthers oblong, 1.5–1.7 mm long, cleft to below the middle, sagittate, on filaments nearly 2 mm long. Capsules ellipsoid, 4–5 mm long, placentation basal-central, the valves with low septa. Seeds numerous, narrowly cylindric-oblanciform, ca. 1.5–1.7 mm long, including a pale, narrowly conic apiculus ca. 0.3 mm long (loose outer integument), the body pale reddish brown, translucent, finely but distinctly longitudinally ribbed.

Distribution. High-elevation tepuis, in boggy savanna, over 2,000 meters, southeastern and southern Estado Bolívar, Venezuela.

Additional specimens examined. VENEZUELA. BOLÍVAR: Cumbre del Ilu-(Uru-)tepui, sector centro-meridional, 2,630 m, 29 Apr. 1984, *Huber 9509* (MYF, VDB); cumbre del Tramen-tepui, la porción mas noroccidental del Macizo del Ilu-(Uru-)tepui, 2,650 m, 23 Jan. 1985, *Huber 10053* (MYF, VDB); Ilu-tepui, Gran Sabana, wet places in open low bush, Mesa Ridge, 6,000 ft., 13 Mar. 1952, *Maguire 33408* (NY)—this is the tallest example on record, with leaf tips more as in *X. albescens*; summit Mt. Roraima, NW portion N and NW of Summit Camp, 2,620–2,720 m, 27 Sep. 1944, *Steyermark 58806* (F, NY, US, VEN); Chimantá Massif, upper mossy slopes, NW part summit of Abacapa-tepui, above first line of sandstone bluffs, *Steyermark 74998* (C); Cerro Roraima: cumbre parte NE de Venezuela inmediata al sur del hito que marca los limites con Guyana, Brazil, and Venezuela, 2,750–2,800 m, 26 Aug.–2 Sep. 1976, *Steyermark et al. 112618* (VEN); Cumbre de Auyan-tepui, cerca de las orillas del sector oriental, al norte de la Misión de Camarata, 1,940 m, 27 Feb. 1978, *Steyermark et al. 116115* (VEN).

This endemic is vegetatively a stubby version of *X. bicephala* Gl., but even a first

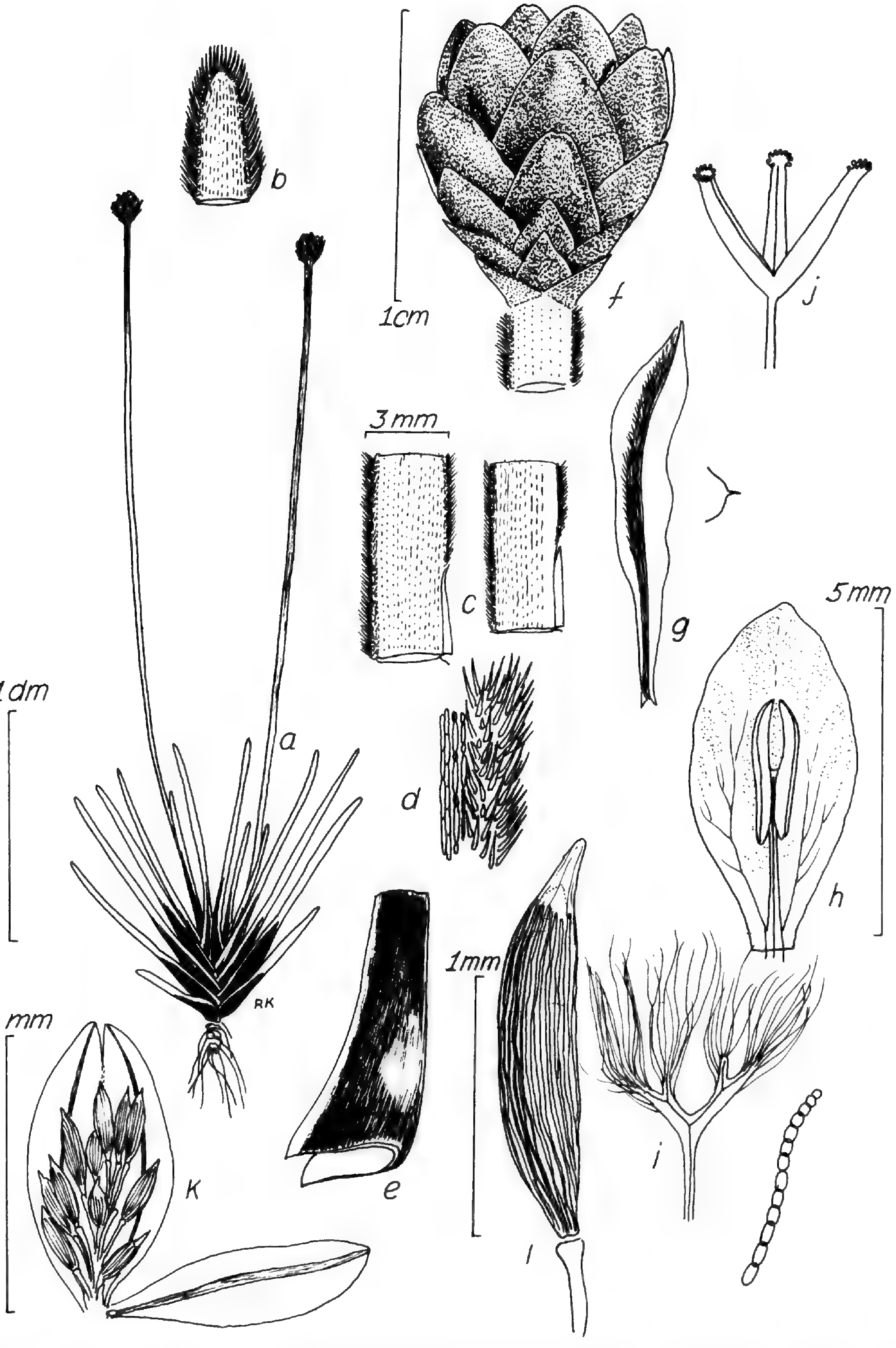


FIGURE 35. Xyris decussata *(from the type, except for flower).—a. Habit sketch.—b. Leaf tip.—c. Two samples of leaf-sheath junction.—d. Enlarged sector of edge of leaf blade.—e. Leaf base.—f. Spike, upper scape.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode and enlarged tip of beard hair.—j. Stylar apex.—k. Capsule, showing placentation; one valve removed.—l. Seed.*

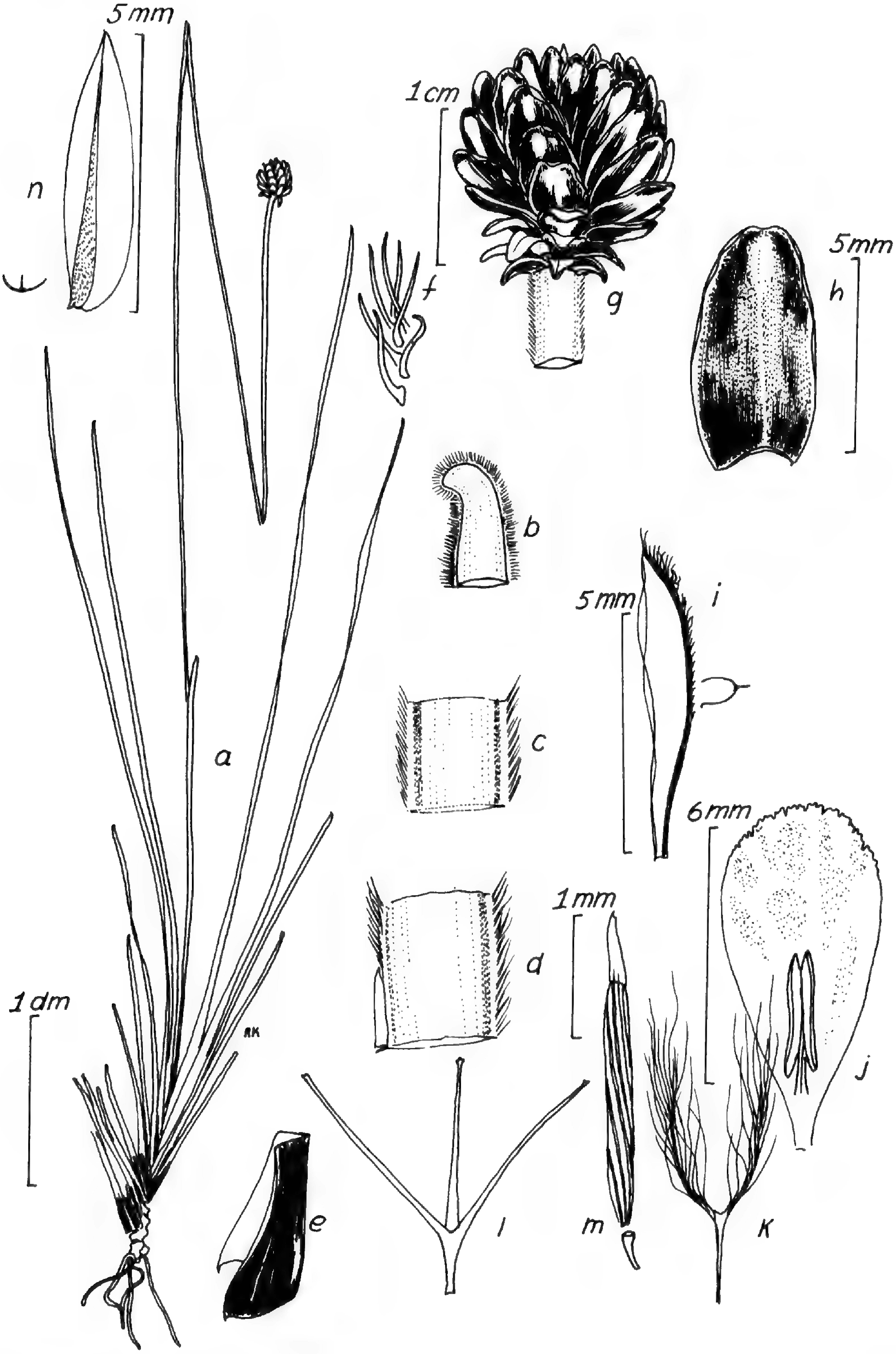


FIGURE 36. Xyris albescens (Steyermark 59734).—*a. Habit sketch.—b. Leaf tip.—c. Sector of leaf, mid-blade.—d. Leaf blade at junction with sheath.—e. Leaf base.—f. Trichomes from edge of leaf blade (much enlarged).—g. Spike.—h. Fertile bract.—i. Lateral sepal.—j. Petal blade and stamen.—k. Staminode.—l. Style branches.—m. Seed.—n. Capsule, valve removed, showing septum (shaded).*

glance reveals the distinctive dense fringe of rust-colored hairs marginally on the leaf blade. Taller material with more lustrous bracts and longer leaves but having such ciliation has been obtained from Chimantá, Ptari-tepui, and Ilu-tepui. This material appears to be from populations "influenced" by other species such as *X. albescens* Steyerm., or is identified as *X. melanovaginata* Kral & Smith.

36. Xyris albescens Steyerm., Fieldiana Bot. 28(1): 105, fig. 16a, b. 1951. TYPE: Venezuela. Bolívar: Ptari-tepui, *Bonnetia roraimae* forest on southwest-facing shoulder, 2,000–2,200 m, 2 Nov. 1944, *J. A. Steyermark 59734* (holotype, F; isotypes, GH, NY, US). Figure 36.

Robust, cespitose perennial (3.5–)4–10 cm high, the stems short, stout, ascending. Leaves elongate-linear, 2–6 dm long, mostly spreading or ascending; sheaths at least ½ as long as blades, keeled, firm, lustrous, deep red-brown or castaneous, the margins entire, tapering evenly from base to a small, indistinct ligule; blades evenly linear, flat and strongly flattened, pale green, (3–)5–6 mm wide, with apices asymmetrically narrowly acute or (in type) incurved and narrowly rounded, the edges densely white- (rarely pale red-brown-) ciliate, sometimes with a submarginal brown or red border. Scape sheaths much shorter than leaves, short- to elongate-bladed, the blades as in leaves. Scape pale green, distally broad and flattened (2–)2.5–3 mm wide, the edges densely pale ciliate as in leaf blades. Spike broadly ovoid, globose or hemispheric, (1–)1.5 cm long, blunt, rich, lustrous brown or castaneous, multiflowered; sterile bracts very many, triangular-ovate, the lowermost small, often squarrose, grading larger into the fertile bracts, these narrowly ovate to oblong, firm, 6–9 mm long, apically rounded, entire, sometimes somewhat cucullate, the dorsal area absent or inconspicuous, the backs rounded-convex, ecarinate. Lateral sepals equilateral, oblong-linear to linear-oblanceolate, mostly acute, 6–7 mm long, pale except for dark, scabro-ciliate to villosulous keel. Petal blades narrowly obovate, ca. 6–7 mm long, yellow, apically broadly rounded, erose. Staminodia bibrachiate, the slender branches long-penicillate from base to tip. Anthers lanceolate, ca. 2.5 mm long, apically deeply retuse, basally sagittate, on filaments ca. 1 mm long. Capsule narrowly ellipsoid, ca. 5 mm long, the valves deeply septate at base, placentation appearing central but axile at base. Seeds narrowly fusiform-cylindric, 2–3 mm long, pale brown, including a white, triangular-linear scale 0.5–0.7 mm long, the fruit body spirally coarsely parallel-ribbed.

Distribution. Moist to rather dry rocky savanna, high elevations of tepuis, southern Estado Bolívar, Venezuela.

Additional specimens examined. VENEZUELA. BOLÍVAR: Cima del Roraima, Jan. 1977, *Delascio & Brewer-Carias 4802* (VEN); en el paso entre Ptari-tepui y Sororopan-tepui, al N de Kavanayen, 1,370 m, 28 June 1983, *Huber & Alarcon 7725* (NY); Cumbre del Yuruani-tepui, ca. 12 km al NNE del Kukenan-tepui, 29 Feb. 1984, *Huber 9088* (MYF, VDB); Cumbre del Yuruani-tepui, al NNW del Cerro Kukenan, 27 Apr. 1984, *Huber 9414* (MYF, VDB); Kukenan-tepui, cumbre del sector mas septentrional, algo separado del macizo principal, 2,500 m, 28 Apr. 1984, *Huber 9446* (MYF, VDB); Ptari-tepui, vic. "Cave Rock" Camp below southern face of mountain, 1,600–2,000 m, 14–19 Aug. 1970, *Moore et al. 9817* (NY, US); Mt. Roraima, escarpment, 7,600 ft., 1 Nov. 1973, *R. Persaud 149* (K); vic. rd. campamento 150 at km 150 in valley of savanna of Río Urarama below Urarama-tepui, NE of Luepa, 1,220 m, 24–25 Apr. 1960, *Steyermark & Nilsson 641* (NY, VEN); Ptari-tepui, dry sandy and rocky sandstone exposures on plateau portion of southeast-facing slopes, 1,600 m, 1 Nov. 1944, *Steyermark 59683* (F, NY); Chimantá Massif, elfin forest on plateau of southeast-facing upper shoulder of Apacará-tepui, 2,000 m, 19 June 1953, *Steyermark 75757* (F, NY, VEN); Meseta del Jaua, el Este del trib. del Río Marajano, 1,800 m, 26 Feb. 1974, *Steyermark et al. 109558* (F, K, US, VEN)—this differs from all other specimens in its longer spikes to ca. 2 cm; Macizo del Chimantá, altiplanicie en la base meridional de los farallones superiores del Apacará-tepui, sector norte del Macizo, 2,200 m, *Steyermark et al. 128393* (VEN, VDB).

Material of this from Guyana, Upper Mazaruni District, north slope of Mt. Roraima, alt. 2,000–2,300 m, 16 Feb. 1985, *J. Renz 14266*, was lent by U. Other material with affinities, lent by NY, from T. F. Amazonas of Venezuela is Cerro Marahuaca, 2,500 m, 16 Feb. 1981, *Steyermark 124439*.

37. Xyris fuliginea Kral & Lyman B. Smith, sp. nov. TYPE: Venezuela. T. F. Amazonas: Dept. Atabapo, Cerro Marahuaca—FHUIF Cumbre, zona boscosa en la falda este del riachuelo, 2,480–2,500 m, 3°35′N, 65°20′W, 1–2 Feb. 1982, *J. Steyermark, M. Guariglia, N. Holmgren, J. Luteyn & S. Mori 125978* (holotype, VEN; isotype, VDB). Figure 37.

Planta perennis caespitosa, rigida, 3–5.6 dm alta. Radices graciles. Caules breves aut usque ad 5 cm longi. Folia principalia vulgo flabellate expansa, 1.5–3 dm longa, vaginis scaporum parum longiora; laminae vaginas aequantes vel eis leviter aut 1–2-plo breviores, linearotriangulatae, planae, compressae, 3–5 mm latae, olivaceae, glabrae; apices gradatim contracti, acuti, leviter incrassati; margines tenues, subtiliter dense albociliati vel albociliolati; vaginae carinatae, atrocastaneae, nitidae, integrae, ad basin dilatae, in laminas gradatim decrescentes, eligulatae. Vaginae scaporum prope basem castaneae, teretes, tortae, multicostatae, apicem versus apertae, carinatae, laminis brevibus. Scapi apicem versus ancipiti, ca. 2–2.5 mm lati, albociliati, olivacei. Spicae multiflorae, obovoideae, 1–1.5 cm longae, obtusae. Bracteae erectae, subdecussatae vel laxe spiraliter imbricatae, firmae, ecarinatae, fuligineae, sine area dorsali, integrae tum laceratae; bracteae steriles plures, triangulato-ovatae, pari infimo valde carinato, carinis ciliatis, anguste acuto, ca. 3-plo spica brevius, paribus intimis fertilibus breviores, in fertiles gradatim transientes; bracteae fertiles latae oblongae vel oblongo-lanceolatae, 7–9 mm longae, late acutae vel anguste rotundatae. Sepala lateralia libera, subaequilatera, ca. 7–8 mm longa, atroferruginea, leviter curvata, late acuta; ala carinali lata, a medio ad apicem rufociliata. Laminae petalorum late obovatae, 5.5–6 mm longae, luteolae, apice late rotundatae, erosae. Staminodia bibrachiata, brachiis longipenicillatis. Antherae lanceolatae, ca. 2 mm longae, profunde emarginatae et sagittatae; filiis latis, ca. 1 mm longis. Capsula ellipsoidea, 5 mm longa, placentae centralis sed valvis capsulae ad basim profunde septatis, sic placentio subaxilis. Semina numerosa, anguste ellipsoidea vel anguste claviformes, ca. 1.5 mm longa, longitudine prominente spiraliter multicostata, conicam pallidam squamellam ca. 0.5 mm longam includens.

Stiff tufted perennial 3–5.5 dm high. Roots slender, fibrous. Stems short or up to 5 cm long. Principal foliage leaves commonly spreading flabellately, 1.5–3 dm long, slightly longer than the scape sheaths; blades equal to sheaths or to ½–⅔ as long, linear-triangular, level, flattened, 3–5 mm wide, olivaceous, smooth; apices gradually narrowed, acute, slightly thickened at tips; margins thin, finely densely white ciliolate or white ciliate; sheaths carinate, deep-castaneous, shining, entire, dilated at base, narrowing gradually into blades, eligulate. Sheaths of scapes castaneous toward base, terete, twisted, multicostate, opening toward apex, carinate, with short blades. Scape ancipital toward apex, ca. 2–2.5 mm wide, white-ciliate, olivaceous. Spikes multiflorous, obovoid, 1–1.5 cm long, obtuse. Bracts erect, subdecussate to loosely spirally imbricate, firm, ecarinate, fuligineous (charcoal brown), without dorsal area, entire, lacerate; sterile bracts several, triangular-ovate, the lowest pair strongly carinate, carinae ciliate, narrowly acute, ca. 3 times shorter than the spike, the inner pairs shorter than the fertile pairs, grading into them; fertile bracts broadly oblong to oblong-lanceolate, 7–9 mm long, broadly acute to narrowly rounded. Lateral sepals free, subequilateral, ca. 7–8 mm long, deep red-brown, slightly curvate, broadly acute; keel broad, red ciliate from middle to apex. Petal blades broadly obovate, 5.5–6 mm long, yellow, broadly rounded apically, erose. Staminodia bibrachiate, the branches long-penicillate. Anthers lanceolate, ca. 2 mm long, deeply emarginate and sagittate on broad filaments ca. 1 mm long. Capsule ellipsoid, 5 mm long, the placentae central but the capsule valves deeply septate toward base, thus the placentation subaxile. Seeds numerous, narrowly ellipsoid to narrowly claviform, ca. 1.5 mm long, longitudinally spirally prominently ribbed, and including a pale, conical scale ca. 0.5 mm long.

Distribution. Confined to the Cerro Marahuaca, wet high altitude, rocky savanna, elevation over 2,000 m, T. F. Amazonas, Venezuela.

Paratypes. Summit, northeast, headwaters of small stream, 2,500 m, 16 Feb. 1981, *Steyermark et al. 124439* (MO, NY, VDB, VEN); same locality, date, and collectors as type, *Steyermark et al. 125991, 125993* (VEN), *126018* (VDB, VEN); extremo noreste, 3°50′N, 65°28′W, 2,580–2,600 m, 30 Mar.–1 Apr. 1983, *Steyermark & Delascio 129224* (VDB, VEN); cumbre parte central de la Meseta Sur-Este, a lo largo de la Quebrada Yekuana, afluente del Río Negro, 2,560 m, 10–12 Oct. 1983, *Steyermark 129470* (VDB, VEN).

This species has been more of a problem than most in that it appears to be a meld of

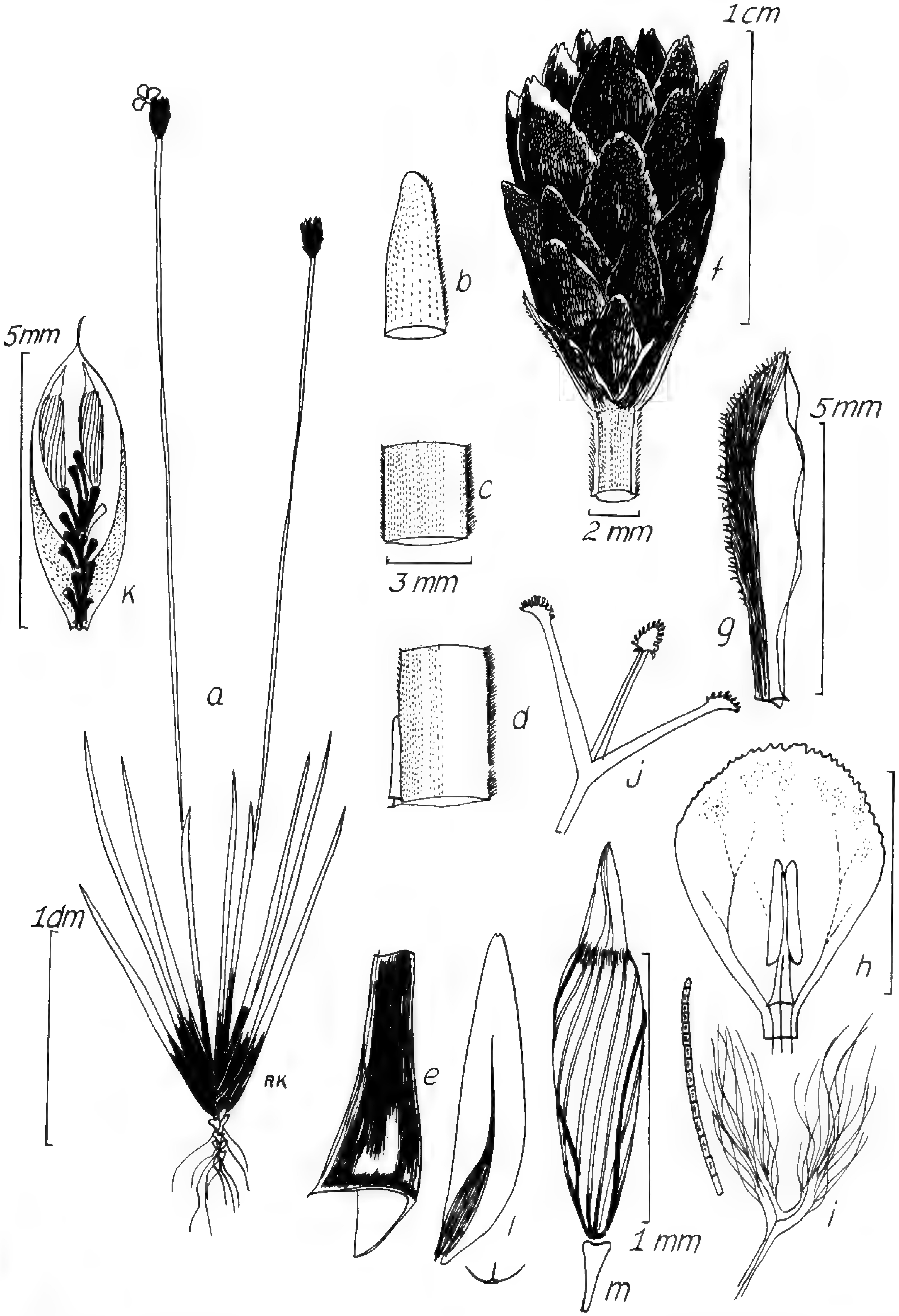


FIGURE 37. Xyris fuliginea *(from the type)*.—*a. Habit sketch.*—*b. Leaf apex.*—*c. Leaf blade, midsector.*—*d. Leaf blade-sheath junction.*—*e. Leaf base.*—*f. Spike.*—*g. Lateral sepal.*—*h. Petal blade, stamen.*—*i. Staminode, enlarged beard hair.*—*j. Stylar apex.*—*k. Capsule, ideal longisection showing two septa (stippled), placentae, two seeds.*—*l. Capsule valve showing septum (dark shading)*.—*m. Seed.*

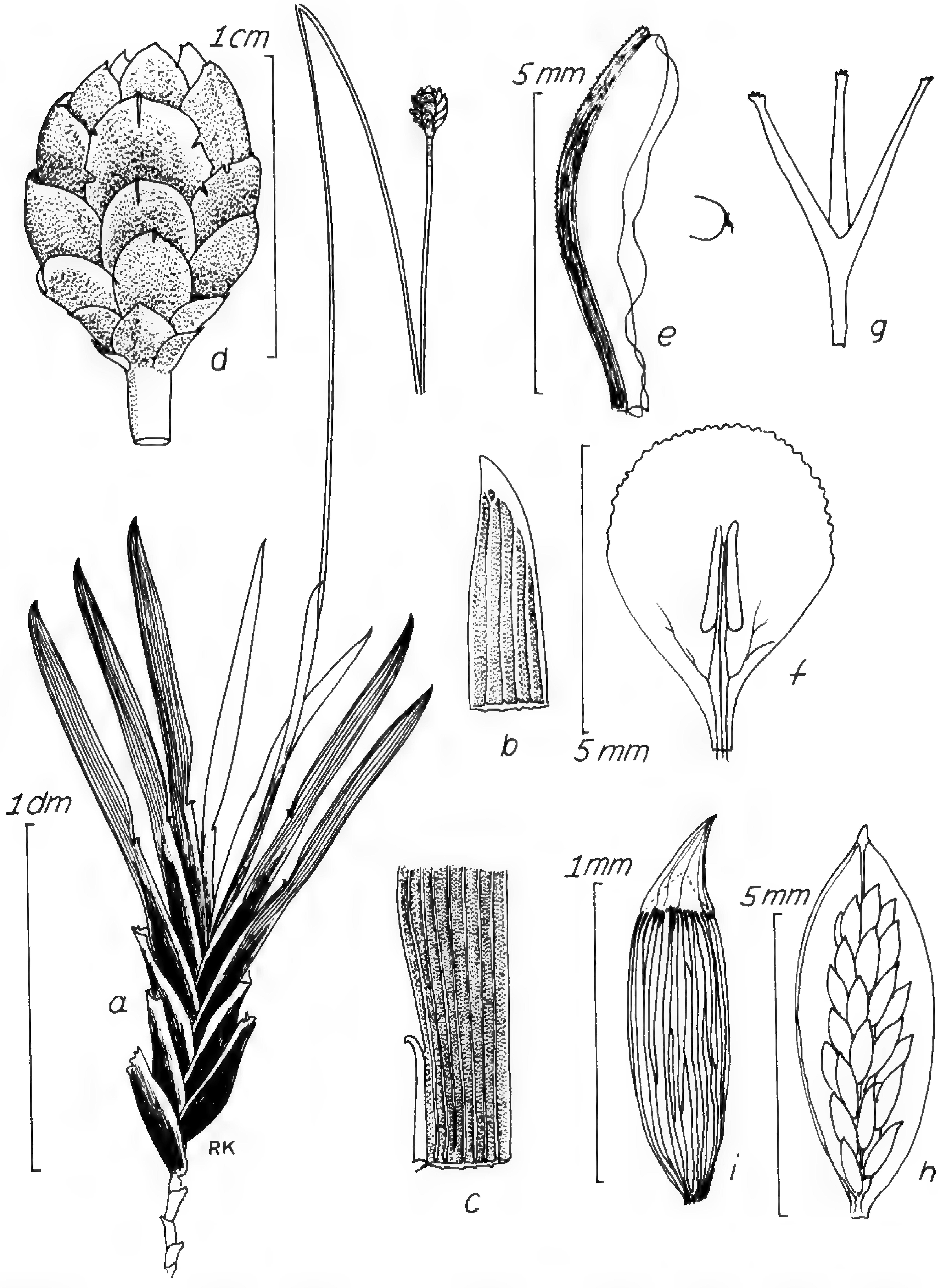


FIGURE 38A. Xyris ptariana *(*Steyermark 105124, *except lateral sepal and stylar apex from the type).—a. Habit sketch.—b. Leaf apex.—c. Leaf blade–sheath junction.—d. Spike.—e. Lateral sepal.—f. Petal blade, stamen.—g. Stylar apex.—h. Capsule.—i. Seed.*

three other high-country species: *X. albescens* (ancipital scape, white-ciliate leaf and scape edges), *X. culmenicola* (obovoid, sooty brown spikes, ciliate, linear-triangular leaf blades), and *X. lugubris* (similar bract, spike and leaf characters). Yet the uniformity of the now rather large set of samples from Cerro Marahuaca collected by Steyermark and oth-

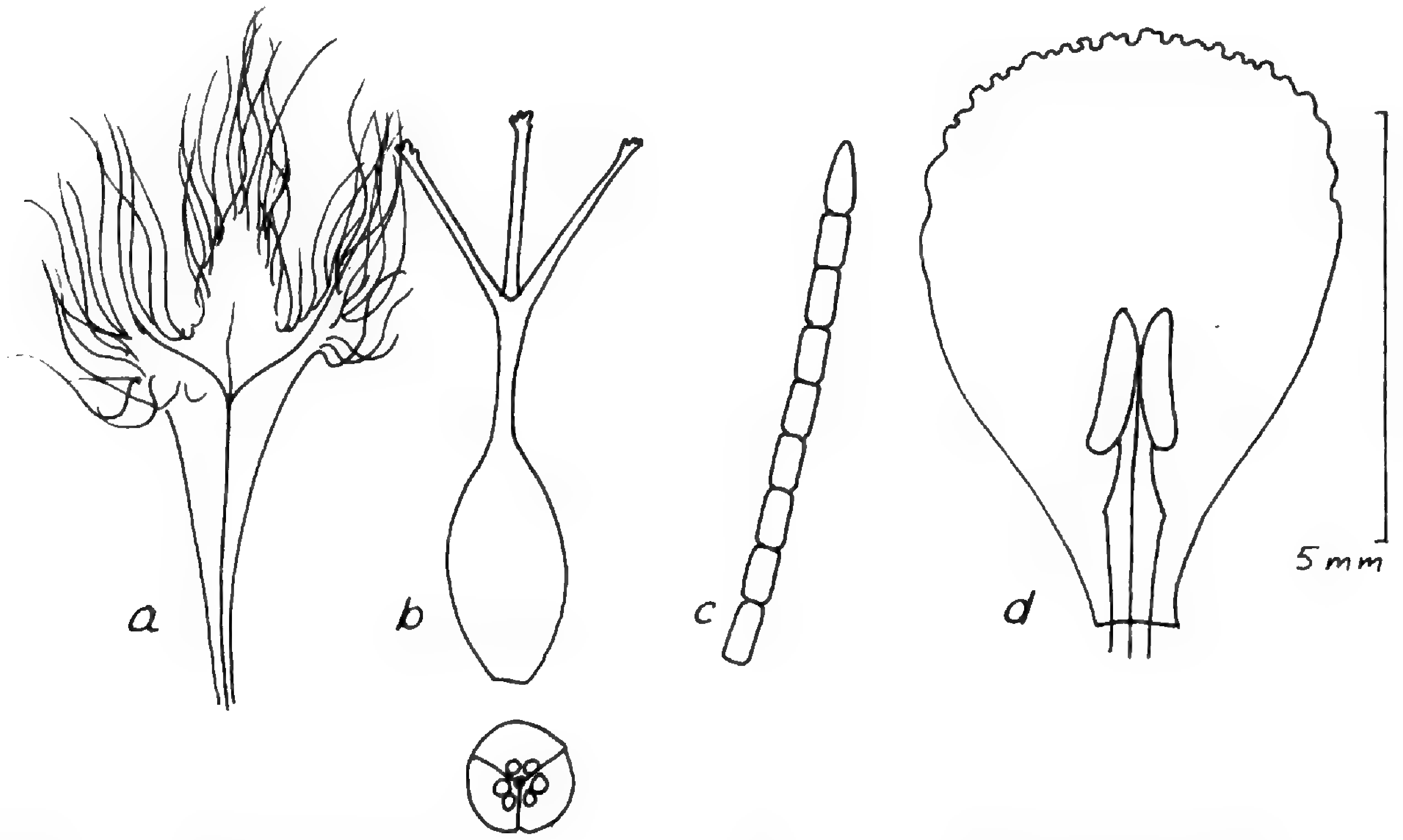


FIGURE 38B. Xyris ptariana *(from the type).—a. Staminode.—b. Ovary and style branches; cross section below.—c. Enlarged staminodial beard hair tip.—d. Petal blade, stamen.*

ers makes description of this cryptic morphology necessary.

38. Xyris ptariana Steyerm., Fieldiana, Bot. 28(1): 110, fig. 16I, J. 1951. TYPE: Venezuela. Bolívar: forming dense tufts, wet bluffs, 2,000 m, Ptari-tepui, Gran Sabana, *Steyermark 59919* (holotype, F; isotypes, F, NY, US, VEN). Figure 38A, B.

Robust, densely cespitose, usually smooth, perennial to 1 m high, the stems elongate, branching from the base and rebranching, the ultimate branches forming frondlike plates of leaves. Leaves spreading-ascending, 1.5–3.5 dm long; sheaths mostly deep red-brown, sometimes pale brown, nearly as long as blades or longer, entire-edged, strongly keeled, narrowing evenly from the dilated base to the blades, there producing a triangular, scarious, spreading or recurved-tipped ligule to 3 mm long; blades flat, straight, linear-ensiform, (3–)3.5–12 mm wide, the apex incurved-acute, flat, the margins usually entire (on Abacapa-tepui densely red ciliate) or papillose-tuberculate, the base narrowed ca. 2–3 cm from ligule on ventral side, the surfaces deep green, strongly multinerved. Scape sheaths shorter than leaves, proximally tubular and multicostate, lustrous brown, distally opening, strongly keeled, with a short blade. Scapes slender but stiff, straight or slightly flexuous and slightly twisted, distally flattened or in cross section narrowly ovate or elliptic, sometimes ancipital, 1.5–3 mm wide, the costa(e) 1–2, usually making up edges, smooth to tuberculate-scabrid or (on Abaca-tepui) red ciliate. Spikes ellipsoid to broadly obovoid, 1–1.5(–2) cm long, blunt, pale brown or olivaceous brown to reddish brown, of many spirally imbricate, thinnish bracts without dorsal areas, the lowest sterile bracts much smaller than the fertile bracts, ovate, obtuse-angled to acute, slightly keeled, grading into the larger, flatter fertile bracts, these obovate-oblong, 0.8–1 cm long, the apex broadly rounded, entire to erose, the backs but slightly convex, toward apex often with a low, lustrous costa. Lateral sepals free, subinequilateral, oblanceolate or spathulate, 6–8 mm long, blunt, thin, with a broad, darker, entire to ciliolate keel. Petal blades broadly obovate to suborbicular, 6–7 mm long, yellow, the broadly rounded apex erose. Staminodia clavate-trilobate when present (in the type), distally densely long-penicillate. Anthers lance-oblong, 1–2 mm long, deeply bifid and sagittate, on filaments 1–1.5 mm long. Capsule ellipsoid, ca. 6–7 mm long, the placentation appearing free-central but the 3 valves with strong, deep septa reaching the capsule axis, thus placentation actually axile. Seeds very numerous, asymmetrically ellipsoid, 1–1.5 mm long, pale amber with a pale, narrowly conic apical scale, longitudinally finely but distinctly ribbed.

Distribution. Boggy, seepy, rocky areas of savanna, at elevations of 1,300 meters or more, Territorio Federal Amazonas and Estado Bolívar, Venezuela.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: Cerro Sipapo (Paraque) common in bogs about pool, Caño Negro savannas at 1,400 m, 15 Dec. 1948, *Maguire & Politi 27703* (GH, K, US, VEN)—very large material as to plant height, leaf width, spike, etc.; summit, Cerro Marahuaca, 2,685 m, 15 Jan. 1981, *Maguire 65634* (NY); Cerro Sipapo, wet cliffs below escarpment, 1,300 m, frequent, Dec. 1948, *Maguire & Politi 27498* (F, NY, US); Cerro Paraque, 1,800 m, Feb. 1946, *Phelps 47* (US); summit of Cerro Duida, on high moist ridgetop, 1,820–2,075 m, 4 Sep. 1944, *Steyermark 58350* (F); Cumbre del Cerro Autana: sabana y afloramientos expuestos, 1,230–1,240 m, 20–22 Sep. 1971, *Steyermark 105124* (F, MO, US); summit of Mount Duida, 5,500–6,000 ft., 26 Nov.–16 Dec. 1927 *G. H. H. Tate 417* (NY)—this with scape broader than norm. BOLÍVAR: Cerro Apacara, 2,300 m, Río Caroni, 11 Nov. 1946, *F. Cardona 1942* (US); Cumbre del Aprada-tepui, sector sur, ubicado ca. 30 km al E de Uriman, 2,500 m, 30 June 1984, *Huber 9565* (MYF, VDB); Chimantá Massif, NW part of summit of Abacapa-tepui, above first line of sandstone bluffs, 2,125–2,300 m, 14 Apr. 1953, *Steyermark 74998*—this material with red-bordered scapes and leaf blades (F, NY, VEN).

This species may be a complex of varieties held together by a combination of elongate and elongate-branched axes producing frondlike plates of leaves, by the curious ligule, and by the distinctive, indented ventral margin of leaf blade just above the sheath. At one end of the variation is the type, narrowest example of *X. ptariana* in leaf and scape, and which differs the least from *X. witsenioides* F. Oliver. At the other extreme, to the far west in Territorio Federal Amazonas, is *X. xiphophylla* Maguire & Lyman B. Smith. Several summit elevations in Estado Bolívar and some in Amazonas are now known to have this taxon, and populations on each are distinguishable, yet not sufficiently to allow a specific treatment.

39. Xyris witsenioides F. Oliver, Thurn, Timehri 5: 207. 1886; Trans. Linn. Soc. II. 2: 285, pl. 50, figs. 9–15. TYPE: "British Guiana, Roraima, ledge 7,300 ft.," *Everard F. im Thurn*, 14 Dec. 1884 (lectotype, K). Figure 39A, B.

Densely cespitose, multibranched perennial (1.2–)2–6 dm tall, the primary branches elongate, ascending, rebranching to form frondlike plates of leaves, the whole producing large dome-shaped masses with bases buried in substrate. Leaves ascending, rarely spreading, 5–20 cm long; sheaths eciliate, the bases tightly imbricate, distichous on the elongate stems, castaneous or light brown, often persistent long after blades, fully as long as blades, strongly keeled, narrowing gradually to scarious, triangular, erect ligules 1–2 mm long; blades gladiate-linear, flattened, straight or falciform, 1–3(–4) mm wide, gradually narrowing from just below middle to apex, there incurved-acute or erect-acute, slightly thickened; margins thin, smooth or scaberulous-papillate, rarely ciliolate; surfaces yellow-green, smooth, finely but evidently multinerved. Scape sheaths shorter than leaves, closed at base, ciliate-keeled, multicostate, above with short, erect, ciliate blades. Scapes straight or flexuous, distally subterete to slightly compressed and oval or narrowly oblong-elliptic in cross section, 0.7–1 mm wide, ecostate or 1(–2 or more) costate, the costae smooth, scaberulous or rarely ciliolate, the surfaces otherwise smooth. Spikes ellipsoid to obovoid, drying broader, 0.7–1.4 cm long, olive-brown or red-brown, of loosely spirally imbricate thin bracts without evident dorsal areas; sterile bracts several, the lowest much smaller and narrower than the fertile bracts, these oblong to obovate, shallowly convex, low-carinate toward apex, 5–7 mm long, rounded, entire, aging lacerate. Lateral sepals free, subequilateral, ca. 5–7 mm long, oblong-curvate, obtuse, the broad thin keel subentire to ciliate, aging lacerate. Petal blades broadly obovate to suborbicular, yellow, 5–6 mm long, the broad, shallowly rounded apex erose-denticulate to nearly entire. Staminodia distally above a short geniculation producing a single,

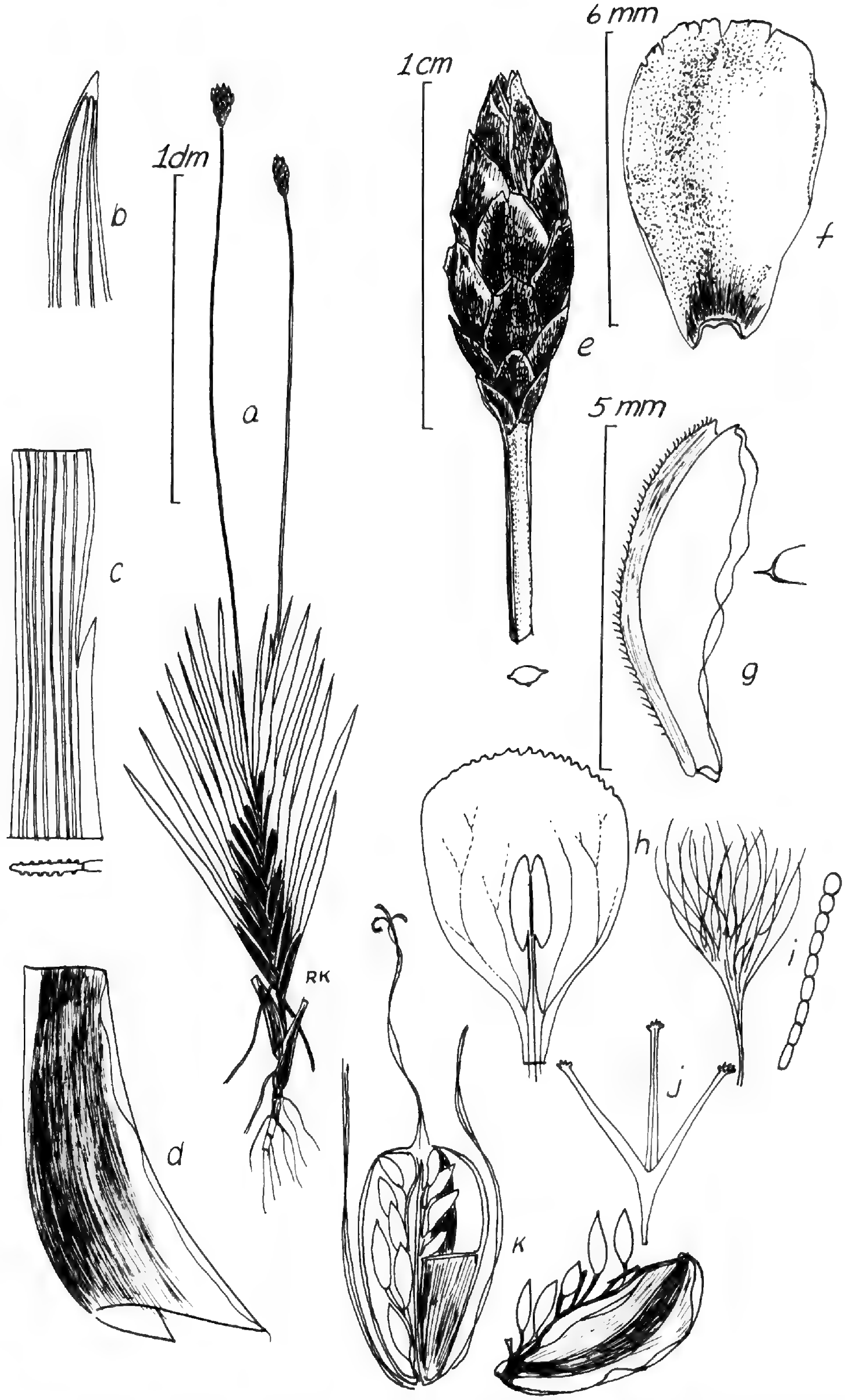


FIGURE 39A. Xyris witsenioides (Kral 70395).—*a. Habit sketch.—b. Leaf apex.—c. Leaf blade-sheath junction.—d. Leaf base.—e. Spike, upper part of scape, cross section of scape.—f. Fertile bract.—g. Lateral sepal (rather broader and shorter than most).—h. Petal blade, stamen.—i. Staminode, enlarged hair.—j. Stylar apex.—k. At left, a longisector through capsule, with a placental strand showing its proximal and distal attachment; at right, another septum with upper part removed showing neighboring locule, a valve removed showing septum and placental strand (dark-shaded).*

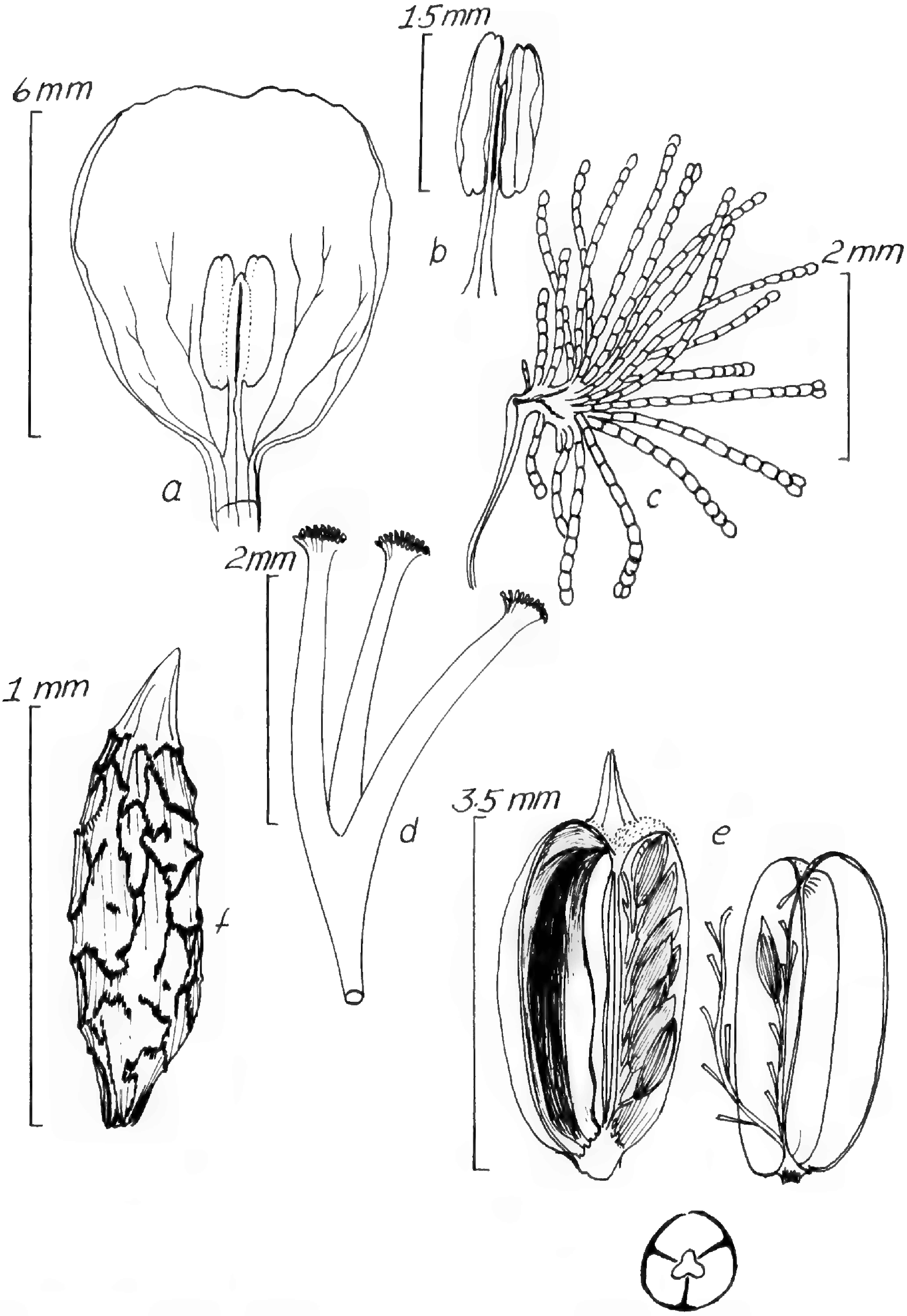


FIGURE 39B. Xyris witsenioides (Maguire et al. 432334).—*a. Petal blade, stamen.—b. Stamen, removed.—c. Staminode, much enlarged to show geniculation, beard hairs.—d. Stylar apex, much enlarged over petal, showing glandular stigmas.—e. Two views of capsule parts: left, most of one locule shown, together with contiguous valves (septum shaded dark at left); right, a fruit section removed to show septum, two placental strands; at base, a transverse section showing placental strands (center), valve edges, and septa.—f. Seed.*

densely penicillate pubescent blade. Anthers oblong, 1.5–1.7 mm long, deeply bifid and sagittate, on filaments ca. 1 mm long. Capsules narrowly obovoid, 3.5–4 mm long, the valves with complete septa, at fruiting maturity with placentae separating from each other except at base and apex and from the septa. Seeds fusiform, ca. 1–1.3 mm long, deep to pale amber, finely longitudinally ribbed, the fine ribs overlain by a coarser, broader, subanastomosing ribbing.

Distribution. Steep bluffs and rocky wet savanna, summits of tepuis, southern Territorio Federal Amazonas and Estado Bolívar in Venezuela, east to the boundary of Venezuela with Brazil and Guyana at the type locality: Roraima.

Additional specimens examined. BRAZIL: Roraima, Dec. 1909, *E. Ule 8547* (L). GUYANA: Mt. Roraima, Nov.–Dec. 1931, *Abbensetts 20* (U); Summit Roraima, *McConnell & Quelch 658* (K); Roraima escarpment, 21 Oct. 1973, *Persaud 88* (NY, UC); N slope of Mt. Roraima, 2,300 m, 16 Feb. 1985, *Renz 14270* (U); Summit Roraima, Autumn 1894, *Quelch & McConnell 95* (K); N slope of Mt. Roraima, 2,300 m, 16 Feb. 1985, *Renz* (U); N ridge scarp of Mt. Roraima, ca. 6,500–7,000 ft. at 6,600 ft., 26 Mar. 1978, *Warrington et al. K. E. R. 62* (K). VENEZUELA. T. F. AMAZONAS: Cerro de Marahuaca above Salto Los Monos, 2,555 m, 26 Feb. 1985, *Liesner 17992* (MO, VDB); Neblina, upper escarpment slopes E of Camp III, 1,600–1,800 m, 27 Dec. 1953, *Maguire et al. 36932* (NY, US); Neblina, Cumbre Camp, 1,700 m, 5 Jan. 1954, *Maguire et al. 37064* (GH, MO, NY, US); Neblina, E of Camp III, 1,600 m, 24 Jan. 1954, *Maguire et al. 37371* (NY, US); Neblina, banks of Caño Grande, E of Cumbre Camp, 1,100 m, 24 Nov. 1957, *Maguire et al. 42200* (GH, K, NY, VEN); Neblina, upper Cañon Grande, 1,900 m, 11 Dec. 1957, *Maguire et al. 42334* (F, K, NY, US, VEN); Cerro Marahuaca, cumbre, sección suroriental, 2,685 m, 15 Jan. 1981, *Maguire et al. 65634* (NY, VEN); headwaters of Cañon Grande, SE portion, 1,900 m, *Steyermark 104007* (NY, US, VEN); Cerro Marahuaca-FHUIF, cumbre, altiplanicie de rocas expuestas, 2,330–2,470 m, 3–4 Feb. 1982, *Steyermark et al. 126079* (NY, VDB); same area and collectors, 9–10 Feb. 1982, *Steyermark et al. 126313* (NY, VDB, VEN); Cerro Marahuaca, cumbre extremo noreste, 2,580–2,700 m, 1 Apr. 1983, *Steyermark & Delascio 129297* (VDB, VEN); Cerro Aratitiyope, ca. 70 km al SSW de Ocamo con riachuelos afluente al Río Manipitare, 1,550 m, 24–28 Feb. 1984, *Steyermark et al. 130287* (VEN). BOLÍVAR: Alto Caroni, Guyana, del Cerro Yaipan, 7,800 m, *F. Cardona 2421* (VEN); Valle Encantado, Lado derecho del Salto Angel, Auyantepuy, 15 Aug. 1968, *Foldats 7109* (VEN); Cumbre del Yuruani-tepui, ca. 12 km al NNE del Kukenan-tepui, 2,200 m, 29 Feb. 1984, *Huber 9078* (MYF, VDB); Macizo del Guaiquinima, sector centro-noroccidental, 1,350 m, 2 Apr. 1984, *Huber 9364* (MYF, VDB); Cumbre del Ilú-(Urú-)tepui, sector centro-meridional, 29 Apr. 1984, *Huber 9493* (MYF, VDB); sección mas septentrional del Brazo occidental del Auyantepui, ca. 25 km al SE de Canaima, 13 Nov. 1984, *Huber 9727* (MYF, VDB); cumbre del Ptari tepui, ca. 22 km al NNW de la Misión de Kavanayen, ca. 2,400 m, 19 Nov. 1984, *Huber 9828* (MYF, VDB); Kukenani-(Mataui-)tepui, cumbre meridional, 2,700 m, 15 June 1985, *Huber & Alarcon 10525* (MYF, VDB); Serranía Guanay, sect. nororiental, cabeceras mas orientales del Río Parguaza, ca. 1,700 m, 20–28 Oct. 1985, *Huber 10968* (MYF, VDB); Altiplanicie del Auyan tepui, sector centro-oeste, 1,860 m, 19 Jan. 1986, *Huber 11237* (MYF, VDB); Ptari-tepui along trail from camp to SW shoulder of mt., vic. Cave Rock Camp, 1,600–2,000 m, 14–19 Aug. 1970, *Moore et al. 9807* (VEN); Mt. Roraima, 9,000 ft., *H. S. Irwin 441* (NY, US); Uaipantepui, summit of West Peak, 1,980 m, 4 Mar. 1967, *Koyama & Agostini 7438* (NY, US); Cerro Guaiquinima, 1,500 m, 31 Dec. 1951, *Maguire 32883* (NY, US); Cerro Guaiquinima, open savanna 1 km S of Cumbre Camp, 1,800 m, 29 Dec. 1951, *Maguire 32799* (K, NY, US, VEN); ca. 6.5 km N of Pioneer Monument by Ven. 10, summit La Escalera, ca. 1,200 m, *Kral 70395* (F, K, L, MO, NY, SP, U, US, VDB, VEN); Cerro Guaiquinima, North Valley, 1,600–1,700 m, 4 Jan. 1952, *Maguire 32957* (NY, US, VEN); Ilu-tepui, Gran Sabana, 6,000–7,000 ft., 16 Mar. 1952, *Maguire 33433* (NY, US); Mt. Roraima, 2,100–2,255 m, 27 Sep. 1944, *Steyermark 58719* (F, NY, US, VEN); Ptari-tepui, 2,000–2,200 m, 2 Nov. 1944, *Steyermark 59736* (F, US, VEN); Sierra de Lema, base of uppermost waterfall of Río Chicanan, *Steyermark 89551* (NY, US, VEN); Auyan-tepui, cumbre, 1,760 m, 11 May 1964, *Steyermark 93665* (F, NY, US, VEN); Auyan-tepui, cumbre de la parte sur, 2,050–2,300 m, 15 May 1964, *Steyermark 93966* (F, NY, US, VDB, VEN); Cerro Roraima (near boundary markers), *Steyermark et al. 112501* (F, K, NY, US, VEN); Cumbre de Cerro Guaiquinima, 26 Jan. 1977, *Steyermark & Dunsterville 113518* (NY, VEN); Ptari-tepui, 2,360–2,420 m, 23 Feb. 1978, *Steyermark et al. 115716* (F, MO, US, VEN); Aprada-tepui, 2,460–2,500 m, 25 Feb. 1978, *Steyermark et al. 115895* (F, MO, NY, U, US, VEN); Auyan-tepui, 1956, *Vareschi & Foldats 4907* (VEN).

The above citations, while far from complete, help illustrate the considerable variation in habit, leaf, and spike characters displayed sometimes even on the same tepui. This is perhaps one of the most distinctive morphologies in the genus, individual plants forming enormous dome-shaped clumps of foliage from which the slender scapes stand out like long pins from a pincushion. Out of so many collections, some represented by many duplicates, few capsules with full seed can be found, thus this species appears to be one of the poorest seed setters in *Xyris*. The question then arises as to why it is so widespread and seemingly successful.

40. Xyris xiphophylla Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 20–21, fig. 6A–E. 1963. TYPE: Venezuela. T. F. Amazonas: abundant in wet escarpment savanna, 4–8 km south of Cumbre Camp, 1,850–1,900 m, Cerro de La Neblina, Río Yatua, 15 Jan. 1954, *B. Maguire, J. J. Wurdack & G. S. Bunting 37312* (holotype, NY; isotypes, US, VEN). Figure 40.

Robust, densely cespitose, smooth perennial 5–8 dm high, the stems short and stout or up to 5 or 6 cm long; sheaths eciliate, as long as blades or longer, with broad, dark reddish brown or castaneous bases, gradually narrowing to blades and with a triangular erect or divaricate ligule to ca. 2–3 mm long; blades straight, strongly flattened, narrowly lance-linear, 5–10 mm wide, broadening just above ligule, then narrowing evenly to an acute, erect or slightly falcate apex, the tip slightly thickened; margins smooth, edges thin, producing a narrow, subcartilaginous border; surfaces deep green, smooth, with numerous low, wide nerves. Scape sheaths shorter than most leaves, deep brown, multicostate, carinate at base, opening and producing a short blade above. Scapes somewhat flattened distally (narrowly elliptic or ovate in cross section), sometimes slightly ancipital, 2–3 mm wide, the edges blunt, the surfaces smooth, sometimes striate. Spikes narrowly cylindric-obovoid, to ca. 2 cm long, the base acute to attenuate, the apex blunt, the inflorescence of many, loosely imbricate but firm, dark brown or pale brown, dull bracts in nearly vertical rows and without dorsal areas, the sterile bracts much smaller, narrower than the fertile bracts and grading into them, the fertile bracts oblong, 10–15 mm long, apically narrowly rounded, with a short, subapical, glossy carina or apiculus, the margins entire, aging lacerate. Lateral sepals free, subequilateral, lineal, 10–12 mm long, acute, the narrow, dark keel entire or papillate toward apex. Petal blades broadly obovate, 6–7 mm long, yellow, the shallowly rounded apex crenulate. Staminodia not evident. Anthers narrowly oblong, 2–2.5 mm long, deeply bifid and sagittate, on short filaments to ca. 0.5 mm long. Capsule cylindric, 6–8 mm long, strongly septate from tip to base, the placentation axile, the placental axis extending ¾ up the fruit. Seeds lance-ovoid, 1.5–2 mm long, pale to deep amber, finely longitudinally anastomosing-ribbed.

Distribution. Wet, rocky savanna, summit elevations, Cerro de La Neblina, Territorio Federal Amazonas, Venezuela, locally abundant.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: low bush slopes near Cumbre Camp, 1,800 m, 4 Jan. 1954, *Maguire et al. 37051* (paratype, NY, US); planicie de Zuloaga, Río Titirico, 2,300 m, 10–15 Oct. 1970, *Steyermark 103825* (K, NY, US, VEN). More recent collections, not yet fully distributed, are: Valle de Titirico N of Pico Phelps, ca. 2,300 m, 1 Dec. 1984, *Kral 71914*; Camp 2, 2.8 km NE of Pico Phelps, 2,100 m, open bog, 15 Apr. 1984, *Stein & Gentry 1578* (MO, VDB, etc.); al norte del campamento base a lo largo del Río Mawarinuma, afluente del Río Baria, 1,880 m, 7–8 Feb. 1984, *Steyermark & Luteyn 129819* (MO, NY, VDB).

This species is another with the tendency to form frondlike plates of leaves and is superficially closest to forms of *X. ptariana* Steyerm. In the savanna of the Valle de Titirico it is the dominant xyrid, its pale yellow flowers unfolding in morning.

41. Xyris spruceana Malme, Bih. Svensk. Vet. Akad. Handl. 26(3)[19]: 12, pl. 1, f. 2. 1901. TYPE: Venezuela: ad fluv. Guainía v. Río Negro supra ostium fluvensis Casiquiari, in 1854, *R. Spruce 2993* (isolectotypes, GH, NY). Figure 41.

X. applanata Idrobo & Lyman B. Smith, Caldasia 6(29): 239–240, fig. 27a–h. 1954. TYPE: Colombia. Vaupés: Río Kananari, Cerro Isibukuri, piedra de arenisca, 250 m, 28 Oct. 1951, *R. E. Schultes & I. Cabrera 14466* (holotype, COL; isotypes, F, GH, MG, US, VDB).

Low, cespitose annual 0.8–2.5 dm tall, the stems contracted. Leaves ascending or spreading flabellately, mostly 5–15 cm long; sheaths from ½ as long to longer than blades, eciliate, sharply keeled, brown at very base, above stramineous, pink or pale purple, shading to pale green, progressively narrowing into blade, there either eligulate or with a narrowly triangular ligule less than 1 mm long; blades ensiform-linear, flat, 1.5–3 mm wide, narrowing gradually to an acute apex above middle, the margins slightly incrassate, papillose

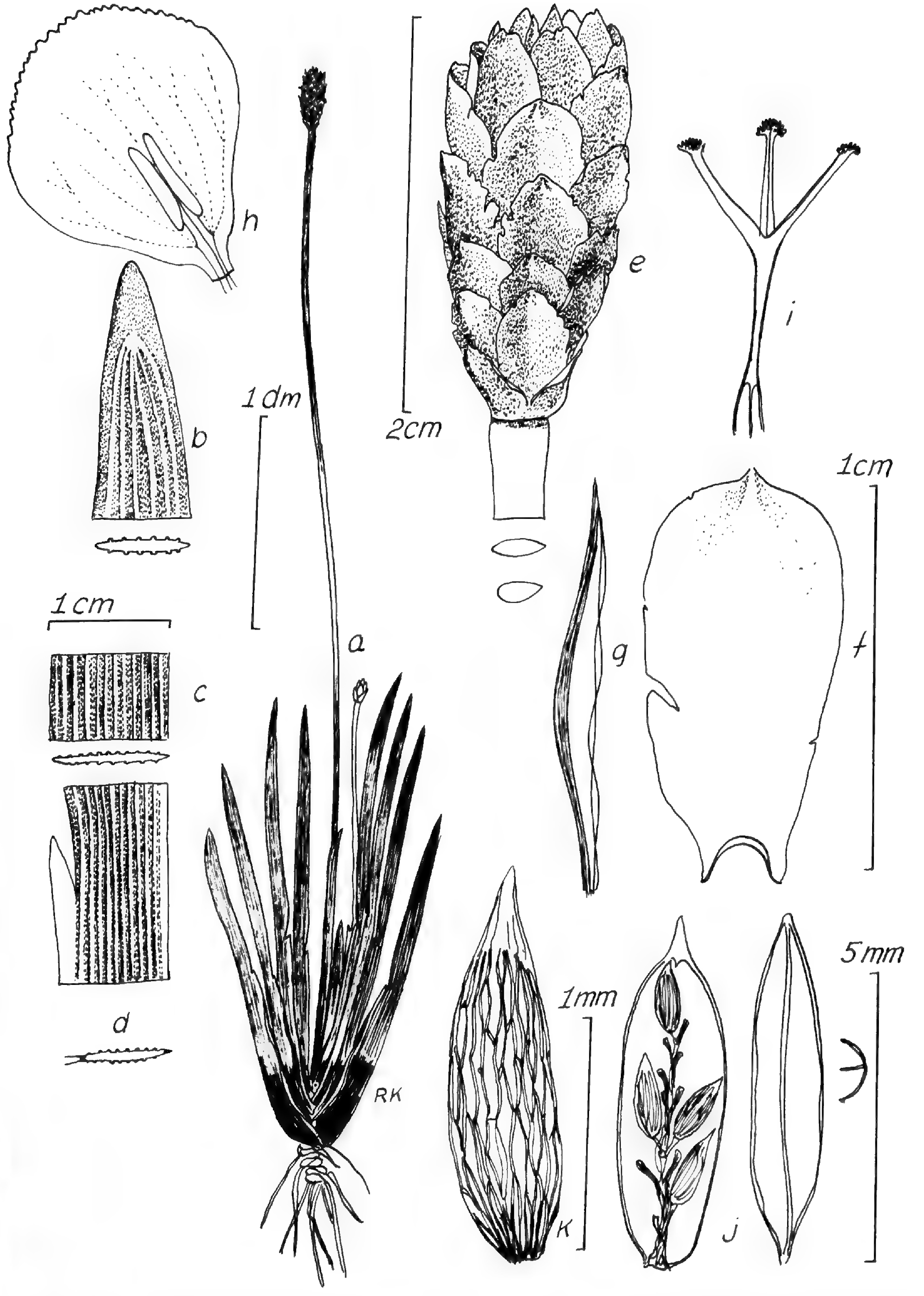


FIGURE 40. Xyris xiphophylla *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Sector of leaf blade at widest point.—d. Leaf sheath–blade junction.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Stylar apex.—j. At left, median long view of capsule, showing placentae; at right, inside view of one valve, cross section of valve to show septum.—k. Seed.*

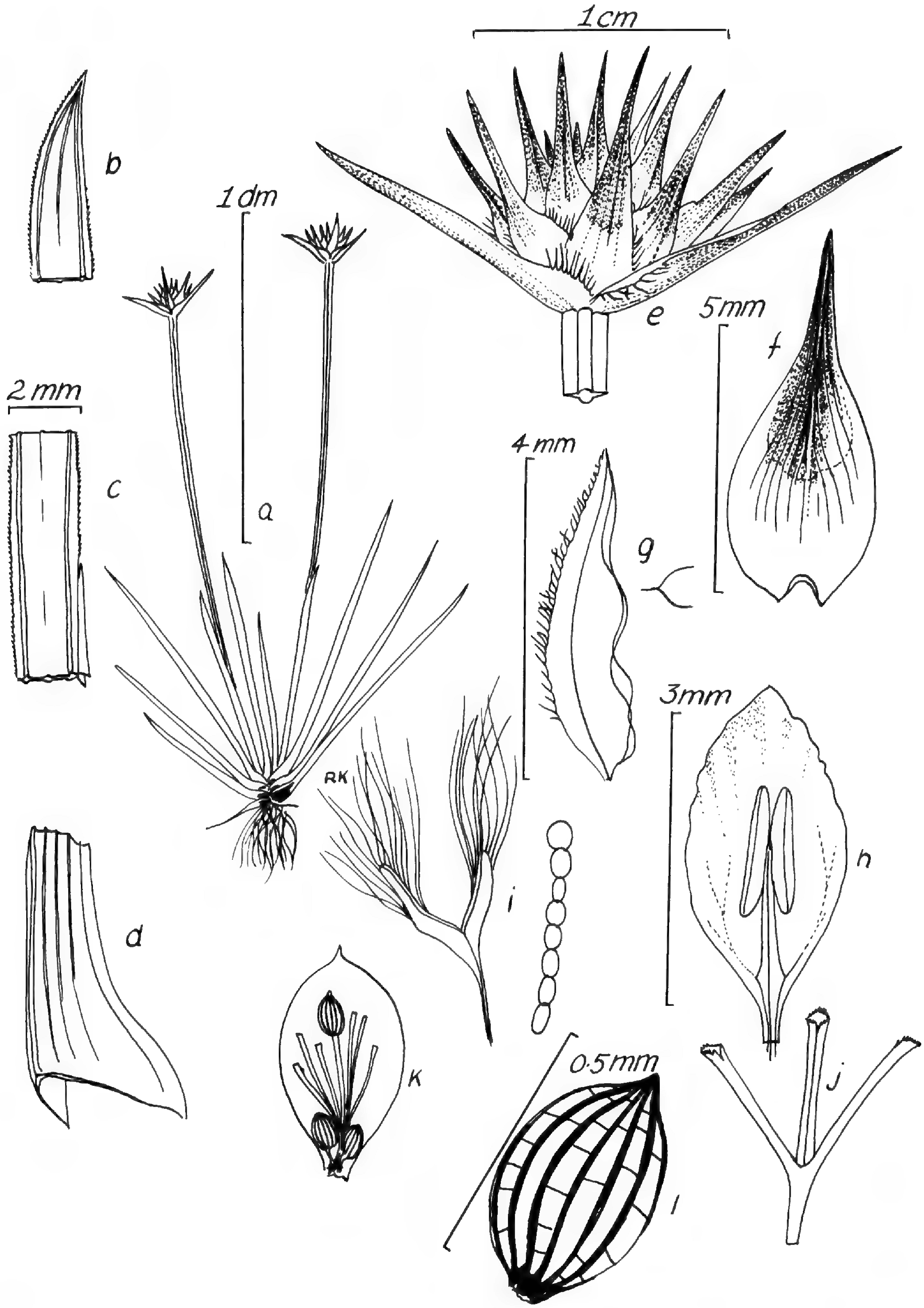


FIGURE 41. Xyris spruceana (Clark 6455).—*a. Habit sketch.*—*b. Leaf apex.*—*c. Leaf sheath–blade junction.*—*d. Leaf base.*—*e. Spike.*—*f. Fertile bract.*—*g. Lateral sepal.*—*h. Petal blade, stamen.*—*i. Staminode, enlarged beard hair tip.*—*j. Stylar apex.*—*k. Capsule, showing basal placentation, valve outline.*—*l. Seed.*

to scabridulous or minutely ciliate, the surfaces green, often bordered by a pale brown band and a strong submarginal nerve, smooth, multinerved. Scape sheaths carinate at base, strongly bladed, similar to foliage leaves. Scapes appearing strongly flattened, distally 2–3 mm wide, scape body slightly flattened, usually with 1–2 ribs/side, the lateral costae alate, broader than scape body, ciliolate or papillate or entire. Heads turbinate to hemispheric, 0.7–1 cm high, with several spirally and loosely imbricate bracts, involucrate, with at least some sterile bracts leaflike with foliaceous, spreading or ascending, green-keeled blades, the blades elongate, sharply and ciliately keeled, spreading or overtopping, longer than the spike to slightly shorter, and with bases broadly margined, scarious, reddish, fimbrio-ciliate; fertile bracts ovate or lance-ovate, 5.5–6.5 mm long, strongly carinate, the large green, venose dorsal area excurrent to form an acuminate-subulate apex, or merely acute. Lateral sepals free, inequilateral, thin, broadly lanceolate, ca. 4 mm long, acute, the darker firmer keel ciliolate or villose with rusty hairs. Petal blades elliptic, 3.5–4 mm long, yellow, subacute, the margin undulate. Staminodia bibrachiate, the oblong, flat branches long-penicillate-ciliate. Anthers oblong, ca. 1 mm long, deeply bifid and sagittate, on filaments ca. 1 mm long. Capsule obovoid, 2–3 mm long, placentation basal, the valves without septa. Seeds numerous, ovoid to ellipsoid, ca. 0.5 mm long, apiculate, lustrous but opaque, with ca. 14 strong, dark brown, longitudinal ribs.

Distribution. Locally common in wet, sandy, savanna–forest transition or in white-sand savanna, along the Rio Negro and tributaries from Amazonian Brazil (Amazonas) northward into southern Colombia and southern Territorio Federal Amazonas, Venezuela.

Additional specimens examined (only Colombian and Venezuelan records are cited here). COLOMBIA. VAUPÉS: Río Apaporis, Jirijirimo, 250 m, 26 Nov. 1951, *García-Barriga 13729* (NY); Puerto Colombia (opp. Maroa), 130 m, 12 Oct. 1957, *Maguire et al. 41848* (F, NY); Río Negro, El Castilo, San Filipe, 12 Dec. 1947, *Schultes & López 9333A* (NY); Cachivera de Jirijirimo, ca. 250 m, 13 June 1951, *Schultes & Cabrera 12392* (GH, NY); Río Apaporis, Cachivera de Jirijirimo, 13 June 1951, *Schultes & Cabrera 12392* (GH); same locality, 12 Aug. 1951, *Schultes & Cabrera 13512* (GH, NY); same locality, 16 Sep. 1951, *Schultes & Cabrera 14055* (F, GH); same locality, 21 Jan. 1952, *Schultes & Cabrera 14949* (COL, F, GH, US, VDB); Río Kananarí, ca. 250 m, Cachivera Palito, 25 July 1951, *Schultes & Cabrera 13187* (GH); Cerro Isibukurí on summit, 6 Aug. 1951, *Schultes & Cabrera 13401* (GH); Cerro Yapoboda, ca. 450 m, 5 Oct. 1951, *Schultes & Cabrera 14263* (GH); Río Kananarí, Cerro Isibukurí, 29 Oct. 1951, *Schultes & Cabrera 14535*; Cerro Isibukurí, *Schultes & Cabrera 14466* (isotype of *X. applanata*, F, GH, MG, NY, US, VDB); Raudal Jirijirimo below mouth of Kananarí, ca. 900 ft., 21 Jan. 1949, *Schultes & Cabrera 14949* (F, GH); Río Piraparana, Aug. 1952, *Schultes & Cabrera 17116* (GH); 18 Sep. 1952, *Schultes & Cabrera 17504, 17553* (GH); Río Negro, San Felipe and vic., Puerto Colombia, 31 Oct.–2 Nov. 1952, *Schultes et al. 18189* (GH); Río Piraparana, Cerro E-ree-ee-ko-mee-o-kee, 30 Aug.–18 Sep. 1952, *Schultes & Cabrera 17499* (F, GH, MG, VDB, US); Río Guainía, Caño del Caribe, 2 Nov. 1952, *Schultes et al. 18249* (GH); Río Vaupés, falls of Yurupari, 12 Apr. 1953, *Schultes & Cabrera 19002* (GH); same locality, Nov. 1951, *Schultes & Cabrera 19732* (GH); Mitu and vic. along Río Vaupés at Circasia, 14 Sep. 1976, *Zarucchi 2049* (GH). VENEZUELA. T. F. AMAZONAS: San Carlos de Río Negro, 28 Sep. 1978, *Clark 6827* (NY); 3 km NE of San Carlos, 31 Dec. 1977, *Clark 6455* (MO, NY); raudal "pereza" en el Río Autana, 9 Nov. 1984, *Guanchez & Melgueiro 3426* (TFAV, VDB); km 11 de la carretera San Carlos–Solano, 16 Sep. 1980, *Huber et al. 5677* (US); carretera San Carlos–Solano, entre los km 4 y 20, 15 Sep. 1980, *Huber & Medina 5639* (US); 4 km E San Carlos de Río Negro, 11 Nov. 1977, *Liesner 3365* (NY, MO); 1–2 km SE and E of San Carlos, 22 Apr. 1979, *Liesner 6870* (MO, VDB); Río Guainía, Yavita–Pimichín trail near Pimichín at 140 m, 22 Nov. 1957, *Maguire et al. 36337* (GH, NY); Bana, 2 km N de San Carlos, 6 Feb. 1977, *Morillo & Hasegawa 5155* (VEN); same locality, 6 Feb. 1977, *Morillo & Villa 5355* (VEN).

A number of specimens are cited above to illustrate the degree of variation in involucral bract and fertile bract in the species. This variation includes, as a continuum, *X. applanata* Idrobo & Lyman B. Smith.

42. Xyris uleana Malme, Repert. Spec. Nov. Regni Veg. 3: 113. 1906. TYPE: Auf nassem Sandbogen, Bl. Gelb., Manaos, Rio Negro, Mai 1902, Amazonas Expedition *E. Ule*, Herbarium Brasiliense No. *6171* (lectotype, B; isolectotypes, GH, L, U; phototype, F).

X. duidensis Malme, Bull. Torrey Bot. Club 58: 325. 1931. TYPE: Venuezuela. T. F. Amazonas: summit of Mount Duida, 4,000 ft., Gorge of Caño Negro, Savanna Hills, *G. H. H. Tate 811* (lectotype, NY; isolectotype, US).

X. vaupesiana Idrobo & Lyman B. Smith, Caldasia 6(29): 237–238, fig. 26a–f. 1954.

This complex of little plants varies so much as to leaf and scape, trichomal features, relative length of spike and sterile bracts, and degree of sepal connation, that it is understandable that several variants have been described as species. Certainly two varieties appear, as follows:

KEY TO VARIETIES OF *XYRIS ULEANA*

1a. Scapes distally ancipital, the costae produced as 2 flat wings comprising the edges; leaf blades over 1 mm wide .... 42a. *X. uleana* var. *uleana*
1b. Scapes at most low-costate, terete, rarely with 1–few low costae; leaves 1 mm wide or less .... 42b. *X. uleana* var. *angustifolia*

42A. Xyris uleana Malme var. **uleana.** Figure 42.

Cespitose, soft-based annual 0.6–1.5(–2.2) dm high, the stems contracted. Leaves erect to spreading flabellately, 3–10 cm long; sheaths eciliate, keeled, ½ as long as blades or more, brownish or tan, narrowing gradually to blades and usually eligulate; blades linear, strongly flattened, 1–3.5 mm wide, tapering to incurved-acute tips; margins thin or comprising a yellowish-incrassate nerve, smooth or papillate toward leaf apex; surfaces green or tinged with pink or maroon, finely nerved or with some strong, yellowish nerves, glabrous. Scape sheaths mostly shorter than leaves, keeled and multicostate proximally, distally with strong blades similar to leaves. Scapes straight, slightly twisted, appearing strongly flattened, 1–3 mm wide, with scape body actually often round and with 2 lateral costae, alate, in combined width broader than scape body, the wings smooth or scaberulous-ciliate, sometimes scape faces with 1 or 2 more low costae. Spikes broadly to narrowly ovoid, 3–5(–10) mm long, acute, of several tightly imbricate bracts, these with large dorsal areas, otherwise thin, scarious, papillose, pilose-ciliate, the lowest pair sterile, often with backs alate-keeled, with excurrent-bladed dorsal areas, often longer than the other bracts, sometimes exceeding spike and with tips incurved-cucullate or erect; fertile bracts 2–3.5 mm long, broadly obovate or suborbicular, cucullate, broadly rounded at apex, ecarinate, papillate, the margins usually pilose-ciliate. Lateral sepals free or connate at base, strongly inequilateral, 2.5–3 mm long, blunt, the broad, curvate keel ciliolate and/or papillate. Petal blades very broadly obovate, ca. 2 mm long, yellow, the wide, shallowly rounded apex coarsely few-toothed. Staminodia bibrachiate, the narrow, flat branches long-penicillate-ciliate. Anthers lance-oblong, ca. 0.5 mm long, deeply bifid and auriculate, on flat filaments ca. 0.5 mm long. Capsule broadly obovoid, ca. 1.5 mm long, the placentation basal. Seeds narrowly ovoid or ellipsoid, 0.5–0.7 mm long, pale amber, longitudinally with many wavy, narrow, sharp lines, sometimes also with a few, irregular, stronger, dark red ribs.

Distribution. Sandy wet savanna at low to high elevations, northern South America west of the Andes, the Amazon system and tributaries, southern Colombia east to the Guianas, also including the upper Orinoco and tributaries; northern Brazil from Mato Grosso and Amazonas east into Pará. Only some of the collections from Colombia, Venezuela, and the Guianas are cited below.

Additional specimens examined. COLOMBIA. VAUPÉS: Río Atabapo, 1 km W Cacagual, *Maguire et al. 36293* (NY, VEN); Río Kubiyú, Cerro Kanenda, ca. 800–900 ft., 10 Nov. 1952, *Schultes & Cabrera 15398* (id. as *X. applanata* Idr. & Sm.—COL, F, GH, MG, US, VDB), *18337* (GH), *18398* (COL, GH, VDB); Río Kuduyari, Yapoboda, ca. 900–1,000 ft., 18 Nov. 1952, *Schultes et al. 18531* (F, GH). GUYANA: Kaieteur Savanna, 1,200 ft., 7 Sep. 1937, *Sandwith 1422* (K, U); Kaietuk savana, 1,100 ft., 20 Aug. 1933, *Tutin 497* (K, U); Kaietur summit, 1,100 ft., 31 Aug. 1959, *Whitton 217* (K). SURINAM: wet-sand savanna in upper Sipaliwini area, 4 Sep. 1966 (U); Weyneweg, between Albina and Moengotapoe, savana-forest, 14 Aug. 1933, *Lanjouw 433* (U); *Lanjouw 433a* (an older plant—U). VENEZUELA. T. F. AMAZONAS: laja en raudal "pereza" en el Río Autana, 9 Nov. 1984, *Guánchez & Melgeiro 3422* (TFAV, VDB); hasta el pie occidental del Cerro Yapacana, ca. 100 m, 14–28 Feb. 1978, *Huber 1600* (US); al E del Caño Perro de Agua a unosa 30 km al SE de la confluencia Orinoco–Ventuari, 30 Nov.–1 Dec. 1978, *Huber & Tillett 2814* (US); cabeceras del Caño Cotua y la base occidental del Cerro Yapacana, *Huber & Tillett 3014* (US); *Cerro Moriche,* 120 m, 19 Feb. 1979, *Huber 3198* (US); base of

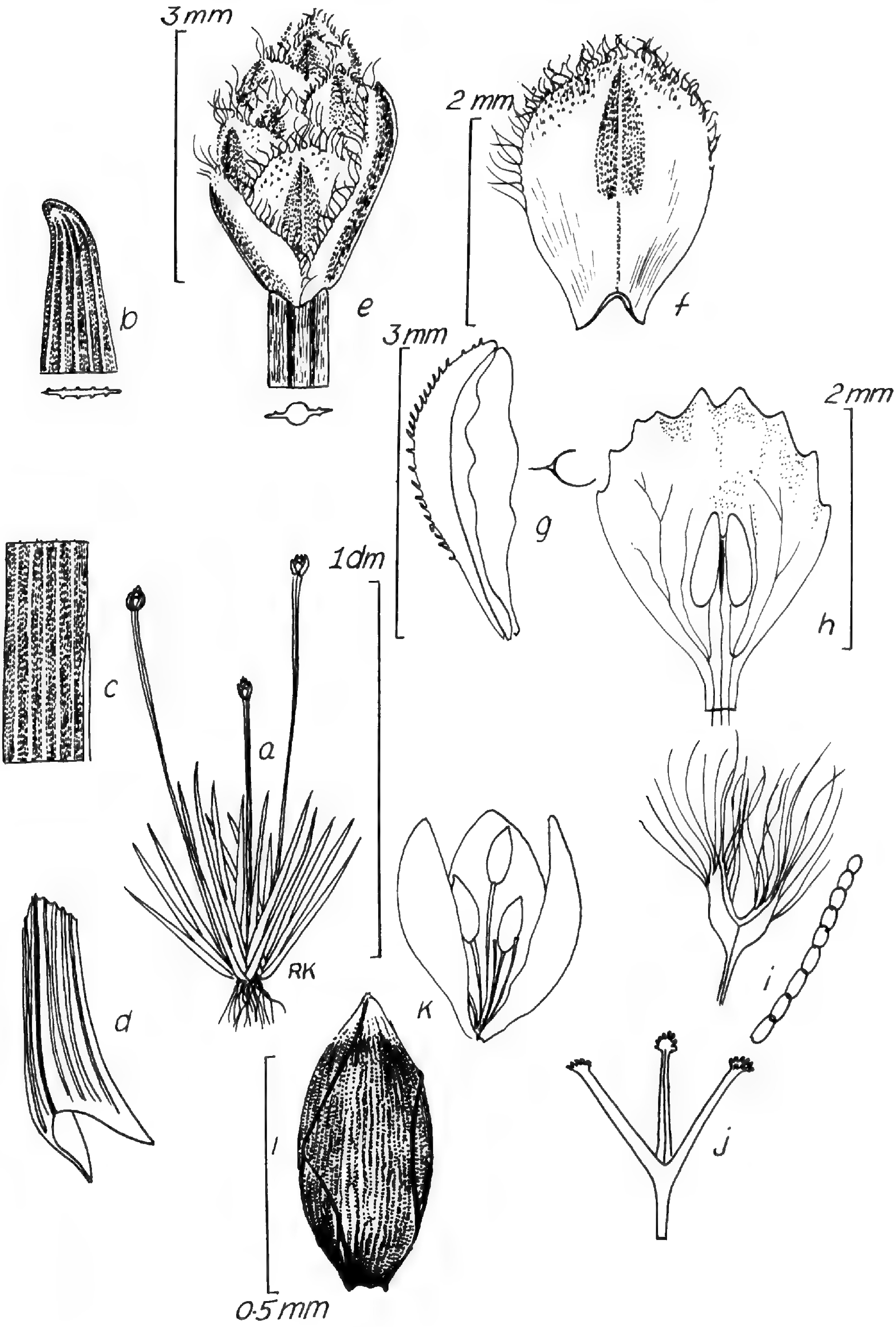


FIGURE 42. Xyris uleana (Kral 70610).—*a. Habit sketch.—b. Leaf apex.—c. Leaf sheath-blade junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode, enlarged apical part of beard hair.—j. Stylar apex.—k. Dehisced capsule showing basal placentation.—l. Seed.*

Cerro Yapacana, *Kral & Huber 70680, 70701* (F, K, MO, NY, SP, US, VDB, VEN); 30 km N of Puerto Ayacucho, 80 m, 5 Nov. 1980, *Maas & Huber 5149* (U, US, VDB); Salto Yutaje, 8 Nov. 1980, *Maas & Steyermark 5174* (U, VDB, VEN); summit Cerro Guanay, 1,800 m, 2 Feb. 1951, *Maguire et al. 31704* (id. as *X. duidensis*—GH, K, NY, US, VEN); near Pimichín, 140 m, 22 Nov. 1953, *Maguire et al. 36338* (GH, NY, US); Cerro Sipapo, 1,400 m, 25 Dec. 1948, *Maguire & Politi 27916* (NY); ibidem, savanna vic. base camp, 125 m, 30 Dec. 1948, *Maguire & Politi 28041* (NY); Danta Falls, Río Cuao, Río Orinoco, 30 km below La Urbana, 14–15 May 1949, *Maguire & Politi 29083* (F, US); Cerro Duida, Río Cunucunuma, Caño Culebra, 1,000–1,100 m, 18 Nov. 1950, *Maguire et al. 29519* (NY, US, VEN); summit Cerro Duida, Brocchinia Hills, 1,700–1,980 m, 1 Sep. 1944, *Steyermark 58145* (id. as *X. duidensis*—F, GH, MO, NY, US, VEN); topotype, 1 Feb. 1975, *Tillett & Talukdar 752-142* (K, NY, U, VEN). BOLÍVAR: region de Canaima, Salto Hacha, 16–17 Feb. 1964, *G. Agostini 266* (VEN); top of Salto Aicha near E base of Uaipan-tepui, 1,100 m, 27–28 Nov. 1982, *Davidse & Huber 22857* (MO, VDB); Vallé Encantado, lado derecho del Salto Angel, Auyantepuy, *Foldats 7178* (id. as *X. duidensis*—VEN); Serania Guayay sector nor-oriental, 20–28 Oct. 1985, *Huber 10967* (MYF, VDB); S foot of peaks of Uaipan-tepui, 1,200 m, 6 Mar. 1967, *Koyama & Agostini 7513* (NY, US, VEN); along Río Karuai, NW of Kavanayen, 1,220 m, 30 Nov. 1944, *Steyermark 60823* (F, US, VEN); Sierra Ichun, Salto Maria Espuma del Río Ichun, 28 Dec. 1961, *Steyermark 90340* (F, NY, US, VEN); Sierra Pakaraima, 4–5 May 1973, *Steyermark 107266* (F, MO, U, VEN, US); cumbre de Cerro Guaiquinima, Salto del Río Szczerbanari, 750 m, 20–25 Jan. 1977, *Steyermark et al. 113150* (MO, NY, US, VEN); Cerro Marutani, 1,200 m, 11 Jan. 1981, *Steyermark 123881* (NY, VDN). Two *Kral* numbers from the Gran Sabana collected with *A. Gonzalez* in 1983 and with distributions to F, MO, NY, US, VDB are *Kral 70389* and *70610*; two more from the Gran Sabana in Dec. 1984 and awaiting full distribution are *72157* and *72192*.

This variety is one of the weediest of the annual *Xyris* species, coming in solidly in disturbed sandy moist savanna and sandy washes in the Guayana Highland. It can, in dense populations, range from dwarf plants a few centimeters tall to quite tall. Generally, well-spaced individuals on moist, peaty sites range between one and two decimeters in height. The pale yellow flowers open in the morning.

42B. Xyris uleana var. **angustifolia** Lanj., Kew Bull. 1939: 562. 1939. TYPE: Guyana: Kaieteur Savanna, in damp sand, ca. 1,200 ft., petals deep orange-yellow, 7 Sep. 1937, *N. Y. Sandwith 1421* (holotype, K; isotypes, NY, U).

X. connectens Malme, Ark. Bot. 19(13): 2. 1925. TYPE: Brazil. Pará: cerca Belem, *Ducke* (type at BM).

The plants usually more slender and lower than in the type variety, the leaf blades narrower, mostly 0.5–1 mm wide, the edges smooth or papillate, the lower bracts typically shorter than the larger fertile ones, all bracts with papillate-tuberculate dorsal areas as in the type variety but bracts themselves with acute tips and entire to lacerate, eciliate margins. Lateral sepals mostly free.

Distribution. Low- to medium-elevation savanna, from Territorio Federal Amazonas in Venezuela west through southern Estado Bolívar to Guyana, infrequent. Also in Amazonas and Pará, Brazil.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: Rincones de Chacorro, 30 km N of Puerto Ayacucho, savanna, 80 m, 5 Nov. 1980, *Maas & Huber 5127* (US). BOLÍVAR: seeps among sandstone boulders by Ven. 10, ca. 800 m, N of Río Yuruani Ferry at Puente Kumerepa, 12 Dec. 1985, *Kral 72193* (MYF, VDB, VEN, and to be distributed). GUYANA: Pakaraima Mt., Mt. Aymatoi, 1,150 m, 15 Oct. 1981, *Maas et al. 5687* (U); Kaietuk Savanna, 1,100 ft., Aug. 20, 1933, *Tutin 497* (K).

This low variety of *X. uleana* is often in mixed populations with the type variety but is less frequent and could be mistaken for smaller, shorter-spiked *X. paraensis* var. *paraensis*. However, the dorsal areas of the latter are not strongly papillose-tuberculate. The terete scapes have sharp but low costae, very unlike the usually winged costae of the type variety.

43. Xyris calderonii Kral, Lyman B. Smith & Wanderley, sp. nov. TYPE: Brazil. Amazonas: Transamazon Highway, 9 km W of Rio dos Pombos, ca. 1.5 km E of Igarapé dos Pombos, and ca. 64 km E of the Aripuanã. Common in white sand campina, flowers yellow, 18 June 1979, *Cleofé E. Calderón, O. P. Monteiro & J. Guedes 2549* (holotype, INPA; isotypes, US, VDB). Figure 43.

Planta humilis, annua, praeter inflorescentiam glabra. Radices filiformes. Folia linearia, solum basalia, 3–7 cm longa, flabellate expansa, vulgo vaginis scaporum longiora. Laminae vaginis 2–4-plo longiores, 0.5–1 mm latae, planae, rectae, longitudine paucicostatae, a basi ad apicem compressae, porphyreae vel flavovirentae, apicibus abrupte contractis, incurvato-acutis, marginibus integris, non incrassatis; vaginae carinatae, porphyreae, pluricostatae, praeter costas scariosae, marginibus scariosis stramineis, in laminas gradatim convergentibus aut ad apicem ligulam scariosam curtam latam fascientibus, infime gradatim expansae, acies integrae. Vaginae scaporum laxae, plerumque apertae, rectae, carinatae, laminis aut similis laminis foliorum aut brevibus. Scapi subteretes, filiformes plus minusve spiraliter torti, 5–10 cm alti, 0.4–0.5 mm crassi, distaliter leviter multicostati, costis laevibus. Spicae subglobosae vel late ovoideae, 3–5 mm longae, pluriflorae, obtusae, involucratae. Bracteae steriles 2–4, subdecussatae, villosiciliatae; par infimum foliaceum, rigidum, spica 2–5-plo longiorum, lanceolatum vel oblongum, 2–3 mm longum, carinatum, areis dorsalibus linearibus, viridibus et laminis similis laminis foliorum sed triangulatis; par intimum ovatum, convexum, scariosum, acutum vel acuminatum, profunde villosiciliatum, areis dorsalibus valde papillosis, vulgo sine laminis. Bracteae fertiles late ovatae vel suborbiculatae, 2.5–3 mm longae, valde rotundato-convexae, villosiciliati, areis dorsalibus ovatis, valde granulato-papillosis. Sepala lateralia libera, oblonga vel ovata, 2–2.5 mm longa, valde inaequilatera; ala carinali lata, a basi ad medium integra, a medio distante ciliata, apicem versus lacerata. Laminae petalorum late obovatae, ca. 3 mm longae, luteolae, ad apicem late rotundatae et valde erosae. Staminodia bibrachiata, brachiis parce longipenicillatis. Antherae oblongae, sagittatae, ca. 0.5 mm longae; filamenta ca. 0.8–1 mm longa. Capsula matura late obovata, planoconvexa, ca. 1 mm longa, placenta basalia. Semina late ellipsoidea, ca. 0.3 mm longa, pallide brunneola, plus minusve reticulata.

Low annual, smooth except for the inflorescence. Roots filiform. Leaves linear, strictly basal, 3–7 mm long, spreading flabellately, commonly longer than the scape sheaths. Leaf blades 2–4 times longer than sheaths, 0.5–1 mm wide, flat, straight, longitudinally few-costate, flattened from base to apex, brown to yellow-green, the tips abruptly narrowed, incurved-acute, the margins entire, not thickened; sheaths carinate, brown, many-ribbed, scarious except for the ribs, with the thin edges stramineous, gradually narrowing into the blades or apically producing a short, scarious, broad ligule, gradually dilating toward base, the edges entire. Sheaths of scape lax, mostly open, straight, carinate, with blades similar to those of foliage leaves or shorter. Scapes subterete, filiform, ± spirally twisted, 5–10 cm high, 0.4–0.5 mm thick, distally with many low, smooth costae. Spikes subglobose to broadly ovoid, 3–5 mm long, several-flowered, obtuse, involucrate. Sterile bracts 2–4, subdecussate, villous-ciliate, the lowermost pair foliaceous, rigid, 2–5 times longer than the spike, lanceolate to oblong, 2–3 mm long, carinate, the dorsal areas linear, green, with blades similar to those of foliage leaves but triangulate; inner pair (if present) ovate, convex, scarious, acute, very villous-ciliate, the dorsal areas strongly papillate, without blades. Fertile bracts broadly ovate to suborbicular, 2.5–3 mm long, strongly rounded-convex, villous-ciliate, the dorsal areas ovate, strongly granular-papillose. Lateral sepals free, oblong to ovate, 2–2.5 mm long, very inequilateral, with keel broad, distantly ciliate from base to middle, lacerate toward apex. Petal blades broadly obovate, ca. 3 mm long, yellowish, broadly rounded and strongly erose at apex. Staminodia bibrachiate, the branches sparsely long-penicillate. Anthers oblong, sagittate, ca. 0.5 mm long; filaments ca. 0.8–1 mm long. Mature capsule broadly obovoid, plano-convex, ca. 1 mm long, the placenta basal. Seed broadly ellipsoid, ca. 0.3 mm long, pale brown, ± reticulate.

There is no question that the affinities of this little plant are with *X. uleana* Malme; in the production of narrow leaf blades it is most similar to var. *angustifolia* Lanj., which also sometimes produces long-tipped basal bracts. However, the lateral sepals are smaller with a somewhat different keel configuration, and the dorsal areas are consistently long-excurrent to produce acicular blades several times longer than the subtended spike. The scapes are uniformly terete.

44. Xyris esmeraldae Steyerm., Fieldiana, Bot. 28(1): 109, fig. 16c. 1951. TYPE: Venezuela. T. F. Amazonas: Esmeralda Savanna, 200 m, Cerro Duida, 22 Aug. 1944, *J. Steyermark 57821* (holotype, F; isotype, NY). Figure 44A (44B—see synonym).

Xyris rugulosa Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 29, fig. 13A–E. 1963. TYPE: Venezuela. T. F. Amazonas: Cerro Sipapo (Paraque), frequent along banks of small shaded stream savanna about pool, Caño Negro, 1,300 m, 15 Dec.

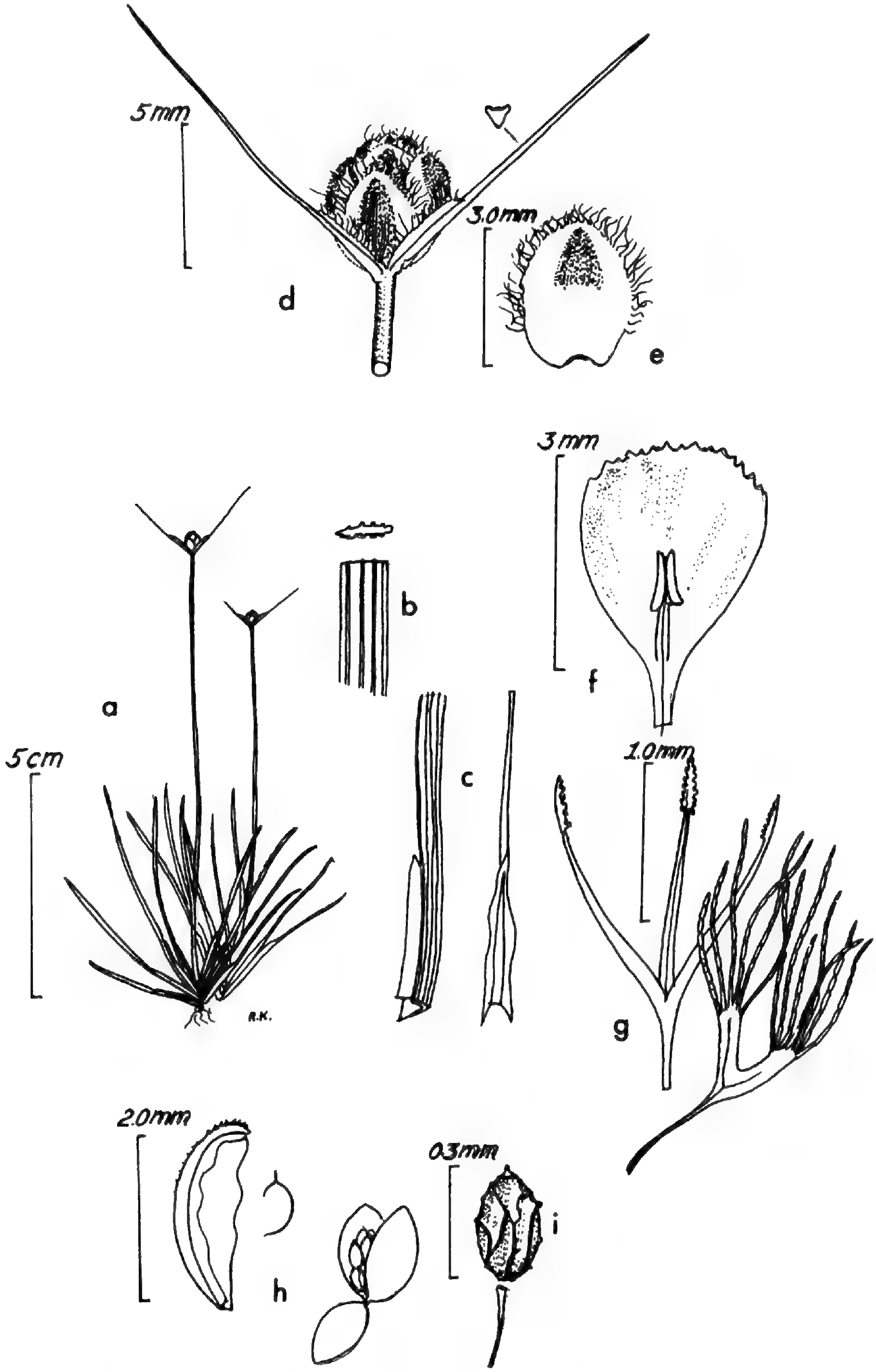


FIGURE 43. Xyris calderonii (Calderon et al. 2549).—*a. Habit sketch.—b. Leaf at midblade.—c. Leaf blade-sheath junction, side (left) and ventral (right) views.—d. Mature spike.—e. Fertile bract.—f. Petal blade and stamen.—g. Stylar apex, staminode.—h. Lateral sepal, capsule.—i. Seed.*

1948, *B. Maguire & L. Politi 27699* (holotype, NY; isotypes, US, VEN). Figure 44B.

Low, slender, cespitose, smooth to papillose-rugulose annual 0.5–3 dm high, the stems contracted, the roots filiform. Leaves ascending or spreading flabellately, 1–5 cm long, often absent by full anthesis or represented only by scalelike sheaths; sheaths of longer foliage leaves less than ½ as long as blades, pale lustrous brown, tapering gradually from base to blade, there with a narrowly triangular, erect ligule to 2 mm long, at this level broader than blade is wide, the blades linear, flat or somewhat twisted, much compressed, ca. 1 mm wide, green or maroon, gradually narrowing toward apex, to a narrowly acute or acuminate tip, this dorsally scabrid, the margins mostly pale-incrassate, scaberulous or smooth, the surfaces strongly few-ribbed, smooth, rugose or rugulose. Scape sheaths shorter than most leaves, the base tubular, ribbed, keeled, the apex short-bladed or with a cusplike blade. Scapes much twisted, straight or flexuous, flattened distally, ca. 0.8–1 mm wide, ancipital with smooth or tuberculate-scabrid costae making edges, the surfaces ribless or with 1–2 ribs per side, smooth or rugulose-scabrid. Spikes elliptic-lanceolate, 3.5–5 mm long, acute, uniflorous, subtended by a narrow castaneous collar, of few, strongly convoluted, erect, reddish brown, decussate bracts with distinct dorsal areas; sterile bracts 2 pair, shorter than the fertile bracts, the lowest pair ovate to lance-triangular, acute, strongly keeled, the inner pair ovate-triangular, slightly keeled, distally with a strong, narrow midnerve, acute or narrowly rounded, entire or lacerate; fertile bract solitary, narrowly to broadly obovate, much inrolled, ca. 4–6 mm long, broadly acute or narrowly rounded, with broad dorsal area and strong midnerve. Lateral sepals ca. ⅓ connate, 4–4.5 mm long, the lobes oblong, subequilateral but excentrically folded, pale red-brown, acute, the narrow firm keel scabrociliate at least from middle to apex. Petal blades obovate or elliptic-oblong, 2–3 mm long, yellow, the rounded apex lacerate-dentate. Staminodes either not evident or with obreniform, beardless blades. Anthers oblong, ca. 1 mm long, deeply bifid and sagittate on filaments ca. 1 mm long. Capsules obovoid, 2–3 mm long, the valves eseptate, the placentation basal. Seeds several on long funiculi, ellipsoid, 0.7–1 mm long, including a short, silvery apiculus (outer integument), the body deep amber, finely longitudinally and spirally anastomosing-ribbed.

Distribution. Low (mostly under 500 m) savanna, southeastern Colombia eastward along the upper Río Orinoco and the Río Negro and tributaries in Venezuela.

Additional specimens examined. COLOMBIA. AMAZONAS: Río Caquetá, Araracuara, sabana de la Angostura, 400 m, 21 Dec. 1951, *H. García-Barriga & Schultes 14165* (NY); Araracuara, Río Caquetá, 5 Sep. 1959, *Maguire et al. 44131* (NY); Río Miritiparaná, 8 May 1952, *Schultes & Cabrera 16410* (GH, NY). VAUPÉS: Río Vaupés, Caño Pacú, 6 Mar. 1944, *Schultes 5830* (NY); Río Kananarí, Cerro Isibukuri, 29 Oct. 1951, *Schultes & Cabrera 14536* (GH, VDB); Río Piraparaná, Caño Pacá, 19 Sep. 1972, *Schultes & Cabrera 17567* (GH, VDB); Río Kananarí, Cerro Isibukuri, 28 Oct. 1951, *Schultes & Cabrera 14445* (GH); Río Piraparaná, Raudal Na-hoo-gaw-he, 30 Aug. 1952, *Schultes & Cabrera 17110* (GH); San Filipes & vic., ca. 600 ft., 25 Oct. 1952, *Schultes et al. 18026* (GH); Río Parana Pichuna, ca. 700 ft., June 1953, *Schultes & Cabrera 19933* (GH). VENEZUELA. T. F. AMAZONAS: Río Negro, base Cerro Cucuy, 2 Mar. 1944, *Baldwin 3240* (VEN); middle part of Caño Yagua at Cucurital de Yagua, 8 May 1979, *Davidse et al. 17376* (MO, VDB); Cerro Duida, 1,000 m, Jan.–Feb. 1969, *Farinas et al. 436* (NY, VEN); S de la Sierra de Untuyan en las cabeceras del Río Mavacá, 550 m, *Guánchez 805* (TFAV, VDB); "Cerro la Trampa" al norte del medio Río Autana, 12 Nov. 1984, *Guánchez & Melgueiro 3531* (TFAV, VDB); IVIC Study area 4 km E of San Carlos de Río Negro, 120 m, 12 Nov. 1980, *R. Liesner 3381* (MO, NY, VDB); 10 km NE of San Carlos, white sand area, 7 Apr. 1979, *Liesner 6286* (MO); Cerro de La Neblina, Puerto Chimo Camp on Río Mawarinuma, 5 km E of Neblina Base Camp, 150 m, 13 Feb. 1984, *Liesner 15884*; Cerro Sipapo, savanna vic. Base Camp, 30 Dec. 1948, *Maguire & Politi 28034* (NY, US); Cerro Sipapo, banks along lower Caño Negro, 25 Dec. 1948, *Maguire & Politi 27916* (NY); Río Guainía, Yavita–Pimichín trail, near Pimichín, 22 Nov. 1953, *Maguire et al. 36326* (GH, NY, US); Cerro Paraque, 1,500 m, Feb. 1946, *Phelps 60* (VEN); 1 km al este de Maroa, 125 m, 20 Apr. 1970, *Steyermark & Bunting 102815* (U, US, VDB, VEN).

It becomes necessary to consider this the same as *X. rugulosa* Maguire & Lyman B. Smith, which does not differ in any essential character but only in the tendency in the latter toward narrower bract tips and more leafiness (cf. Fig. 44A, B). The rugulous epidermal feature supposed to be critical for *X. rugulosa* appears also on leaves of *X. esmeraldae.* Some of the trouble in past interpretation must come from the fact that *X. esmeraldae* proper tends to lose most of its larger foliage leaves as the plants approach seeding. However, when one finds these leaves, they are remarkably the same as those of *X. rugulosa.*

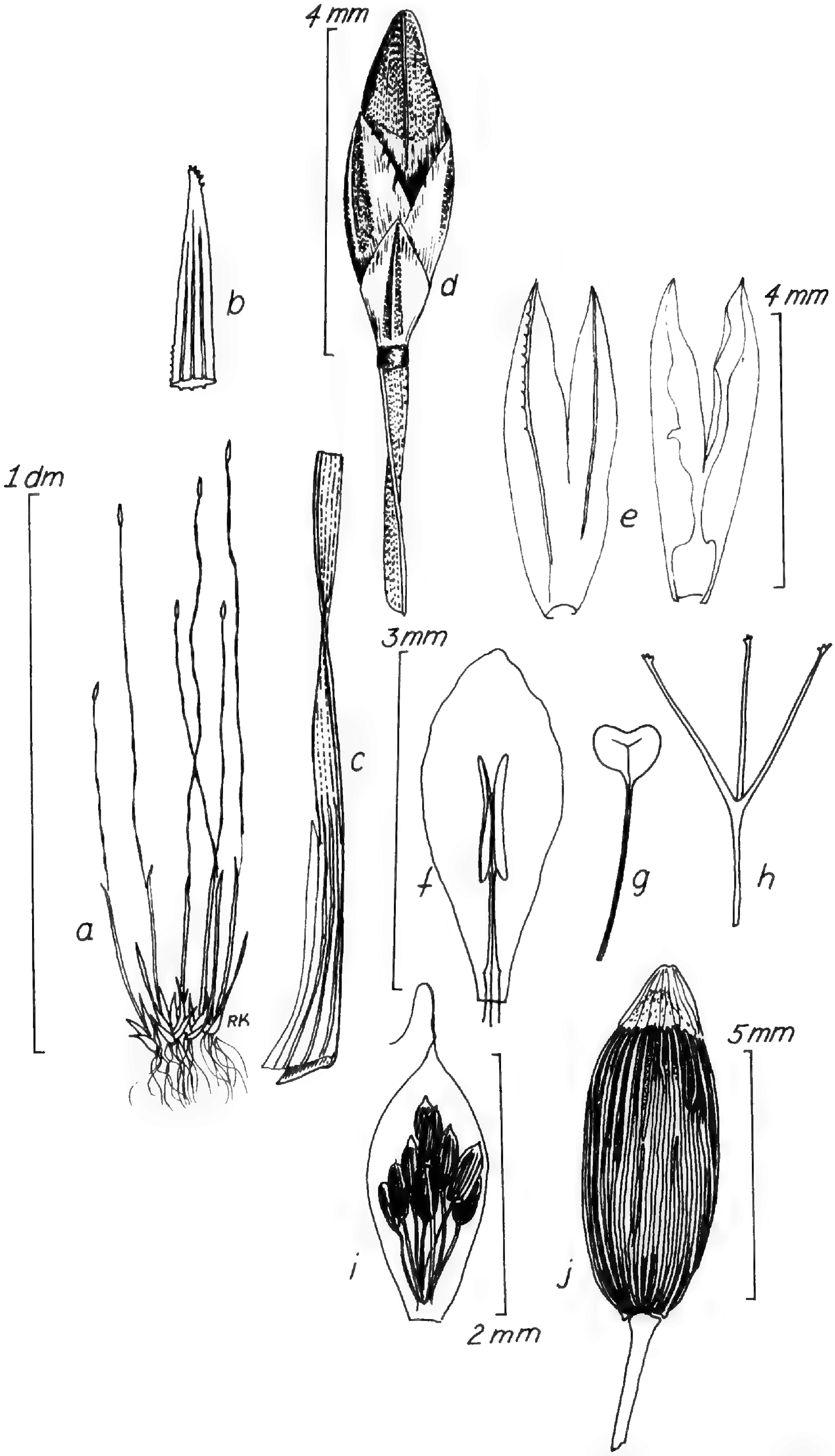


FIGURE 44A. Xyris esmeraldae (Liesner 7035).—*a. Habit sketch.—b. Leaf tip.—c. Leaf, midblade to base.—d. Spike.—e. Lateral sepals, two views.—f. Petal and stamen.—g. Staminode.—h. Stylar apex.—i. Capsule showing placentation.—j. Seed.*

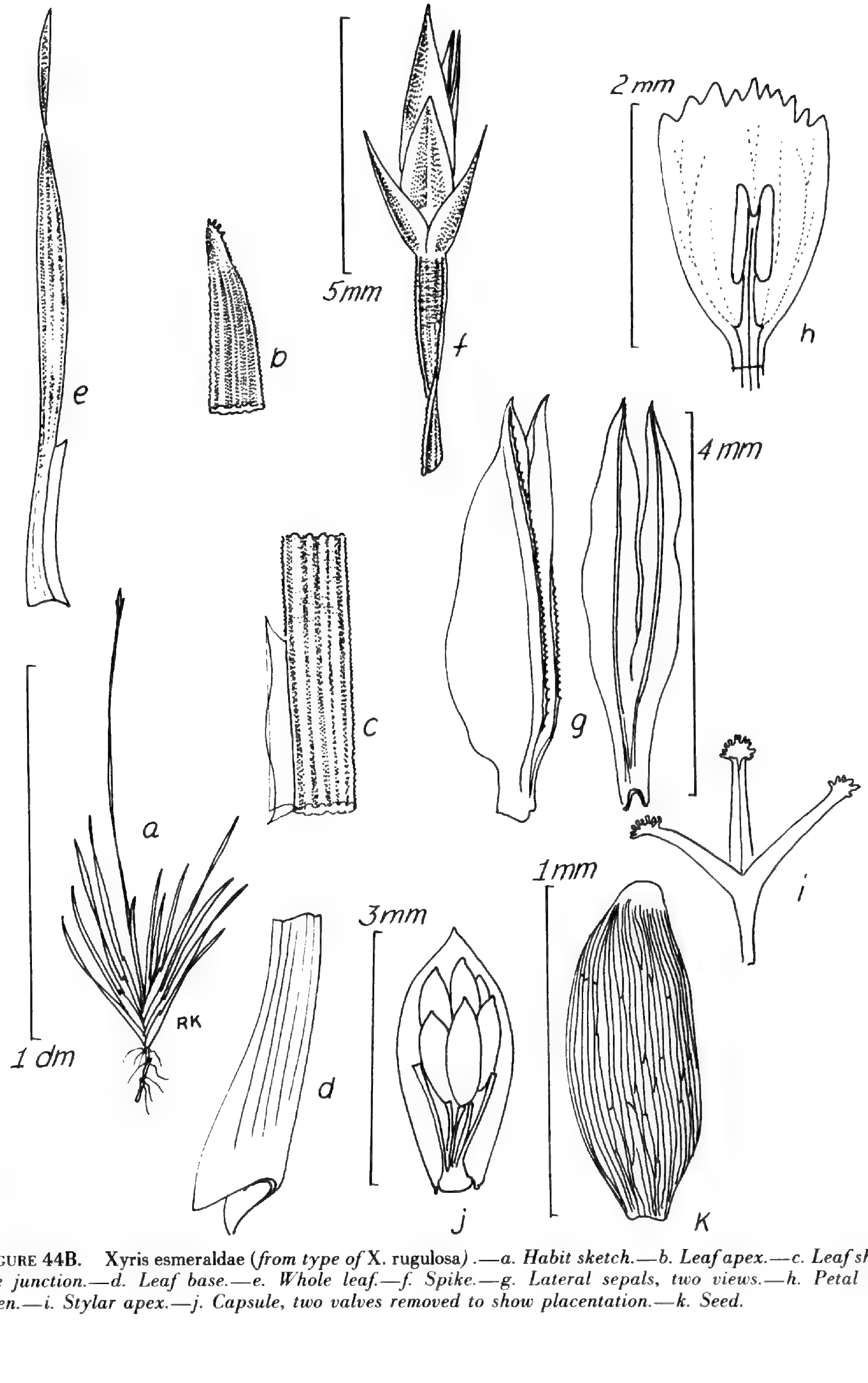


FIGURE 44B. Xyris esmeraldae (*from type of* X. rugulosa). —*a. Habit sketch.*—*b. Leaf apex.*—*c. Leaf sheath–blade junction.*—*d. Leaf base.*—*e. Whole leaf.*—*f. Spike.*—*g. Lateral sepals, two views.*—*h. Petal blade, stamen.*—*i. Stylar apex.*—*j. Capsule, two valves removed to show placentation.*—*k. Seed.*

45. Xyris subuniflora Malme, Rec. Trav. Bot. Neerl. 9: 129. 1912. TYPE: Dutch Guayana: "In arenosis humidis, Suriname," *Splitgerber 990* (lectotype, L; isolectotype, U). Figure 45.

Xyris capillaris Steyerm., Fieldiana, Bot. 28: 107. 1951. TYPE: Venezuela. T. F. Amazonas: between Esmeralda Savanna and southeastern base of Cerro Duida, 200 m, 22 Aug. 1944, *J. A. Steyermark 57835* (holotype, F; isotypes, GH, NY, VEN).

Densely cespitose, low and delicate, smooth, annual or short-lived perennial 3–10 cm high, the stems contracted. Leaves erect or spreading flabellately, 1–7 cm long; sheaths eciliate, soft, ½ as long as blades or less, the bases tan or pink, keeled, tapering evenly into blades or with a short, erect, triangular ligule less than 1 mm long; blades filiform but flat, 0.3–0.5 mm wide, tapering slightly above middle, then abruptly acute-apiculate or incurved-acute, the margins entire, the surfaces very finely nerved, maroon with olive tints. Scape sheaths ca. as long as leaves, twisted, tubular proximally and multicostate, distally open with a strong flat blade as in leaves. Scapes filiform, straight or flexuous, twisted, ca. 0.3 mm thick, distally terete, ecostate, finely striate, olivaceous to maroon. Spikes narrowly ellipsoid or linear-ellipsoid, drying lance-ovoid, 4–5 mm long, few-bracted, uniflorous; bracts with distinct lanceolate dorsal areas, the sterile bracts 4, 2.5–3 mm long, lanceolate, navicular, acute or narrowed-retuse; fertile bracts oblong to ovate, conduplicately folded around floret, ca. 4 mm long. Lateral sepals ca. ½ connate, ca. 3–3.5 mm long, the narrowly triangular, erect lobes inequilateral, acute with very low smooth keels similar to dorsal areas of bracts but narrower. Petal blades broadly obovate, ca. 3 mm long, yellow, the broadly rounded apex denticulate-lacerate. Staminodia bibrachiate, arising from just below sinus between petal blades, the branches short-penicillate-pubescent. Anthers oblong, ca. 0.8 mm long, deeply bifid and sagittate, on filaments ca. 0.5 mm long. Capsule broadly ellipsoid, brown, ca. 1.5 mm long, the placentation basal. Seeds few, broadly ellipsoid, 0.5–0.6 mm long, apiculate, dark brown and opaque, rather coarsely longitudinally ribbed and cross-ribbed.

Distribution. Low-elevation savanna, locally abundant, southeastern Colombia (Vaupés) eastward into Surinam and in contiguous Pará, Brazil.

Additional specimens examined. COLOMBIA. VAUPÉS: Caño del Caribe and vic., 850–900 ft., 2 Nov. 1952, *Schultes, Baker & Cabrera 18276-A* (US). GUYANA: Kaieteur Savanna, ca. 1,200 ft., 5 Sep. 1937, *Sandwith 1373* (K, U). SURINAM: Jodensavanne (Fluv. Suriname), 16 June 1957, *Heyligers 347, 781* (U); Zanderij savanna, Jansma 1 (U); via secta ab Moengo tapoe ad Grote Zwiebelzwamp, savanna near km 10.9, 8 Oct. 1948, *Lanjouw & Lindeman 720* (U); ibidem, ridge E of camp, 14.9 km, 20 Oct. 1948, *Lanjouw & Lindeman 128a* (U); Bronniveau Brinkheuvel, in kleine polletjes, Natur-reservaat Brinkheuvel, 11 Oct. 1967, *Teunissen & Wildschut LBB 11910* (U). VENEZUELA. T. F. AMAZONAS: entre Yavita y Maroa, ca. 204 km hacia Maroa (al sur) desde el empalme con la carretera Yavita–Pimichín, 125–140 m, 6–19 July 1969, *Bunting et al. 3925* (NY, U, VDB); S bank of middle part of Caño Caname, 30 Apr.–1 May 1979, *Davidse et al. 16928* (MO, VDB); km 11 de la carretera San Carlos–Solana, 120 m, 16 Sep. 1980, *Huber et al. 5666* (US); ca. 20 km al SW de Mavaca, Serranía del Vinilla, 760 m, *Huber 6164* (US); sabana en la margen derecha del bajo Río Pasimoni, 8 Feb. 1981, *Huber & Medina 5855* (VDB, VEN); 9 km NE San Carlos, 120 m, 26 Nov. 1977, *Liesner 3913* (MO, NY, VDB); ríos Pacimoni, Yatua, Casiquiare, 110 m, 28 Sep. 1957, *Maguire et al. 41629* (GH, NY, VEN); Triana Savanna, Cerro Pitón, *Maguire et al. 53595* (NY); Bruno (Guaibana), laja de roca ignea, 100 m, 9 Apr. 1970, *Steyermark & Bunting 102490* (F, US, VDB, VEN); terreno arenoso en el camino de Yavita, 128 m, 26 Jan. 1942, *L. Williams 13996* (F, US, VEN). BOLÍVAR: savana bordering forest of Río Karuai, between Kavanayen and base of Ptari-tepui, 1,220 m, 18 Nov. 1944, *Steyermark 60603* (F, NY, VEN).

Perhaps the smallest, certainly the most slender, species of *Xyris*, very easily overlooked among the masses of other weedy *Xyris* of open savanna.

46. Xyris connosepala Lanj. & Lindeman, Bull. Torrey Bot. Club 75: 639. 1948. TYPE: Surinam: Tafelberg (Table Mountain). Frequent, wet sphagnum-filled cracks in rocks, Savanna No. IV, 16 Aug. 1944, *B. Maguire 24395a* (holotype, NY; isotype, U). Figure 46.

Delicate, cespitose, rosulate, smooth annual 1–2 dm high. Leaves spreading-ascend-

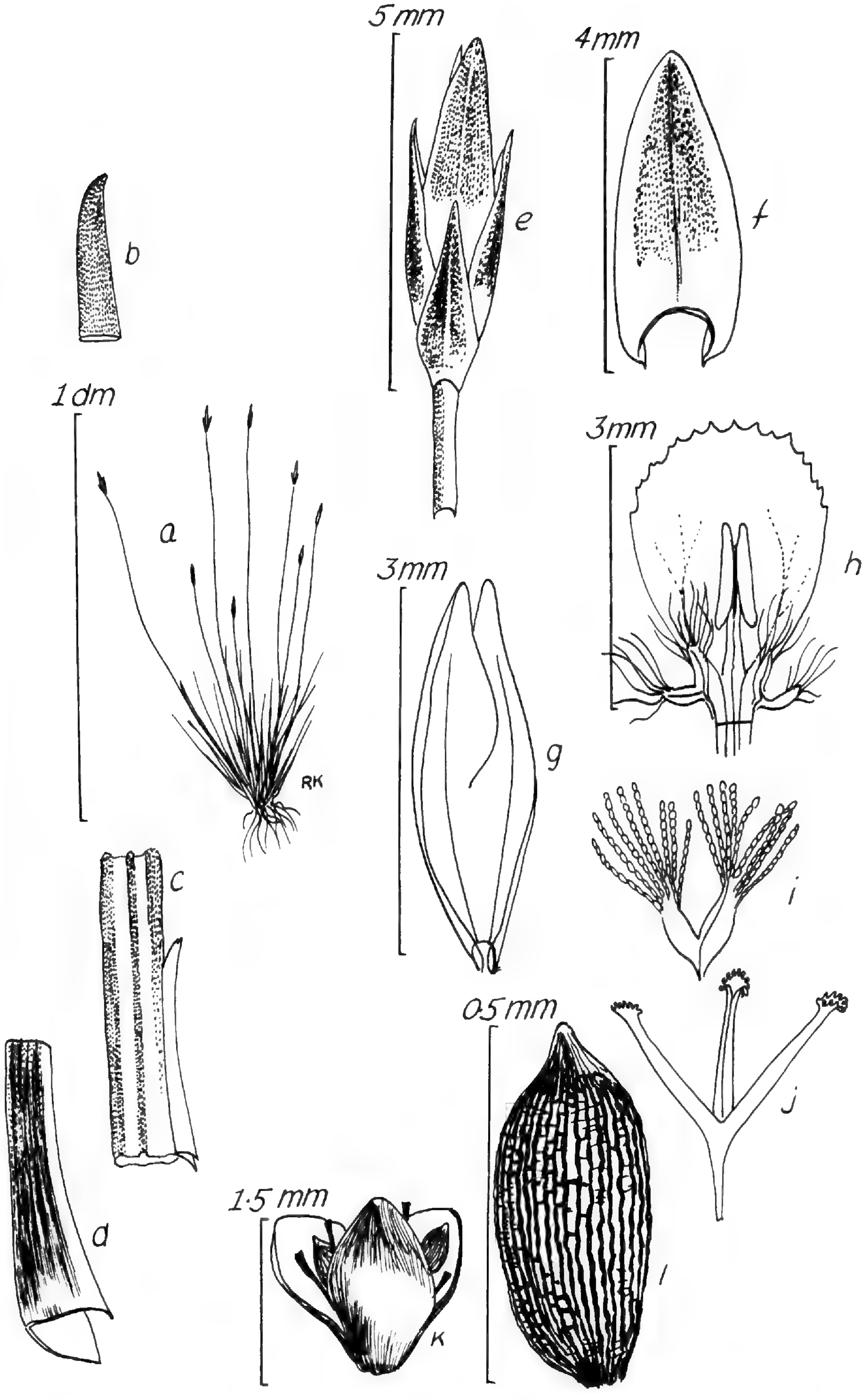


FIGURE 45. Xyris subuniflora (Davidse et al. 16928).—*a. Habit sketch.—b. Leaf apex.—c. Leaf blade-sheath junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepals (inside view).—h. Petal blade, corolla showing attachment of two staminodes.—i. Staminode.—j. Stylar apex.—k. Dehisced capsule.—l. Seed.*

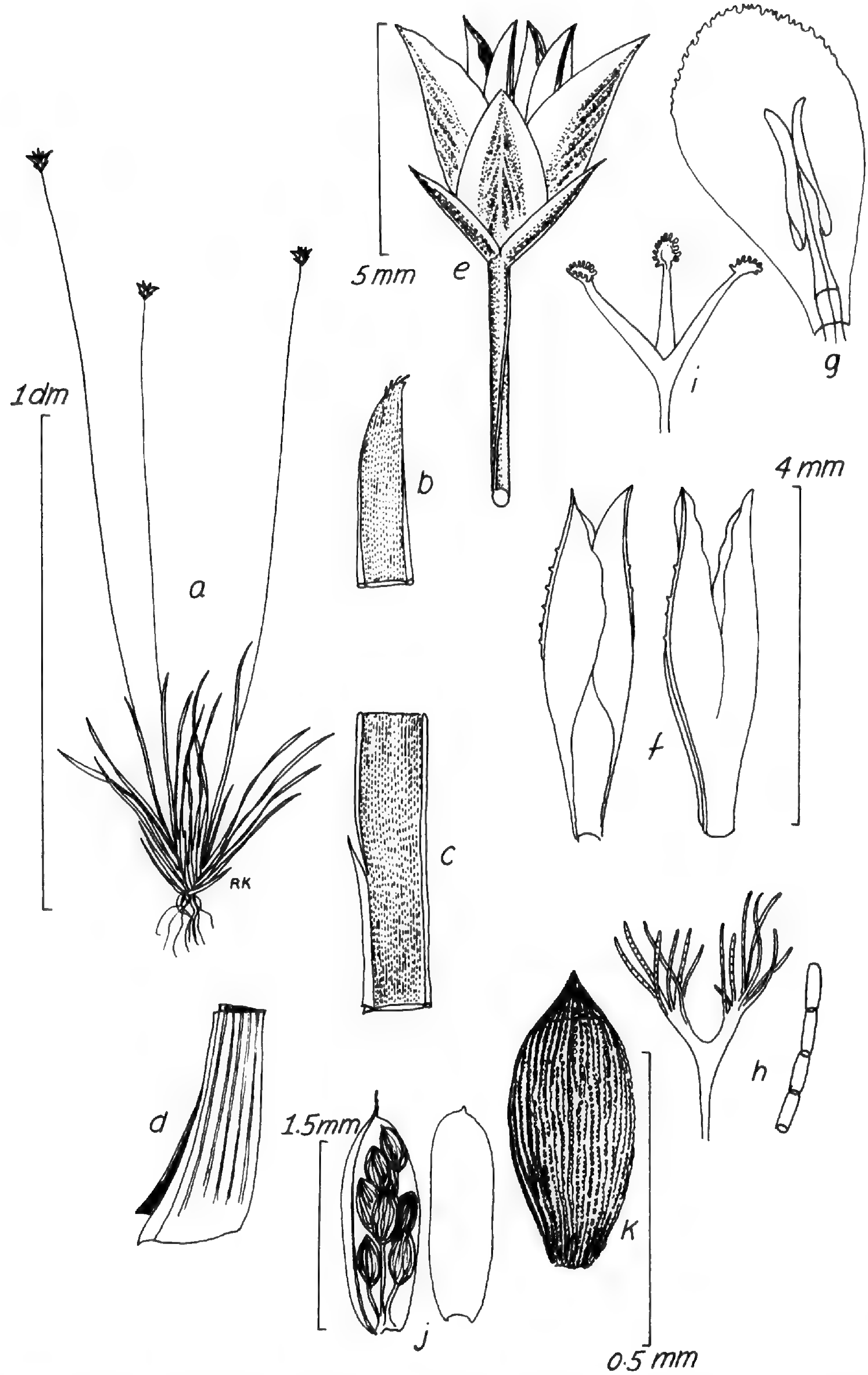


FIGURE 46. Xyris connosepala *(from the type).—a. Habit sketch.—b. Leaf tip.—c. Leaf at sheath-blade junction.—d. Leaf base.—e. Spike.—f. Lateral sepals, front and back view.—g. Petal, stamen.—h. Staminode.—i. Style apex.—j. Capsule, at left open to reveal placenta, at right a valve.—k. Seed.*

ing, 2–5 cm long; sheaths reddish brown, ca. ½ as long as blades, tapering evenly from keeled base to blade, or with an erect, narrowly triangular ligule to 0.5 mm long; blade flat, linear, often twisted, 0.8–1.2 mm wide, the apex incurved-acute, slightly thickened, papillose-tipped, the margin a narrow, pale, cartilaginous band, the surface green or maroon, finely nerved. Scape sheaths ca. the same length as leaves, proximally tubular, multicostate, opening toward middle, at apex bearing a blade similar to that of leaves. Scapes filiform, maroon, terete, with 1 low but strong costa. Spikes ellipsoid, in fruit broadly obconic, ca. 0.5 mm long, red-brown, of 2–3 flowers. Sterile bracts ca. 4, decussate, triangular-ovate, keeled, smaller than and grading into the fertile bracts, these 3–4 mm long, ovate, acute, entire, the backs ecarinate, with prominent lanceolate dorsal areas, excurved in fruit. Lateral sepals ca. 4 mm long, connate in basal ⅓, the lobes subequilateral, oblong, acute, pale brown, firm, keel in middle ⅓ papillate-tuberculate. Petal blades broadly obovate, 3 mm long, yellow, the narrowly rounded apex erose. Staminodia bibrachiate, the flattened branches with sparse penicillate hairs distally. Anthers oblong, ca. 1 mm long, deeply bifid apically, auriculate basally, on filaments ca. 0.5 mm long. Capsule ellipsoid, ca. 1.5 mm long, placentation central. Seeds numerous on elongate funicles, ellipsoid, ca. 0.5 mm long, biapiculate, deep brown, many-ribbed longitudinally.

Distribution. Rocky moist savanna, known only from the type locality (additional material, *Kramer & Hekking 2940*, U).

This species is so similar to the widespread *X. guianensis* as to make the observer doubt their distinctness. However, until more collections from the region show intermediacy in sepal connation, it is perhaps best to include it here as distinct.

47. Xyris guianensis Steudel, Syn. Pl. Glum. 2: 285. 1855. TYPE: Guayana: "Guiana anglica. *Schomburghk No. 1038*" (lectotype, K; isolectotypes, K, L). Figure 47.

Xyris gardneri Malme, Bih. Svensk. Vet. Akad. Handl. 26, Afd. 3(19); 8, pl. 1, f. 1. 1901 (lectotype, S; isolectotype, NY).

Xyris filiscapa Malme, Repert. Spec. Nov. Regni Veg. 3: 112. 1906. TYPE: Brazil. Amazonas: "In arenosis humidis, Manaos, Amazonas, Brasil," *Ule 6172* (lectotype, S; isolectotypes, L, NY, US).

Low, densely tufted, smooth annual 0.5–3 dm high, the stems mostly contracted, sometimes 1–2 cm long. Principal leaves spreading flabellately, often maroon or red-brown, 2.5–7 cm long; sheaths entire, glossy red-brown, ½ the blade length or less, keeled, the keel often papillate-ciliolate, incrassate, tapering gradually to blade, there often with a scarious, narrowly triangular, erect, ligule to 2 mm long or eligulate, the blades flattened, linear, often twisted, 0.5–1 mm wide, the apex narrowly acute to acuminate, the tip sometimes with a tuft of scabrosity, the margins narrow, incrassate, a pale or dark, smooth band, the surfaces finely multinerved and smooth, often with strong maroon tints. Scape sheaths longer than to slightly shorter than leaves, below terete and deep glossy red-brown, distally opening and keeled, producing a blade similar to leaf. Scapes filiform, twisted, sometimes flexuous, ca. 0.5 mm thick, distally terete or slightly compressed, ecostate to low-bicostate, the costae smooth. Spikes ellipsoid, drying obovate or turbinate, 4–7 mm long, pale red-brown with 2–3 (rarely a few more) florets; bracts few, decussate, with strong, green or maroon, lance-ovate dorsal areas bisected by a strong midnerve; sterile bracts mostly 4, the lower pair triangular, keeled, slightly shorter and narrower than the inner pair, the fertile pairs again slightly longer or equal to inner sterile pair, oblong, ca. 4.5–5 mm long, less keeled, more often convex-rounded or rounded-navicular, apically narrowly to broadly rounded, entire, scarious-bordered, the narrow tips often villosulous-ciliate. Lateral sepals pale red-brown, thin, subequilateral, oblanceolate, 4–5 mm long, acute, the narrow, firm keel papillate or ciliolate above middle, or the keel smooth.

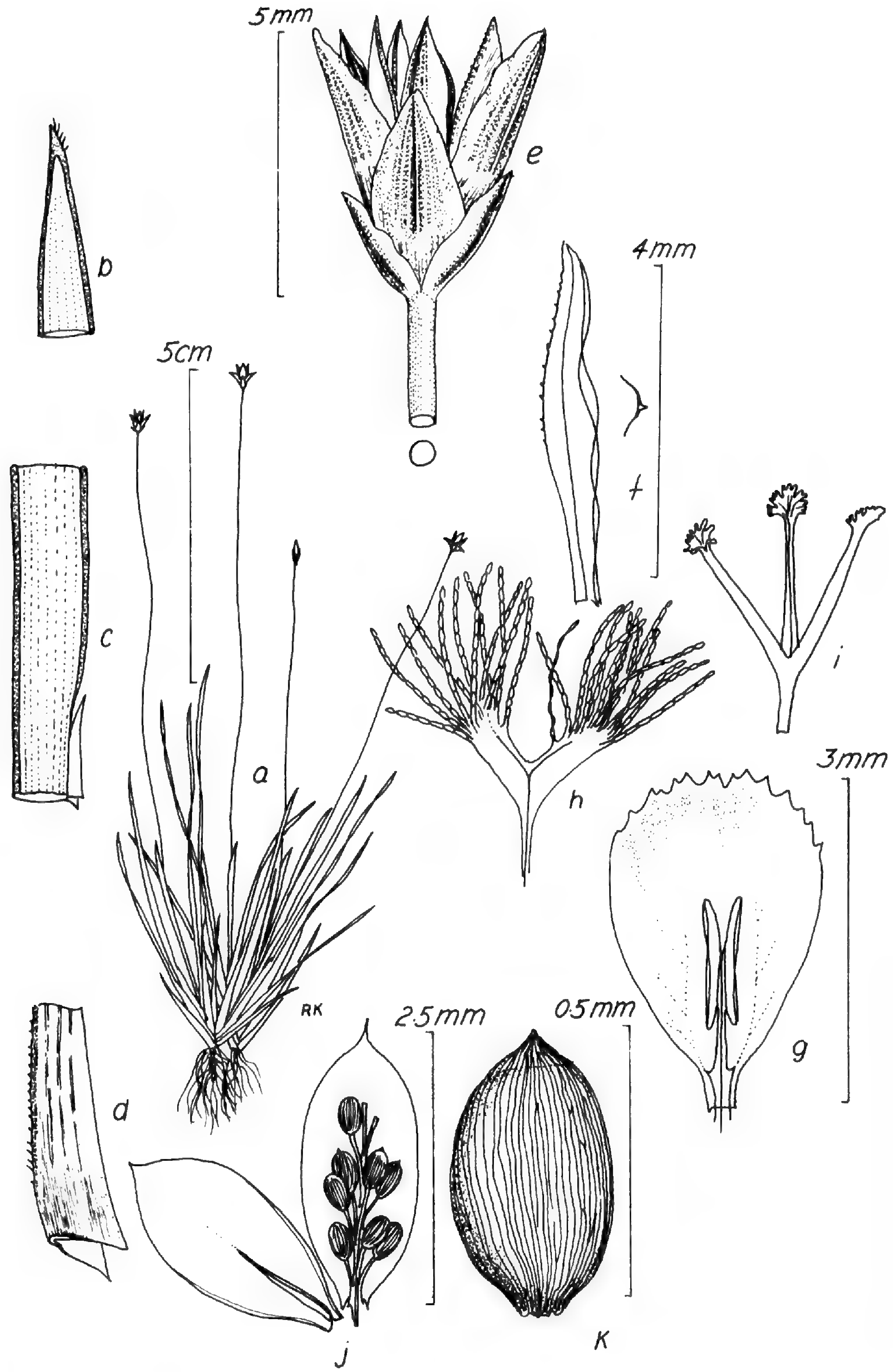


FIGURE 47. Xyris guianensis (Steyermark 75771).—*a. Habit sketch.—b. Leaf apex.—c. Leaf blade–sheath junction.—d. Leaf base.—e. Spike.—f. Lateral sepal.—g. Petal, stamen.—h. Staminode.—i. Stylar apex.—j. Capsule spread to show two of the three valves and placentation.—k. Seed.*

Petal blades broadly obovate, ca. 3 mm long, yellow, the broadly rounded apex lacerate-dentate. Staminodia bibrachiate, the broad, thin branches penicillate-ciliate. Anthers oblong, ca. 1 mm long, deeply bifid and sagittate, on filaments ca. 0.5 mm long. Capsule ellipsoid, ca. 2.5 mm long, the placentation basal-central, the valves with narrow septa below the middle. Seeds numerous, ovoid to ellipsoid, ca. 0.5 mm long, apiculate, dark amber, lustrous, finely ribbed longitudinally.

Distribution. Locally abundant in low- to medium-altitude savanna, southeastern Colombia eastward into Surinam and in adjacent Brazil south into Goiás.

Selected specimens examined. COLOMBIA. AMAZONAS–VAUPÉS: Río Apaporis, Raudal de Jirijirimo, ca. 900 ft., 12 Aug. 1951, *Schultes & Cabrera 13506* (GH). VAUPÉS: Cerro Yapoboda, Río Kuduyarí, ca. 450 m, 5–6 Oct. 1951, *Schultes & Cabrera 14379-B* (GH); Río Kubiyú, Cerro Kanenda ca. 15 mi. up from mouth, 800–900 ft., 10 Nov. 1952, *Schultes & Cabrera 18348* (F, MG, US); Río Vaupés, ca. 800 ft., 20 Apr. 1953, *Schultes & Cabrera s.n.* (GH); same locality, 20 Apr. 1953, *Schultes & Cabrera 19200* (U). GUYANA: Saesdike, Nov. 1973, *Cooper 208* (U); Kaieteur Plateau, 3 May 1944, *Fanshawe* (K, U). SURINAM: savanna inter Zanderij I et Hannover, opn. 125, 8 Oct. 1958, *J. & W. A. E. van Donselaar 363* (U); prope km 103, opn. 308, Gros-savanna, 30 Apr. 1959, *J. van Donselaar 694* (U); Boven Coesewijne, savanne in lijn 5–6 van exploratie 860, 16 May 1956, *Heyligers 14* (U); prope jodensavanne (Fluv. Suriname) tr. 30, p. 74, 30 Mar. 1976, *Heyligers 802* (U); savanne tussen Paranam en Phedra, 5 Feb. 1961, *Kramer & Hekking 2854* (U); Zanderij I, 4 Sep. 1948, *Lanjouw & Lindeman 161* (U); via secta ab Moengo tapoe ad Grote Zwiebelzwamp, ridge E of Camp 14.9, 20 Oct. 1948, *Lanjouw & Lindeman 928* (K, U); Tibiti Savanne, near km 3.2–4, line 2, 11 Jan. 1949, *Lanjouw & Lindeman 1791* (U); near Sapende, upper Commewijne River, 14 July 1953, *Lindeman 4232* (U); Iter secundum Surinamense, pr. Zanderij I, July–Sep. 1920, *Pulle 58* (U); Zanderij, 28 June 1970, *Teunissen LBB 12761* (U); "Suriname" C. Weigelt, from *Schweinitz Herb.* (PH); Nat. Res. "Brinckheuvel," 2 Sep. 1967, *Wilschut & Teunissen 11588* (U). VENEZUELA. T. F. AMAZONAS: alrededores de Yavita (Río Temi), 6–19 July 1969, *Bunting et al. 3714* (MY, NY, U, VDB); Santa Cruz margen del Río Atabapo, 4 Sep. 1960, *Foldats 3689* (NY, VEN); del raudal "Moriche" en el Río Guayapo, 10 May 1983, *Guánchez 3100* (TFAV, VDB); campina near abandoned Petrobras airstrip, mun. Borba, 7 July 1983, *Hill et al. 12975* (MO, NY, VDB); 5 km al N de la punta E del Cerro Yapacana, 28 June 1979, *Huber 3903* (US); 2 km al W de San Antonio del Orinoco, 20 July 1980, *Huber & Tillett 5423a* (VEN); a unos 15 km al N del Cerro Yapacana, 27 July 1980, *Huber & Tillett 5557* (MYF, VDB, VEN); granite outcrop 30 km below La Urgana, 100 m, 14–15 Mar. 1949, *Maguire 29084* (NY, US); Cerro Duida, Río Cunucunuma, along Caño Culebra, 1,000–1,100 m, 18 Nov. 1950, *Maguire et al. 29520* (NY, US); Santa Cruz, small village on Río Atabapo, 17–18 Nov. 1979, *Thomas & Rogers 2688* (NY); Cerro Duida immediatamente N de La Esmeralda, ca. 1,350 m, 29 Jan.–11 Feb. 1975, *Tillett et al. 751-93* (K, MYF, NY, US, VEN); Yavita, 128 m, 26 Jan. 1942, *L. Williams 13996* (F); near Yavita, 10 June 1959, *Wurdack & Adderley 42921* (GH, US, VEN). BOLÍVAR: Salto Camá, ca. 1,000 m, 4 Dec. 1973, *Davidse et al. 4864* (MO); 15 km al NW de Uiaren, *Huber et al. 7602* (MYF, VDB); Macizo del Chimantá, 2,000 m, 26–29 Jan. 1983, *Huber & Steyermark 6874* (VEN); 15–20 km S del empalme Luepa–Kavanayen, *Huber et al. 7252* (MYF); sector SSE altiplanicie suroriental del Acopan-tepui, 13–16 Feb. 1984, *Huber et al. 9012* (NY, VDB, VEN); Macizo del Guaiquinima, 1,350 m, 2 Apr. 1984, *Huber 9365* (MYF, VDB); La Escalera, ca. 7 km N of Pioneer Monument, ca. 1,200 m, 24 July 1983, *Kral 70316* (BM, F, K, L, MO, NY, SP, U, US, VDB, VEN, & others); above El Salto Yuruani, Río Yuruani, *Kral 70571* (MO, NY, US, VDB, VEN); 8 km N of San Rafael, Gran Sabana, 29 July 1983, *Kral 70575* (MO, NY, US, VDB, VEN); ca. 2 km N of Luepa, 20 Dec. 1984, *Kral 72206* (MYF, VDB, VEN); 17 km E of El Pauji, 30 Oct. 1985, *Liesner 19215* (MO, VDB, VEN); Cerro Guaiquinima, 1,600–1,700 m, 4 Jan. 1952, *Maguire 32983* (GH, K, NY, US); Salto Acarima, Río Uriman, 9 Jan. 1955, *Steyermark & Wurdack 44* (NY, US); Roraima, Glycon Swamp & vic., 1,830–1,920 m, 25 Sep. 1944, *Steyermark 58630* (F, NY); Cumbre de Auyan-tepui, sector oriental, al norte de la Misión de Camaratá, 2,140 m, 28 Feb 1978, *Steyermark et al. 116133* (MO, VDB, VEN).

Examination of the type of *X. filiscapa* Malme reveals that this differs in no significant way; that is, a broad range of specimens of *X. guianensis* shows sepal keels varying from entire to ciliolate and leaf blade margins ranging from strongly to weakly incrassate bordered. Elements of the former described as having ciliate sheaths are either ciliate-keeled *X. guianensis* or ciliate-leaf-sheathed *X. tenella* Kunth (*X. steyermarkii* Maguire & Lyman B. Smith). Therefore Colombian material identified as *X. filiscapa* turns out to be *X. guianensis.*

48. Xyris spathacea Lanj., Pulle, Rec. Trav. Bot. Neerl. 34: 484, fig. 4. 1937. TYPE: Surinam: "Sanderij I, Sept. 1914, Leg. *Essed*" (holotype, L; isotype, U). Figure 48A, B.

Xyris exserta Idrobo & Lyman B. Smith, Caldasia 6: 229, f. 21. 1954. TYPE: Colombia. Vaupés: sands in rapids, Río Guaimia, Caño del Caribe near San José, 850–900 ft., 2 Nov. 1953, *R. E. Schultes, R. E. D. Baker & Is. Cabrera 18276* (holotype, COL; isotypes, GH, US).

Xyris yapobodensis Idrobo & Lyman B. Smith, Caldasia 6: 231–232, fig. 22. 1954. TYPE: Colombia. Vaupés: "elevated sandstone savanna known in Kubeo as 'Yapoboda,' Alto Cuduyari, ca. 400 m. alt." 10 Dec. 1943, *P. H. Allen 3287* (holotype, MO).

Mostly low, slender, soft-based, solitary or cespitose, sometimes short-rhizomed ephemerals (5–)10–30 cm high. Leaves erect or spreading, dimorphic, those of dry stages or of innovations 0.5–5 cm long, with sheaths over ½ as long to longer than blades, the broad, scarious margins abruptly converging distally to the short, terete, 0.2–2.5 mm thick, conic-tipped, stiff, often maroon blades, also often producing apically a scarious, triangular or oblong ligule 2 mm long; "wet" or submersed-stage leaves lax, flaccid, filiform, mostly 1–2 dm long, the thin sheaths much less than ½ as long as blades, pale brown or stramineous, sparsely costate, tapering gradually from base to blade, there with a scarious, narrowly triangular ligule to 3 mm long, the blades terete or at intervals somewhat flattened, ca. 0.3 mm thick. Scape sheaths loosely tubular, much raised above the "dry"-season foliage, shorter than the lax "wet"-phase leaves, twisted and fluted, multicostate, distally open, carinate, producing a short, cusplike blade. Scapes soft, filiform, straight or slightly flexuous, slightly twisted, terete, striate, 0.3–1 mm thick, ecostate. Spikes elliptic to obovoid, 3–5 mm long, sometimes proliferous, acute, 2–4-flowered, of a few spirally arranged, scarious-bordered, loosely imbricate bracts with distinct, elliptic-ovate, brown to green, papillose dorsal areas over ½ as long as the bract body; sterile bracts 3–4, narrowly ovate, slightly shorter than the fertile bracts and grading into them, the two lowest keeled, navicular, subacute; fertile bracts broadly elliptic to obovate, ca. 3 mm long, subacute, the margins sometimes white-villosulous-ciliate at apex, the backs rounded-convex, ecarinate, the dorsal areas bisected by a narrow but distinct midnerve. Lateral sepals free, subequilateral or somewhat inequilateral, lanceolate to linear-oblanceolate, ca. 3–3.5 mm long, acute, the broad, low keel sparsely papillose or short-ciliate from middle to apex. Petal blades obovate, 3–3.5 mm long, yellow, the broadly rounded apex lacerate-dentate. Staminodia bibrachiate, the broad, flat branches copiously penicillate apically. Anthers oblong, ca. 1 mm long, bifid to below middle, sagittate, on filaments ca. 0.6–0.7 mm long. Capsule short-cylindric to narrowly obovate, ca. 2.5 mm long, the placentation basal, the valves without septa. Seeds numerous on long funicles, ellipsoid, 0.4–0.5 mm long, pale brown, translucent, with an irregular, coarse, partly anastomosing reticulum of a few strong, deep brown ribs.

Distribution. Locally abundant in low, riverine and intermittently inundated savannas, southeastern Colombia, southern Venezuela, eastward to Surinam and contiguous Amazonian Brazil (Amazonas, Mato Grosso, Pará).

Additional specimens examined. BRAZIL. AMAZONAS: basin of Rio Negro, Rio Uneiuxi, 5 km above mouth, 8 Nov. 1971, *Prance et al. 16183*, with nom. nud. "*X. prolifera* K. & S." (NY, US, VDB). MATO GROSSO: Serra do Roncador, Mun. Barra do Garcas, *G. & L. T. Eiten 8572* (MO, VDB). COLOMBIA. VAUPÉS: types of *X. exserta* and *X. yapobodensis* constituting all known records thus far. SURINAM: Zanderij, d.d. Aug. 1958, *van Donselaar et al., s.n.* (U); Zanderij I, savannah, Aug. 1914, *Essed 112a* (U); prope Jodensavanne, 12 June 1957, *Heyligers 818* (U); Zanderij I, savanna, 4 Sep. 1948, *Lanjouw & Lindeman 109* (U); same locality, 9 Sep. 1948, *Lanjouw & Lindeman 224* (submersed phase) (U); via secta ab Moengo tapoe ad Grote Zwiebelzwamp near km 6.6, 29 Sep. 1948, *Lanjouw & Lindeman 581* (U); Tibiti savanne near km 5.8, 15 Jan. 1949, *Lanjouw & Lindeman 1854a* (U); E of Kopie Peninica R, distr. Commewijne, 16 July 1953, *Lindeman 4375* (U); Zanderij in savanna pool half underwater, *Lindeman 4483* (C); Zanderij, almost dry pool along rd. to old radio station, 22 Nov. 1953, *Lindeman 5068* (NY, U, VDB); Sipaliwini savanna on Braz. frontier, 305 m, 4 km S of "4-Gebroeders" mts., *Oldenburger et al. 188* (U); Zanderij, pool edge, 25 Jan. 1942, *G. Stahel s.n.* (GH, U). VENEZUELA. T. F. AMAZONAS: "Fundo Galletti" Reserva forestal del Río Sipapo, 2 Feb. 1983, *Guánchez 2416* (TFAV, VDB); el medio Caño Yagua y al N del Cerro Cucuritu, 120 m, 18 Jan. 1979, *Huber 3122* (US); a la orilla derecha (W) del Alto Caño Yagua, 18 Feb. 1979, *Huber 3185* (NY); borde del alto Caño Yagua, 28 Feb. 1980, *Huber 4818* (US, VDB, VEN); Savanna II, fls. open in late morning, between Caño Cotua & W base Cerro Yapacana, 100 m, 10 Aug. 1983, *Kral & Huber 70703* (VDB, VEN, and to be distributed).

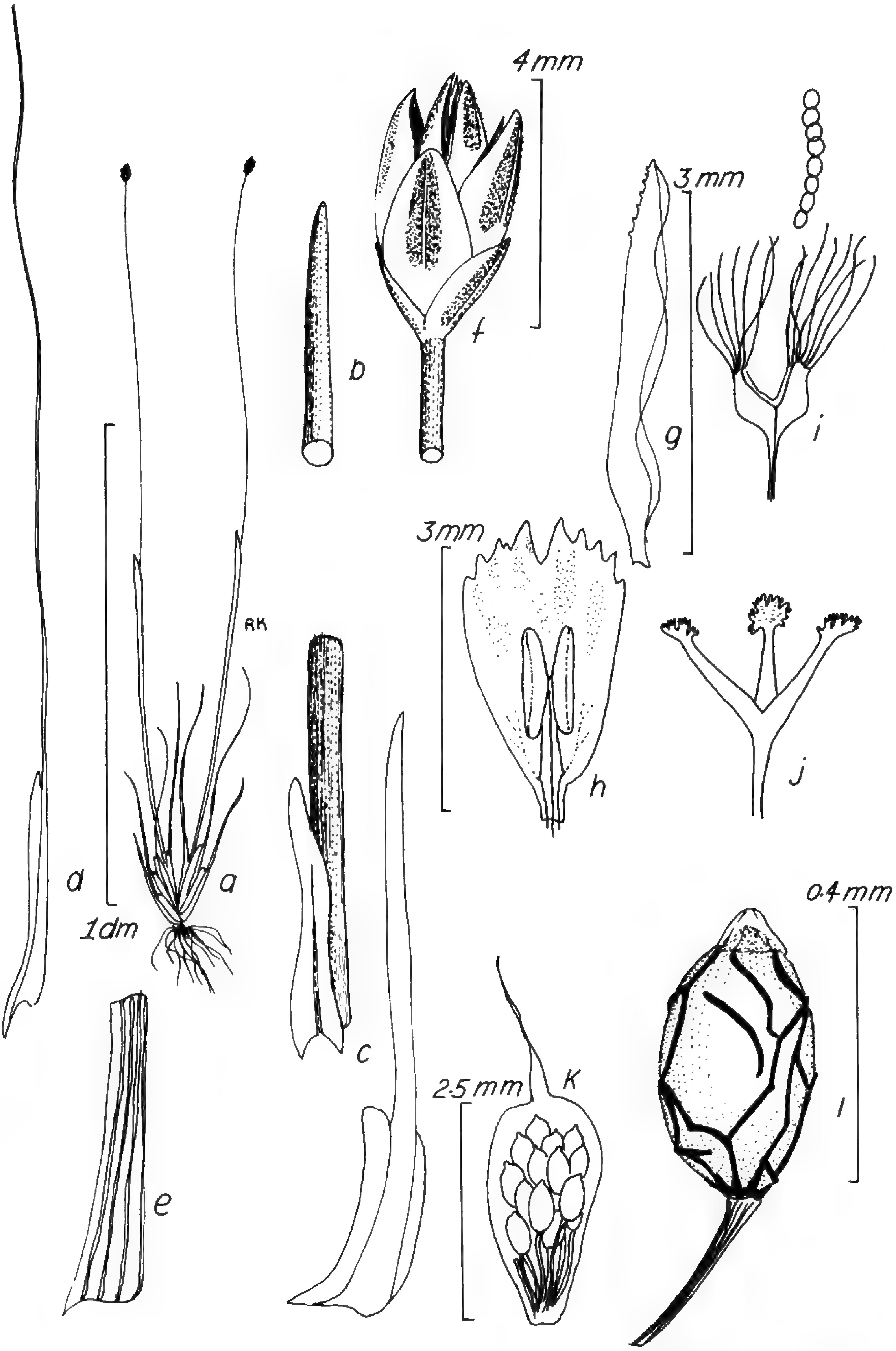


FIGURE 48A. Xyris spathacea *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Leaf blade–sheath junction.—d. Leaf.—e. Leaf base.—f. Spike.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode.—j. Stylar apex.—k. Capsule, median.—l. Seed.*

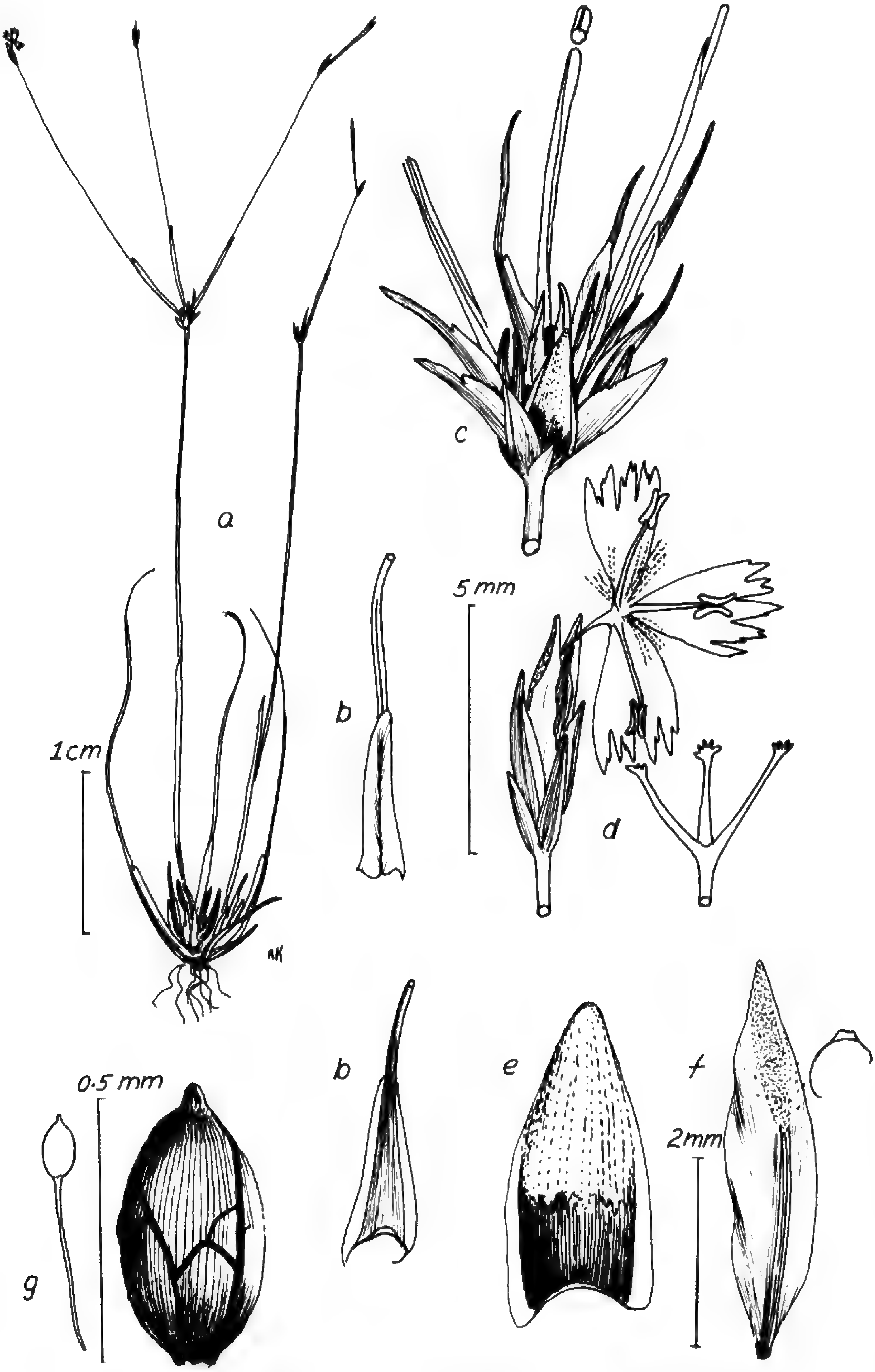


FIGURE 48B. Xyris spathacea (Huber 3185).—*a. Habit sketch.—b. Leaf sheath–blade junction.—c. Spike, showing exserted sepals, proliferous habit.—d. Spike, flower, stylar apex.—e. Fertile bract.—f. Lateral sepal.—g. Seed.*

This species has a low stature and very short leaf blades when developing on drying sites left by retreating waters. On the other hand, such plants produce much longer, laxer leaves when water rises to submerse them or their bases. I find no way to distinguish material of *X. spathacea* (Fig. 48A) from what is being called *X. exserta* (Fig. 48B) from the upper Amazon Basin of western Brazil and from the low savanna of Venezuela and Colombia. The only difference that is of any real interest is the tendency toward proliferative spikes in the latter, doubtlessly this trait induced environmentally. Some such Venezuelan and Brazilian extremes produce strong branches (scapes) that radiate umbel-like from the primary spike and terminate in floriferous spikes (*Huber 3185, Prance et al. 16183*). The type of *X. exserta* differs not at all from longer-leaved *X. spathacea* from Surinam.

49. Xyris cyperoides Gleason, Bull. Torrey Bot. Club 56: 17. 1929. TYPE: Guyana: Kaieteur Savanna, Potaro River, Sep.-Oct. 1881, *G. S. Jenman 1056* (holotype, K). Figure 49.

Xyris epicarae Kral & Smith, Phytologia 53: 436-437, fig. 6. 1983. TYPE: southeast escarpment of Cerro Pitón, 400 m, Cordillera Epicara, Río Chicanan, 5 Sep. 1962, *B. Maguire et al. 53651* (holotype, VEN; isotypes, NY, US, VDB).

Densely cespitose, the firm, pale reddish brown bases covered by persistent old leaf bases, the stems short to somewhat elongated, erect or ascending; roots slender. Principal leaves subdistichous, erect, twisted, flexuous, 0.8-1.8 dm long, longer than the scape sheaths (and often the scapes themselves); blades 5-6 times longer than sheaths, filiform, angulate to terete or somewhat compressed, 0.2-0.4 mm wide, longitudinally strongly nerved, shining, smooth with nerves reddish brown, wider than the greenish intervals; tips gradually narrowed, fimbriolate with clavate trichomes at apex; margins entire or minutely scabrid toward base; sheaths ecarinate, entire, strongly multicostate, smooth, gradually dilating to base, producing an acute, scarious ligule to 1.5 mm long at apex. Scape sheaths similar to leaves but shorter. Scapes filiform, 1.5-2 dm long, 0.3-0.4 mm wide, slightly twisted and flexuous, terete, finely 1-several-costate, olivaceous, smooth. Spikes 2-flowered, ellipsoid or in mature state obconic, ca. 4 mm long; bracts loosely imbricate, decussate, triangular-ovate, mostly 6, smooth, pale lustrous reddish brown, sparsely ciliate toward apex, marginally scarious; sterile bracts 4, unicostate, the lowest pair lanceolate, ca. 2.5 mm long, cymbiform, the inner pair triangular-ovate, ca. 3 mm long, ecarinate; fertile bracts ovate, ca. 3 mm long, strongly convex or navicular, at length excurvate; dorsal area olive, then ferrugineous, conspicuous, large, nearly as long as bract. Lateral sepals oblong, ca. 3.5 mm long, slightly curvate, subequilateral, obtuse and slightly emarginate to acute; keel narrow, entire. Petal blades obtriangular, ca. 3 mm long, yellow, subtruncate at apex, erose. Staminodia bibrachiate, the branches sparsely penicillate apically. Anthers oblong, 1.2 mm long, deeply bifid and sagittate, on filaments ca. 1 mm long. Capsule ellipsoid, ca. 2 mm long, the valves without septa, the placentation central. Seeds numerous, broadly ellipsoid, ca. 0.5 mm long, amber, finely longitudinally multiribbed.

Distribution. Sandy, medium- to high-elevation savanna, apparently rare, from southern Estado Bolívar, Venezuela southward into contiguous Amazonas, Brazil and eastward to Surinam.

Additional specimens examined. BRAZIL. AMAZONAS: Manaus-Caracarai Highway, forest at km 130, *Steward et al. P20348* (specimen bearing nomen nudum *X. sulcata* (US). GUYANA: Kaieteur Plateau, along Mure-mure Creek to ca. 3 mi. above mouth, ca. 1,400 ft., 15-16 Mar. 1962, *Cowan & Soderstrom 2179* (US). SURINAM: Kappel savanna, Tafelberg, 300 m, Natte struik-savanne in het Z. deel, 23 Feb. 1961, *Kramer & Hekking 3308* (U). VENEZUELA. BOLÍVAR: Cerro Pitón, 400 m, cordillera Epicara, Río Chicanan, 3 Sep. 1962, *Maguire & Steyermark 53563* (NY, VDB); same locality, 9-11 Sep. 1962, *Maguire et al. 53713* (NY, VDB); Cerro Guaiquinima, Salto del Río Szczerbanari, 1-2 km río arriba del Salto Szczerbanari, 750 m, 20-25 Jan. 1977, *Steyermark et al. 113116-A* (US, VDB, VEN); cumbre de Auyan-tepui, sector oriental, al norte de la Misión de

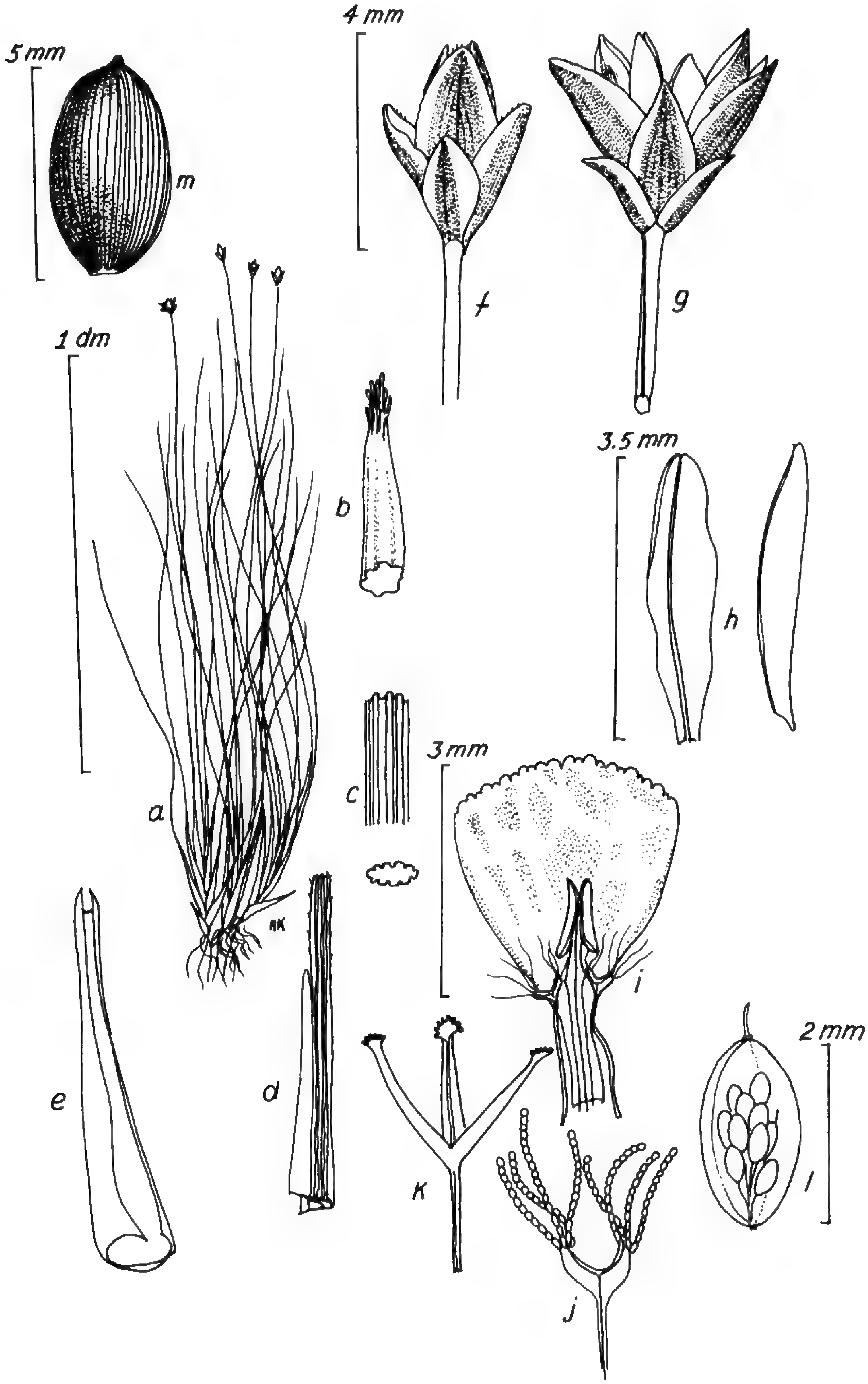


FIGURE 49. Xyris cyperoides *(from holotype of* X. epicarae*).—a. Habit sketch.—b. Leaf apex.—c. Leaf at midblade.—d. Leaf at blade-sheath junction.—e. Leaf base.—f. Spike at anthesis.—g. Spike past anthesis.—h. Lateral sepal.—i. Petal and stamen.—j. Staminode.—k. Stylar apex.—l. Capsule, one valve removed.—m. Seed.*

Camarata, 2,140 m, 28 Feb. 1978, *Steyermark et al. 116133* (MO, VDB, VEN).

In the spike this resembles *X. guianensis* Steud., but it is definitely longer-leaved in relation to scape, and the lateral sepal keels are entire.

50. Xyris toronoana Kral, sp. nov. TYPE: Venezuela. Bolívar: Distr. Piar, Macizo del Chimantá, sector centro-meridional. Amplio valle ubicado entre el borde nororiental del Torono-tepui y la sección central del Chimantá-tepui, drenando hacia el Sur, ca. 6°16′N, 62°09′W, ± 2,100 m, 11–15 Feb. 1985, *O. Huber, Teuvo Ahti & J. J. Pipoly 10,223* (holotype, VEN; isotypes, K, MYF, NY, US, VDB). Figure 50.

Herba humilis, perennis, glabris, caespitosa, rhizomate crassa, brevi, subverticali. Radices fibrosa. Folia linearis, (2–)4–7 cm longa, erecta vel leviter expansa, vaginis scaporum parum longiora. Laminae foliorum principalium compressae, planae vel leviter tortae, 0.9–1.2 mm latae, vaginis ca. 2-plo longiores, longitudine paucinervosae, atrovinosae; apices gradatim contracti, incurvato-acuti, leviter incrassati, ad marginem incrassati, papillosi; margines leviter incrassati, minute ciliati vel scabriduli; vaginae carinatae, integrae, eligulatae, stramineae, infime abrupte dilatatae, marginibus in laminas gradatim contractis. Vaginae scaporum multicostatae, laxae, tortae, laminis brevibus. Scapi recti vel aliquantum flexuosi, torti, 1.2–1.5 dm alti, olivacei, distaliter leviter compressi, ca. 1 mm lati, acute bicostati, costis scabridis. Spicae anguste obovoideae vel ellipsoideae, 5–7 mm longae, ferrugineae, pauciflorae, bracteis laxe imbricatis, distaliter minute papillosis, matricibus tenuibus, ad marginem valde laceratis, ferrugineis vel roseolis. Bracteae steriles 2–4, subdecussatae, ca. 5 mm longae, paro infimo anguste ovato, ca. 5 mm longo, valde carinato, areis dorsalibus anguste linearibus, paro intimo ovato, solum ad apicem carinato, areis dorsalibus brevilinearibus. Bracteae fertiles oblongae, ca. 4, 6–7 mm longae, naviculares, distaliter carinatae, areis dorsalibus linearibus, ca. 3 mm longis. Sepala lateralia libera, inaequilatera, anguste lanceolata, 5.5–6.5 mm longa, acuta, leviter curvata; ala carinali integra. Laminae petalorum angustae obovatae, ca. 5 mm longae, luteolae, anguste rotundatae. Staminodia bibrachiata, brachiis longipenicillatis. Anthera oblongae, sagittatae, 1.5 mm longae; filamenta ca. 0.7–1 mm longa. Capsula anguste ellipsoidea, 3 mm longa; placenta basalis. Semina numerosa, anguste ovoidea, acuminata, 0.6–0.7 mm longa, translucida, ferruginea, longitudine subtiliter multicostata.

Low, densely cespitose, smooth herb, the rhizome thick, short, subvertical; roots fibrous. Leaves linear, (2–)4–7 mm long, erect to slightly spreading, a little longer than the scape sheaths. Principal leaf blades flattened, sometimes slightly twisted, 0.9–1.2 mm wide, about twice as long as the sheaths, few-nerved, dark red-brown; tips gradually narrowed, incurved-acute, slightly thickened, the margins thickened, papillose; blade margins slightly thickened, minutely ciliate to scabridulous; sheaths carinate, entire, eligulate, stramineous, abruptly dilated below, the margins gradually narrowed into the blades. Scape sheaths multicostate, loose, twisted, short-bladed. Scapes straight or somewhat flexuous, twisted, 1.2–1.5 dm high, olivaceous, slightly compressed distally, ca. 1 mm wide, acutely bicostate, the costae scabrid. Spikes narrowly obovoid to ellipsoid, 5–7 mm long, ferrugineous, few-flowered, the bracts loosely imbricate, minutely papillose distally, the matrix thin, strongly lacerate at margin, ferrugineous or roseolate. Sterile bracts 2–4, subdecussate, ca. 5 mm long, the lower pair narrowly ovate, ca. 5 mm long, strongly carinate, with narrowly linear dorsal areas, the upper pair ovate, carinate only at apex, the dorsal areas short-linear. Fertile bracts oblong, ca. 4, 6–7 mm long, navicular, distally carinate, the dorsal areas linear, ca. 3 mm long. Lateral sepals free, inequilateral, narrowly lanceolate, 5.5–6.5 mm long, acute, slightly curvate; carinal keel entire. Petal blades narrowly obovate, ca. 5 mm long, yellow, narrowly rounded. Staminodia bibrachiate, the branches long-penicillate. Anthers oblong, sagittate, 1.5 mm long; filaments 0.7–1 mm long. Capsule narrowly ellipsoid, 3 mm long; placenta basal. Seeds numerous, narrowly ovoid, acuminate, 0.6–0.7 mm long, translucent, red-brown, finely ribbed longitudinally.

The low habit and the delicate, lacerate, thin bracts with narrow, dark dorsal areas would appear to put this species into the *X. tenella* complex. However, the sheaths are entire and long-ciliate, and the lateral sepals are entire and more inequilateral. The tufts of erect or ascending, thick rhizomes covered with leaf bases are distinctive. It is known from only the type locality.

51. Xyris aquatica Idrobo & Lyman B. Smith, Caldasia 6: 206, fig. 9. 1954. TYPE: Colombia. Amazonas: on rocks in swift brook, Río Caquetá, vic. La Pedrara, Apr. 1924, *R. E. Schultes 5855* (holotype, COL; isotypes, GH, US). Figure 51.

Slender, lax, glabrous, soft-based, cespitose and profusely slenderly, scaly-rhizomatous perennial, 3–5 dm high but usually bent and trailing in rapid shoalwater. Leaves very soft, variously elongate, to 3 dm long, polystichous, the sheath less than ½ as long as the blade, the margins entire, the base lustrous pale brown or greenish brown, ecarinate, dilated, narrowing gradually upward to a prominent, narrow, scarious ligule to 6 mm long, there abruptly contracted to a terete, filiform, fluted blade up to ca. 0.5 mm thick. Scape sheath inflated-tubular, tan, opening distally to a bifid or acute apex, bladeless. Scapes straight or slightly flexuous, terete, 1–1.5 mm thick, ecostate. Spikes ovoid, narrowly ellipsoid or cylindric, 1–1.5 cm long, blunt, of many spirally imbricate, brown bracts, the sterile bracts several, ovate, slightly smaller than and grading into the fertile bracts, these oblong to obovate, ca. 5 mm long, broadly rounded, entire, backs rounded-folded, ecarinate, with ovate-elliptic, greenish dorsal areas. Lateral sepals free, curvate, subequilateral, linear-oblanceolate, 4–5 mm long, acute, lustrous brown with a narrow, dark, firm keel, this scabrociliate from below middle to apex, or subentire. Petal blades obovate, ca. 5 mm long, the broadly rounded apex erose. Staminodia bibrachiate, the branches lineal, densely penicillate-pubescent from base to tip. Anthers oblong, ca. 1.5 mm long, the upper ⅓ bifid; filaments ca. 2 mm long. Capsule obovoid, ca. 2 mm long or longer; placentation basal-central; valves eseptate. Seeds numerous, ovoid, ca. 0.5 mm long, apiculate, reddish brown, translucent, finely irregularly longitudinally striate or subreticulate by anastomosing ribs.

Distribution. A true aquatic, usually in shallow rapid shoalwaters of streams in the Amazon Basin of northern Brazil, southeastern Colombia, and T. F. Amazonas in Venezuela.

Additional specimens examined. BRAZIL. AMAZONAS: Mun. Humaitá, estrada Humaitá—km 150, a 65 km ao Sul, rio de nome Branco, *L. O. A. Teixeira et al. 1370* (INPA, NY, VDB); Rio Purus, Rio Ituxi, Rio Curuquetê, São Paulo, 30 km above mouth of Río Coti, 20 Jul 1971, *G. T. Prance et al. 14460* (INPA, NY, VDB); Rio Marmellos, Aug. 1948, *Schultes & López 10307* (US). COLOMBIA. VAUPÉS: Río Piraparaná (trib. of Río Apaporis), Caño Paca, 19 Sep. 1952, *Schultes & Cabrera 17565* (GH, U); Río Paraná Pichuna, ca. 700 ft., June 1953, *Schultes & Cabrera 19908* (NY). VENEZUELA. APURE: 9 km N of Caño Cochina de la Pica, along main rd. between Río Cinaruco and Río Capanaparo, 80 m, 2 Mar. 1979, *Davidse & Gonzalez 15992* (MO). T. F. AMAZONAS: entre el Río Sipapo y El Venado, 25 Nov. 1977, *A. Fernandez 2887* (F, MY); en lajas con caño de morichal de los alrededores de El Sipapo, ca. 100 m, lugares abiertos en carretera hacia el Sipapo, 22 Mar. 1979, *Trujillo & Pulido 15089* (MY); islas del Río Cataniapo en el Raudal Rabipelado a unos 35 km al sur-este de Puerto Ayacucho, 6 Mar. 1981, *Guánchez 904* (MYF, TFAV, VDB, VEN).

One of the few truly aquatic *Xyris*, the whole plant is apparently often totally submersed. Nearest it morphologically are *X. apureana* Kral & Lyman B. Smith and *X. spathacea* Lanjouw, but these usually have smaller spikes, often flatter leaf blades, and larger seeds.

52. Xyris apureana Kral & Lyman B. Smith, Ann. Missouri Bot. Gard. 69: 412–414, fig. 1a–i. 1982. TYPE: Venezuela. Apure: Dist. Pedro Camejo, ca. 2 km S of Caño la Cochina de La Pica along main road south of Paso de San Pablo to the Río Cinaruco, 70 m, 2 Mar. 1979, *G. Davidse & A. C. Gonzalez 15948* (holotype, US; isotypes, MO, VDB, VEN). Figure 52.

Perennial, lax, densely cespitose, smooth herb. Rhizomes slender, short to elongate, ascending (relating to degree of depth in substrate). Roots slender. Leaves linear, 1.5–3 dm long, erect or slightly spreading, subdistichous, longer than the scape sheaths; blades 5–10 times longer than sheaths, 1–2 mm wide, flat, straight, longitudinally few–many-nerved and sulcate, flattened from base to middle, terete or subterete toward apex, the

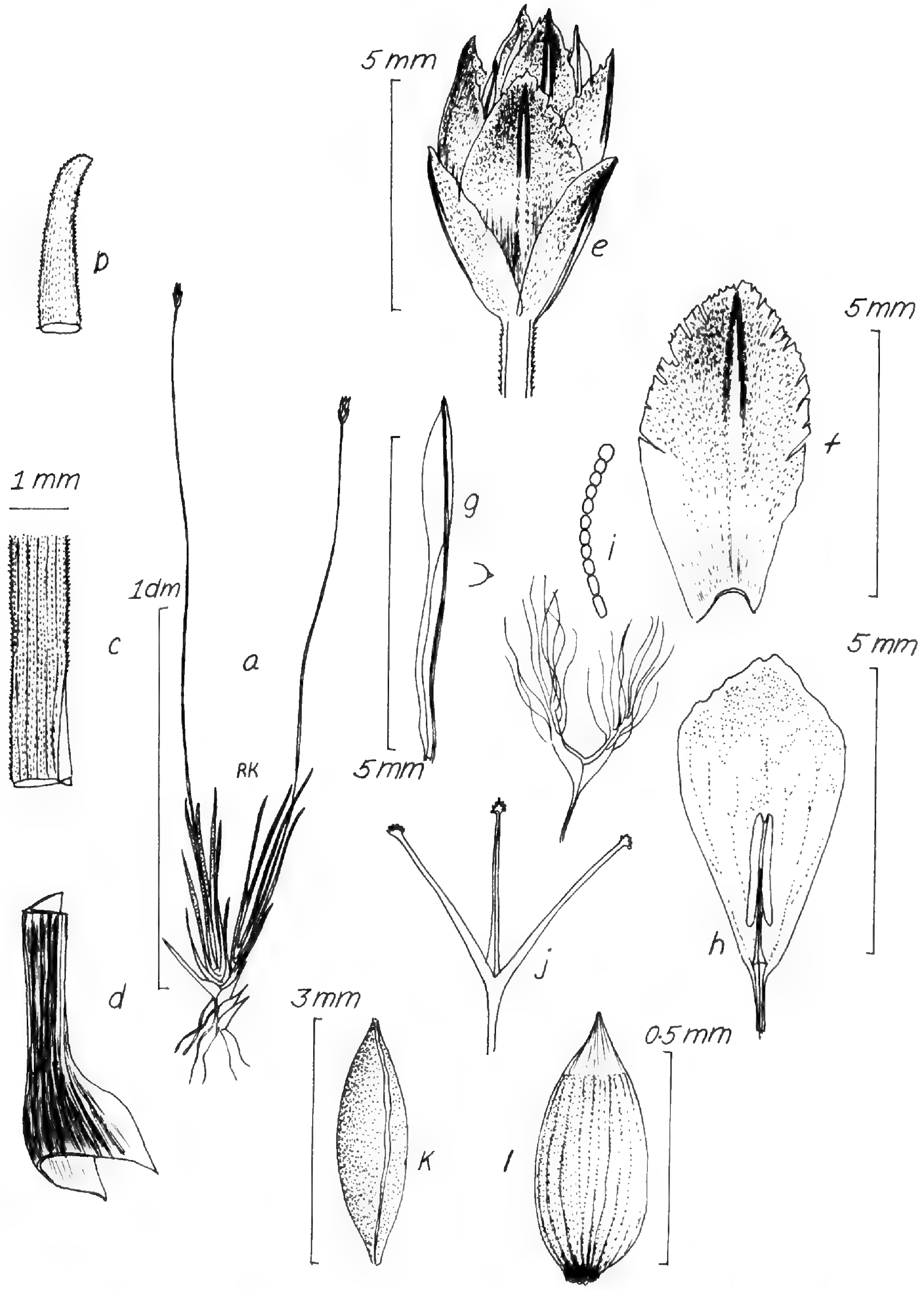


FIGURE 50. Xyris toronoana *(from the type).—a. Habit sketch.—b. Leaf tip.—c. Sector of midblade and sheath junction.—d. Leaf base.—e. Spike.—f. Fertile bract (somewhat flattened).—g. Lateral sepal.—h. Petal blade and stamen.—i. Staminodium and enlarged beard hair.—j. Stylar apex.—k. Capsule.—l. Seed.*

apices narrowed, narrowly rounded, thickened, often channelled; margins entire, not thickened; sheaths carinate, pale shining brown, several-nerved, scarious except for the ribs, the margins entire, gradually converging to blades, there producing a short, broad, scarious ligule. Scape sheaths lax, twisted, multicostate, opening toward apex, carinate, short-bladed. Scapes slender, terete, straight or somewhat flexuous, 2.5–3.5 dm high, 0.5–

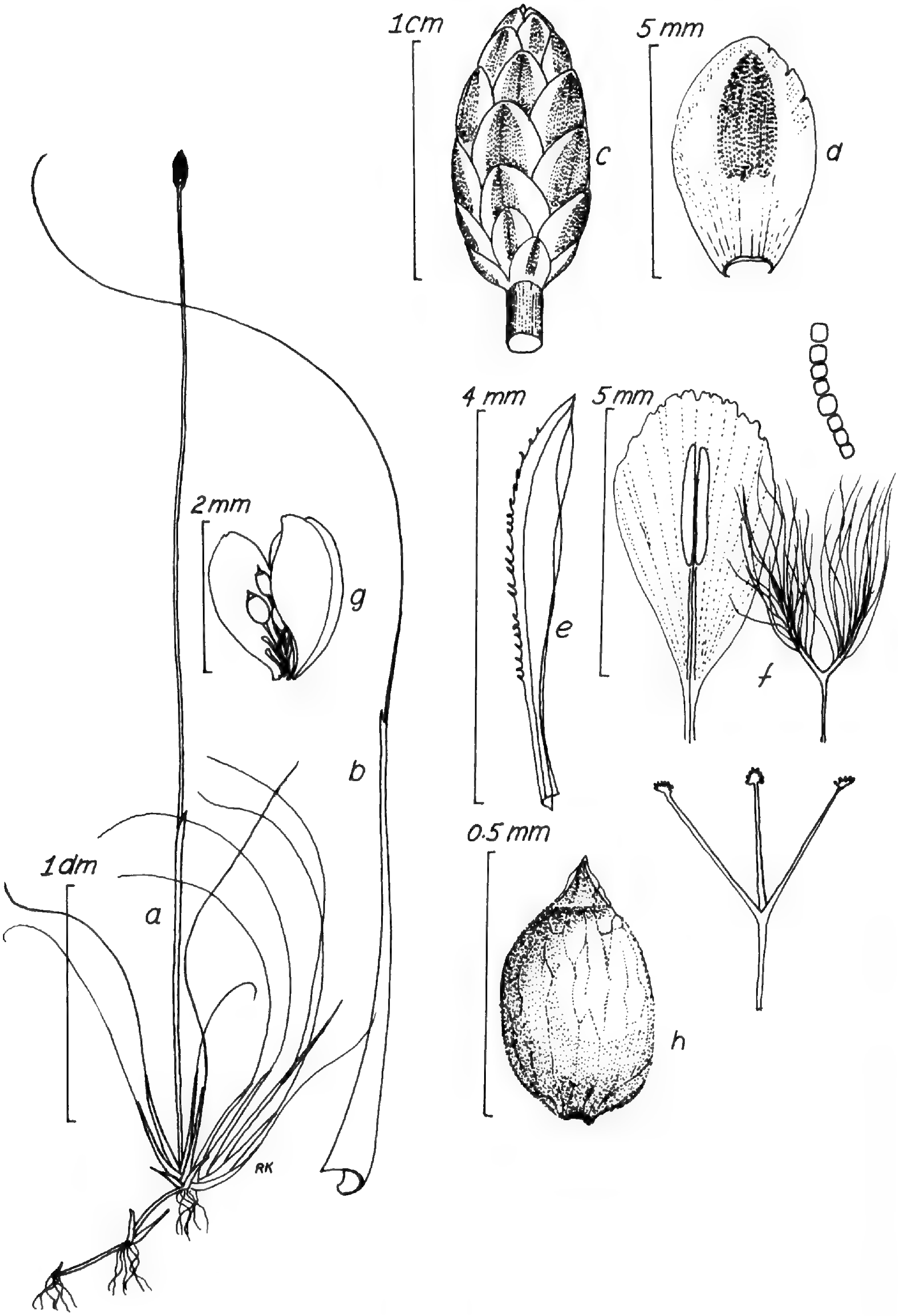


FIGURE 51. Xyris aquatica *(from* Fernandez 2887 *except where noted)*.—*a. Habit sketch (composite from* Schultes & Cabrera 17565, Fernandez 2887*)*.—*b. Leaf.*—*c. Spike.*—*d. Fertile bract.*—*e. Lateral sepal.*—*f. Petal, stamen, staminode, style branches.*—*g. Capsule.*—*h. Seed.*

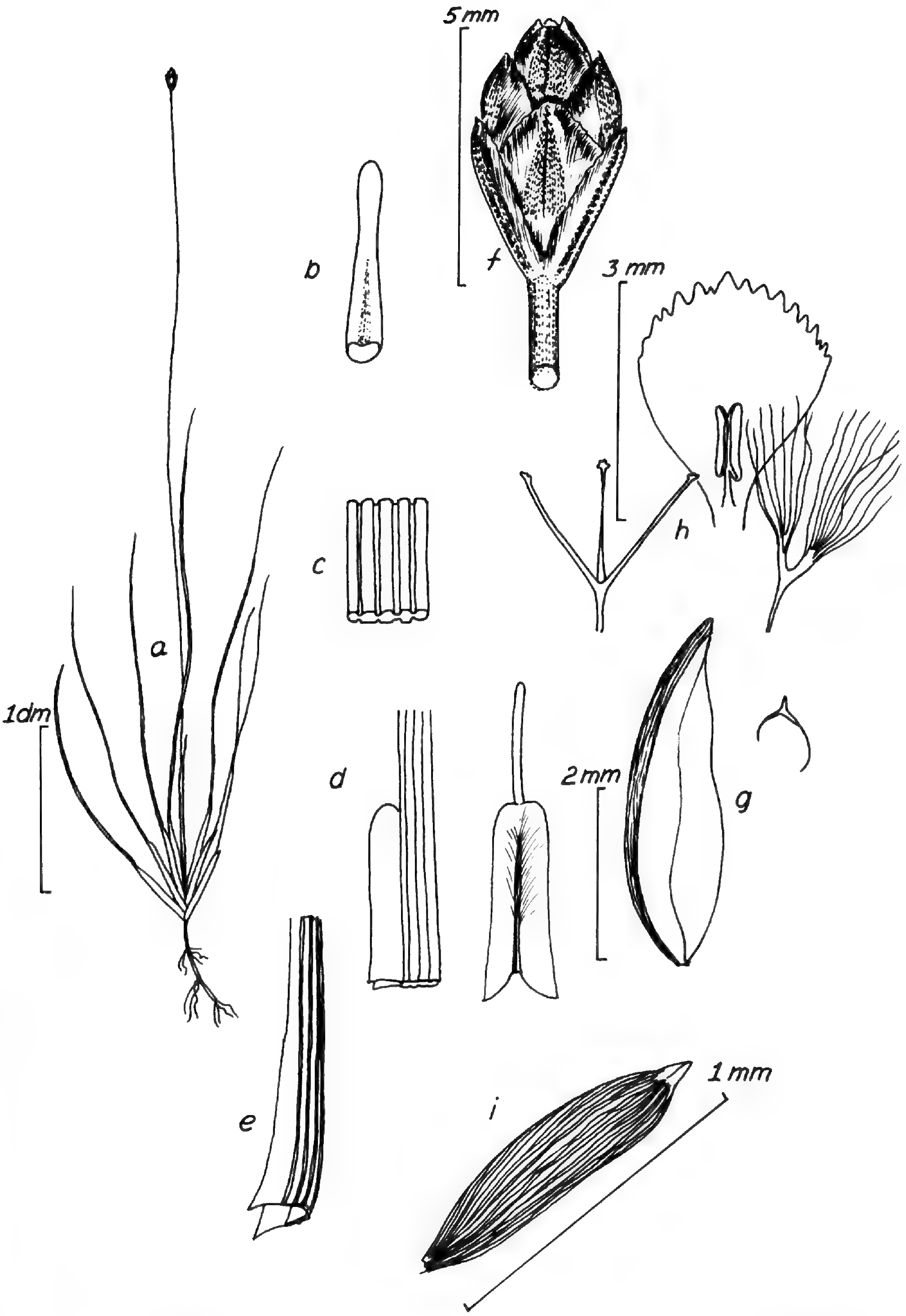


FIGURE 52. Xyris apureana *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Leaf blade sector, mid-blade.—d. Leaf sheath–blade junction.—e. Leaf base.—f. Spike.—g. Lateral sepal.—h. Petal blade, stamen, staminode, stylar apex.—i. Seed.*

0.6 mm thick, olive to reddish. Spikes several-flowered, elliptic, 5–6 mm long, acute, the bracts subdecussate, navicular or convex, ecarinate but medially 1-nerved, scarious, ferrugineous, erose; sterile bracts 4, the lowest pair at least ½ as long as the spike, oblong, the inner pair ovate, ca. 3 mm long; fertile bracts ovate, to 4 mm long, with reddish-scarious, entire to somewhat lacerate borders; dorsal area lanceolate, reddish brown or brown, ½ as long as or equal to the bract. Lateral sepals lanceolate, strongly inequilateral, ca. 4 mm long, acute; carinal keel narrow but strong, entire. Petal blades broadly obovate, 2.5–3 mm long, yellow, broadly rounded, strongly erose, cuneate. Staminodia bibrachiate, the branches long-penicillate. Anthers oblong, ca. 1.5 mm long, retuse and sagittate, slightly longer than the slender filaments. Capsule oblong, planoconvex, 2.5 mm long, amber, longitudinally finely multiribbed.

Distribution. Known thus far only from the type locality in Apure, Venezuela.

This subaquatic is superficially nearest *X. aquatica* on the one hand, and *X. spathacea* on the other. From both it differs in its more slender rhizomes, flattened leaves, and longer seeds.

53. Xyris stenostachya Steyerm., Fieldiana, Bot. 28(1): fig. 16K, L. 1951. TYPE: Venezuela. T. F. Amazonas: among rock outcrops, 100 m, Sanariapo, Río Orinoco, *J. Steyermark 58437* (holotype, F; isotypes, NY, US). Figure 53.

Solitary or cespitose, soft-based annual mostly 1–4 dm high, the stems contracted. Leaves spreading flabellately, 0.3–1.5 dm long; sheaths ½ as long as blades or shorter, tan or roseate, papillose or rugulose, narrowing evenly to blades, there producing a short, erect, scarious ligule, or ligule absent; blades linear-ensiform, flat, 1–3 mm wide, tapering above middle, then abruptly incurved-acute, the tip callused, the margins proximally tuberculate-scabrid or papillose, distally mostly smooth, the edges thickened-rounded, the surfaces maroon to yellow-green, papillose-rugose at least proximally and finely nerved. Scape sheaths as long as or shorter than leaves, tubular, twisted, costate, with short, erect blades similar to leaves. Scapes straight or flexuous, twisted, ca. 0.5 mm wide, subterete or angulate distally, striate and/or with 1–few costae and strongly scaberulous-rugose. Spikes lineal or lance-lineal, flattened, 1.5–5 cm long, the numerous distichous bracts navicular with strong dorsal areas medially unicostate and with narrowly rounded backs; sterile bracts ca. 4, the lowermost sometimes with long-excurrent, green dorsal areas, more often smaller than the fertile bracts and grading into them; fertile bracts lance-ovate to broadly oblong, 5–6 mm long, conduplicately rounded-folded around floret, apically broadly rounded, the margins scarious, a broad, pale entire to (in age) lacerate border around the large, lance-elliptic dorsal areas. Lateral sepals free, subequilateral, elliptic-linear or lance-linear, ca. 4 mm long, apically subulate or narrowly acute, tan, the narrow, firm, brown keel ciliolate to entire. Corollas gamopetalous, the limb ca. 5 mm long, the lobes lance-oblong, ca. 4.5 mm long, yellow, the apex acute, the margin remotely lacerate-dentate. Staminodes subsessile in sinuses of corolla, bibrachiate, the fleshy narrow branches with numerous penicillate, clavate hairs. Anthers lance-oblong, 0.5 mm long, on fleshy filaments ca. 1 mm long. Capsules narrowly ellipsoid, ca. 3 mm long; placentation basal. Seeds 3–6, some on funicles longer than themselves, fusiform, 1–1.5 mm long, amber, finely longitudinally striate, often with an irregular retinaculum of wider, reddish brown ridges.

Distribution. Wet sandy savanna, pools and seeps on and around granite outcrops, southeastern Colombia (not on basis of specimens but on basis of similar geology immediately across the Río Orinoco from an abundance of Venezuelan localities) eastward into the Orinoco of Territorio Federal Amazonas and Estado Bolívar, Venezuela.

Selected specimens examined. VENEZUELA. T. F. AMAZONAS: 12.5 km S of Puerto Ayacucho, 50 m, 2 Nov. 1971, *Davidse 2829A* (MO); la margen derecha del Río

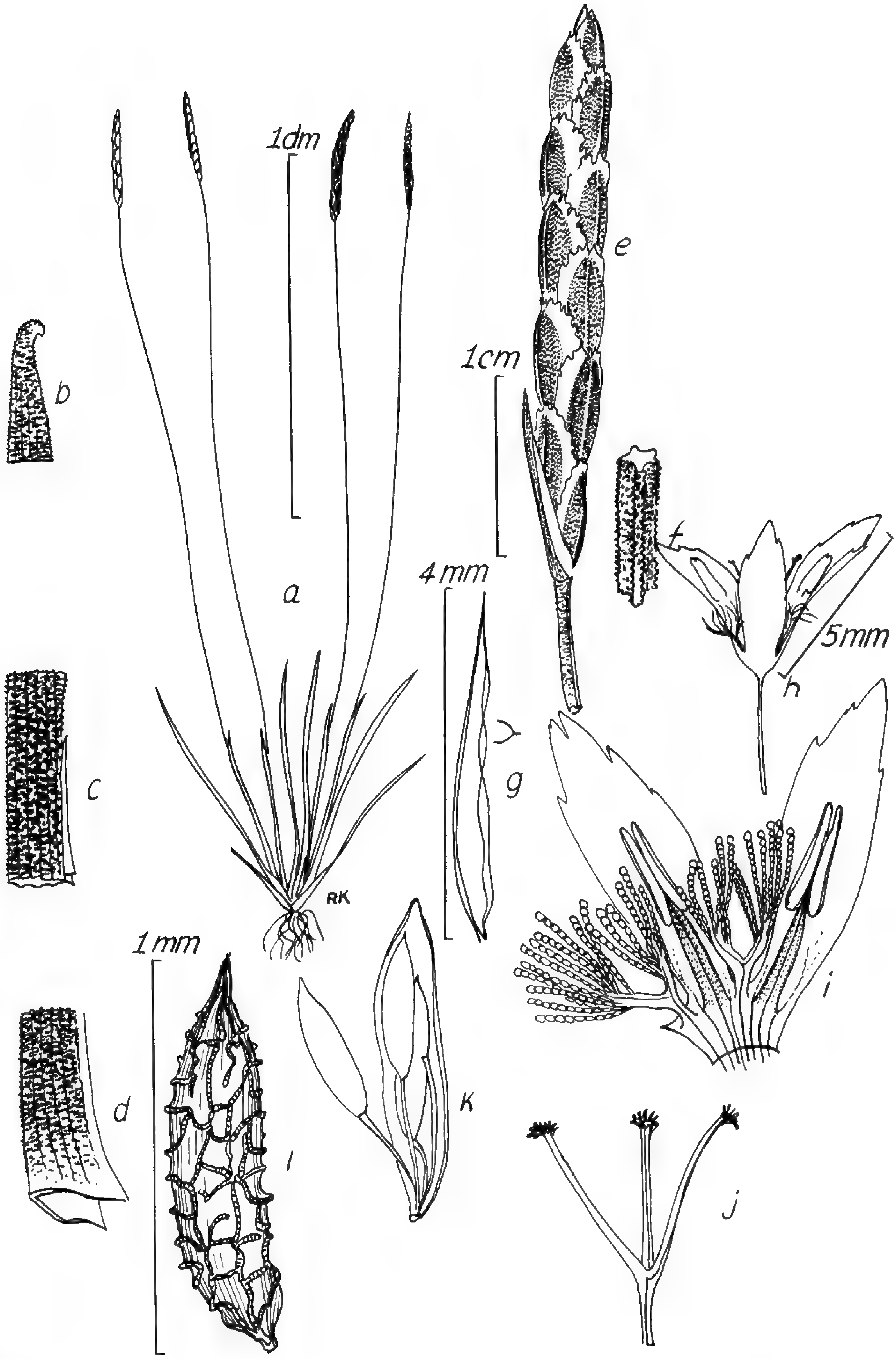


FIGURE 53. Xyris stenostachya (Kral 70681, 70727).—*a. Habit sketch.—b. Leaf tip.—c. Leaf at junction of blade and sheath.—d. Leaf base.—e. Spike.—f. Sector of upper scape.—g. Lateral sepal.—h. Oblique view of corolla limb.—i. Opened corolla showing stamens and staminodes.—j. Stylar apex.—k. Capsule, open to show one valve and placentation.—l. Seed.*

Guayapo, en el "Salto Moriche," 9 Oct. 1983, *Guánchez & Varadarajan 2573* (TFAV); 2 km al sur de Puerto Ayacucho, del Río Autana en raudal "seguera," 8 Nov. 1984, *Guánchez & Melgueiro 3324* (TFAV, VDB); aeropuerto de Puerto Ayacucho, 75 m, 13 Sep. 1977, *Huber 1046* (MYF, NY, VDB, VEN); Cerro Yapacana, ca. 100 m, 14–28 Feb. 1978, *Huber 1546* (US); 20 km SE de San Juan de Manapiare, 140 m, 17 Aug. 1978, *Huber 2340* (US); la región del Caño Corocoro, al N de bajo Río Ventuari, *Huber 2379* (US, VDB, VEN); 5 km al NE de Galipero, 3 Dec. 1979, *Huber 4759* (NY, US); savanna I, Yapacana savannas, 9 Aug. 1983, *Kral & Huber 70681* (BM, F, K, L, MO, NY, SP, TFAV, U, US, VDB, VEN); fisheries lab, granite outcrops, Puerto Ayacucho, 11 Aug. 1983, *Kral 70727* (BM, F, K, L, MO, NY, SP, TFAV, U, US, VDB, VEN, and others); Caño Sambolje near La Urbana, *Maguire 28989* (NY, US); Yapacana Savanna I, at 125 m, 7 Jan. 1951, *Maguire et al. 30787* (C, NY); 35 km SE of Puerto Ayacucho, *Steyermark et al. 122491* (MO, NY). BOLÍVAR: Cerro San Borja, occasional, Río Orinoco at 100–300 m, 12 Dec. 1955, *Wurdack & Monachino 39845*; Río Villacoa, 1–4 km above Salto de Humito, 7 Jan. 1956, *Wurdack & Monachino 41164* (F, NY, US).

This distinctive little annual is most abundant in the shallow pools or seeps in and around granitic lajas within the Venezuelan "piedmont" above the Great Bend of the Orinoco. No other species remotely resembles it. The pale yellow flowers open in the morning.

54. Xyris stenocephala Malme, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 22, Afd. 3(2): 18, tab. 1, fig. 1. 1896; Smith & Downs, Fl. Bras. 9(II): 105–106, tab. 34, figs. 1020–1027. 1968. TYPE: Brazil. Mato Grosso: lugar aberto, pantanoso, cerca de Santa Ana da Chapada, 700–800 m, 28 Nov. 1894, *Malme 1426* (holotype, S; isotype, MO; phototype, F). Figure 54.

Perennial or annual, solitary or cespitose, glabrous plants (1–)2–5 dm high, the stem short. Leaves erect to spreading flabellately, 5–20 cm long; sheaths at least ½ as long as blades, entire, strongly nerved, carinate, pale brown to deep red-brown, sometimes papillose, often with a strong, deep brown, lustrous costa, tapering gradually from a slightly dilated base to the blade, there eligulate or with a short, scarious ligule; blades narrowly linear, flattened, twisted, 1–4 mm wide, strongly nerved, tapering gradually to an incurved-acute, cartilaginous-bordered tip, the margins thickened, lustrous, pale to deep brown, rarely scabrociliate, the sides pale green to reddish green or ferrugineous. Scape sheaths shorter than principal leaves, tubular, ferrugineous, multicostate below, apically with short, flat blades. Scapes flexuous and twisted, distally terete, 1–1.5 mm thick, rarely unicostate with scabrid costa, mostly just striate, olivaceous to green-brown. Spikes mostly ellipsoid, 1–2 cm long, acute, smooth, of several tightly spirally imbricate bracts; sterile bracts usually 4, the lowest pair oblong, carinate, slightly shorter than the fertile bracts, these broadly ovate or obovate to suborbicular, 4.5–5.5 mm long, strongly convex and ecarinate, broadly to narrowly rounded apically, the matrix pale to deep lustrous brown with a pale, thin, entire to erose border, the dorsal areas pale to deep green or brown, ovate, large but subapical, with a strong but fine midrib. Lateral sepals free, strongly inequilateral, strongly curved, acute, ca. 4 mm long, the keel firm and broad, ciliolate from near base to tip; petal blades ca. 4 mm long, obovate, broadly rounded, lacerate, yellow. Staminodia bibrachiate, the branches densely penicillate. Anthers oblong, ca. 1.5 mm long, on filaments 0.5–0.7 mm long. Capsule planoconvex, obovoid, 2–2.5 mm long, the placenta basal. Seeds few, fusiform-curvate, 1.2–1.7 mm long, dark red-brown, translucent, strongly beaked, longitudinally multicostate.

Distribution. Wet, rocky and/or sandy savanna, mostly in northern Brazil, in Amazonas, Pará, Mato Grosso, and with an outlier in São Paulo.

Selected specimens examined. BRAZIL. AMAZONAS. "Estrada do Estanho," road to Igarapé Preto, 60 km SE of Transamazon Hwy., in white-sand savanna, 2 July 1979, *Calderon et al. 2737* (INPA, US, VDB). PARÁ: Mun. Itaituba, estrada Santarem–Cuiaba, BR 163, km 794, Serra do Cachimbo, Base Aérea, campina, solo arenoso, 25 Apr. 1983, *Amaral et al. 934* (INPA, NY, VDB); Campo do Jamaracaru, perto do barracão, Região do Ariramba, *Black et al. 57-19638* (UB); Mun. Itaituba, arredores da Base Aérea do Cachimbo, ca. aõ destacemento km 6 da estrada que vai para o Aeroporto km 794, savana, 25 Apr. 1983, *Silva et al. 82* (INPA, NY, VDB). SÃO PAULO: Mun. Moji-Guacú, "Campos das Sete Lagoas," Fazenda Campininhá, just N of Rio Moji-Guacú, 4 km NNW of Padua Sales, 14 Dec. 1962, *Eiten 5104* (MO, US).

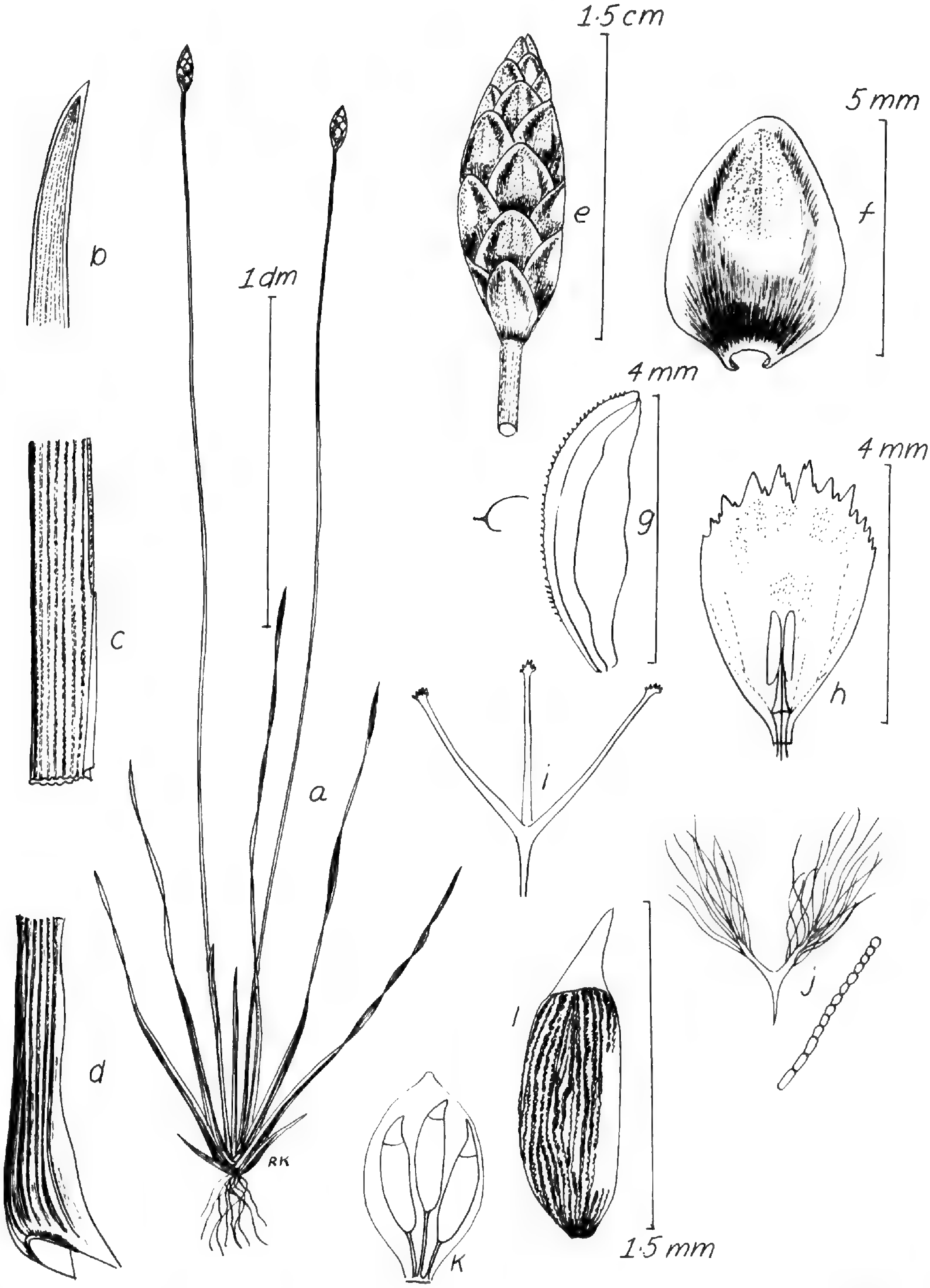


FIGURE 54. Xyris stenocephala (Silva et al. 82).—*a. Habit sketch.—b. Leaf tip.—c. Leaf blade-sheath junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Stylar apex.—j. Staminode.—k. Outline of capsule, showing placentation.—l. Seed.*

This taxon is most abundant in low-elevation, white-sand savanna, particularly in eastern Mato Grosso (Norte) and southwestern Pará but should be looked for in comparable areas north of the Amazon. It borders on larger forms of *X. paraensis*, particularly var. *longiceps*, but differs markedly in its glassy-bordered leaf blades and markedly larger seeds. Populations appear to be sometimes annual, although they are usually perennial. Perhaps this is a matter of degree of disturbance of habitat, particularly the very seasonal nature of moisture in white-sand savanna. Or it could be that crowding produces a depauperate, annual habit.

55. Xyris cylindrostachya Kral & Wanderley, sp. nov. TYPE: Brazil. Amazonas: Mun. Presidente Figueiredo, "Campina das Pedras," ubicada en el km 115, de la Rodovia BR-174 (Manaus–Caracaraí), en el lado oriental del Igarapé das Lajes, 1°58'S, 60°02'W, ca. 100 m, 29–30 June 1985, *O. Huber & Luíz O. Adao Teixeira 10663* (holotype, INPA; isotypes, NY, VDB). Figure 55.

Herba perennis, glabra, densicaespitosa; radices graciles. Caules breves. Folia principalia anguste linearia, 10–30 cm longa, erecta vel flabellate expansa, vaginis scaporum longiora. Laminae foliorum compressae, leviter tortae, 0.8–1 mm latae, vaginis 2–4-plo longiores, longitudine indistincte nervosae, dilute virides; apices gradatim contracti, subulati, subteretes; margines leviter incrassati, integri, pallide brunneoli vel ad basin fuscobrunneoli, persaepe nitidi; vaginae carinatae, integrae, rufobrunneolae vel ferrugineae, papillosae, multicostatae, infime gradatim dilatatae, tum margines in laminas gradatim contractae, ad apicem anguste acutam ligulam scariosam usque ad 2 mm longam efferentes. Vaginae scaporum tortae, tubulosae, multicostatae, ferrugineae, ad apicem apertae, laminis brevibus. Scapi recti vel flexuosi, torti, 30–60 cm longi, ad apicem teretes, 1–2 mm crassi, persaepe rubelli, subtiliter striolati. Spicae ovoideae vel (vulgo) cylindricae, 1–3 cm longae, 5–7 mm crassae, obtusae, multibracteatae, brunneolae, bracteis arcte spiraliter imbricatis. Bracteae steriles 2–4, oblongae, ca. 3 mm longae, naviculares, carinatae, in fertiles leviter transientes; bracteae fertiles late ovatae vel suborbiculatae, 4–5 mm longae, integrae, ecarinatae, valde convexae, areis dorsalibus late ovatis, fuscoviridibus. Sepala lateralia libera, valde inaequilatera, curvata; ala carinali lata, a basi ad apicem ciliolata. Laminae petalorum obovatae, 4–4.5 mm longae, luteolae, latae rotundatae, laceratae. Staminodia bibrachiata, brachiis dense longipenicillatae. Antherae oblongae, sagittatae, 1.5 mm longae; fila ca. 1 mm longa. Capsula planoconvexa, obovoidea, ca. 2 mm longa; placenta basalis. Semina curvato-ellipsoidea, apiculata, 0.6–0.7 mm longa, pallide rufobrunneola, translucida, longitudine subtiliter multicostata.

Smooth, densely cespitose perennial with slender roots. Stems short. Principal leaves narrowly linear, 10–30 cm long, erect to spreading flabellately, longer than the scape sheaths. Blades of leaves flattened, slightly twisted, 0.8–1 mm wide, 2–4 times as long as the sheaths, indistinctly nerved, pale green; tips gradually narrowed, subulate, subterete; margins slightly thickened, entire, pale brown to red-brown at base, often shining; sheaths carinate, entire, red-brown to ferrugineous, papillose, multicostate, gradually dilating below, then gradually narrowed into the blades, at apex producing a narrow, acute, scarious ligule to 2 mm long. Sheaths of scapes twisted, tubular, multicostate, ferrugineous, open at apex, with short blades. Scapes straight to flexuous, twisted, 30–60 cm long, terete toward apex, 1–2 mm thick, usually reddish, finely striate. Spikes ovoid to (commonly) cylindric, 1–3 cm long, 5–7 mm thick, obtuse, multibracteate, brownish, the bracts tightly spirally imbricate. Sterile bracts 2–4, oblong, ca. 3 mm long, navicular, carinate, but slightly grading into the fertile bracts; fertile bracts broadly ovate to suborbicular, 4–5 mm long, entire, ecarinate, strongly convex, with broadly ovate, red-green dorsal areas. Lateral sepals free, strongly inequilateral, curvate; carinal keel broad, ciliolate from base to apex. Petal blades obovate, 4–4.5 mm long, yellow, broadly rounded, lacerate. Staminodes bibrachiate, the branches densely long-penicillate. Anthers oblong, sagittate, 1.5 mm long; filaments ca. 1 mm long. Capsule planoconvex, obovoid, ca. 2 mm long; placenta basal. Seeds curvate-ellipsoid, apiculate, 0.6–0.7 mm long, pale red-brown, translucent, longitudinally finely multicostate.

Paratypes. BRAZIL. AMAZONAS: Mun. Presidente Figueiredo: "Campina das Pedras," ubicada en el km 115 de la Rodovia BR-174 (Manaus–Caracaraí), en el lado oriental del Igarapé das Lajes, 01°58'S, 50°02'W, ca. 100 m, 29–30 June 1985, *O. Huber & Luíz O. Adao Teixeira 10652* (INPA, NY, VDB). PARÁ: Mun. Oriximiná, Campos do Ariramba, campinas inundaveis da margem do Rio Jaramacarú; afloramento arenitoco; 80 m, 8 June 1980, *G. Martinelli 6847* (INPA, NY, VDB).

This species most closely resembles *X. stenocephala* Malme, differing from it primarily in its longer, narrower leaf blades, these less strongly bordered and more inconspicuously nerved. The spikes are very different, being mostly narrowly cylindric and blunt (rather than ellipsoid and acute). The

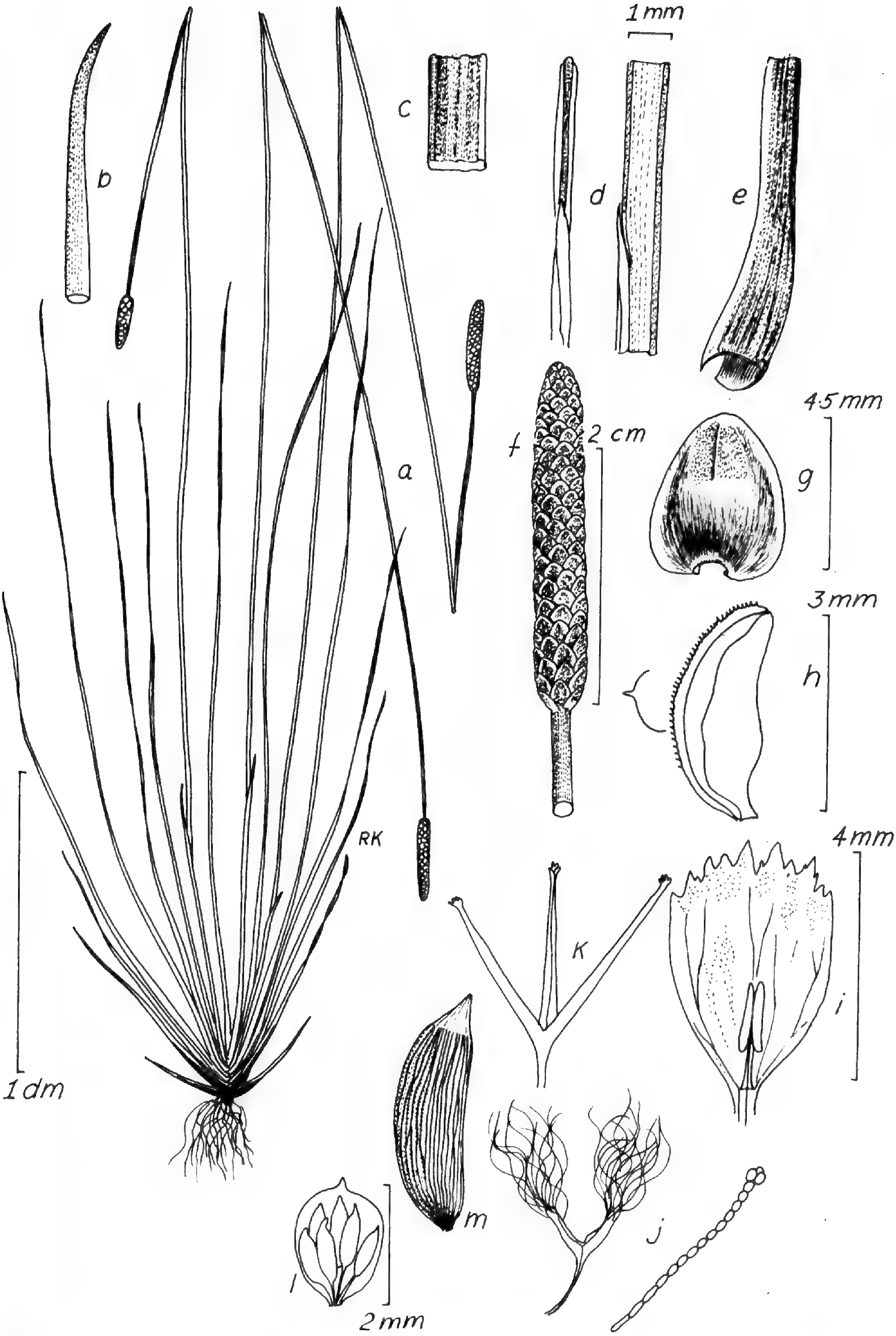


FIGURE 55. Xyris cylindrostachya *(from the type)*.—*a. Habit sketch.*—*b. Leaf apex.*—*c. Leaf midblade sector.*—*d. Two views of leaf blade–sheath junction.*—*e. Leaf base.*—*f. Spike.*—*g. Fertile bract.*—*h. Lateral sepal.*—*i. Petal blade and stamen.*—*j. Staminode and enlarged beard hair.*—*k. Stylar apex.*—*l. Capsule outline, placentation.*—*m. Seed.*

lateral sepals are somewhat shorter and the seeds are significantly shorter (0.6–0.7 mm long vs. 1.2–1.7 mm long). These two species, along with the varieties of *X. paraensis*, *X. savannensis*, *X. uleana*, and *X. mima*, appear to provide an abundant (and perhaps sometimes intergrading) display on the white-sand campinas of the Amazonian savannas. Dense stands are often depauperate and mixed, escaping standard measures and aggravating the taxonomic problem.

56. Xyris brachysepala Kral, sp. nov. TYPE: Brazil. Pará: Serra dos Carajás, 2 km W of AMZA camp N-5, 6°04′S, 50°08′W, ca. 700 m, scrubby vegetation on ferric rock outcrops, moist low areas, 13 May 1982, *C. R. Sperling, R. S. Secco, M. Condon, A. L. Mesquita, B. G. S. Ribeiro & L. R. Marinho 5641* (holotype, INPA; isotypes, MG, NY, VDB). Figure 56.

Planta humilis, annua, glabra. Radices filiformes. Folia linearia, solum basalia, (2–)8–12 cm longa, erecta vel leviter expansa, vulgo vaginis scaporum longiora. Laminae folia principalium vaginis 3–4-plo longiores, spongiosae, tortae, a basin leviter compressae, alter teretes, ca. 0.5 mm crassae, viridulae, ad apicem abrupte contractae, obtusatae; vaginae subcarinatae, roseolae, integrae, in laminas gradatim convergentibus aut ad apicum ligulam scariosam curtam latam fascientibus, infime gradatim expansae. Vaginae scaporum laxae, plerumque apertae, rectae, carinatae, sine laminis aut laminis brevis. Scapi subteretes, subfiliformes, plus minusve spiraliter torti, ca. 0.5 mm crassi, striati. Spicae lanceoloideae vel anguste ellipsoideae, 1–2 cm longae, anguste acutae, pluriflorae, bracteis arcte spiraliter imbricatis, tenuibus, pallide rufobrunneolis, marginibus tenuissimis, latis, pallidis, integris; bracteae steriles 4, oblongae vel anguste ovatae, 2–4 mm longae, acutae vel obtusae, obscure carinatae, fertilibus leviter breviores; bracteae fertiles ovatae, 5–7 mm longae, ad apicem carinatae, acutae; area dorsalis anguste triangulati, subapicales, virides, tum brunneolae, 2–3 mm longae. Sepala lateralia libera, curvata, aequilatera, lanceolata, 2–2.3 mm longa, acuta; ala carinali angusta, integra. Laminae petalorum obovatae, ca. 2 mm longae, luteolae, ad apicem erosae. Antherae oblongae, profunde bifidae et sagittatae, ca. 0.5 mm longae; filamenta plana, ca. 0.5 mm longa. Staminodia parce penicillatis. Capsula leviter dorsali-ventraliter compressa, obovoidea, ca. 3 mm longa; placenta basalis. Semina numerosa, ellipsoidea, 0.6 0.8 mm longa, pallide rufobrunneola, longitudine subtiliter multistriata, translucida.

The plant low, annual, smooth. Roots filiform. Leaves linear, strictly basal, (2–)8–12 cm long, erect to slightly spreading, mostly longer than the scape sheaths. Blades of the principal leaves 3–4 times longer than the sheaths, spongy, twisted, slightly compressed at base, otherwise subterete, ca. 0.5 mm thick, greenish, abruptly narrowed at apex, obtuse; sheaths subcarinate, roseate, entire, narrowing gradually to blades or producing a broad short scarious ligule at apex, gradually dilating below. Scape sheaths lax, commonly open, straight, carinate, without blades or with short blades. Scapes subterete, subfiliform, ± spirally twisted, ca. 0.5 mm thick, striate. Spikes lanceoloid to narrowly ellipsoid, 1–2 cm long, narrowly acute, several-flowered, with bracts tightly spirally imbricate, thin, pale red-brown, the margins very thin, broad, pale; sterile bracts 4, oblong to narrowly ovate, 2–4 mm long, acute to obtuse, obscurely carinate, slightly shorter than the fertile bracts; fertile bracts ovate, 5–7 mm long, carinate at apex, acute; dorsal areas narrowly triangular, subapical, green then (later) brown, 2–3 mm long. Lateral sepals free, curvate, subequilateral, lanceolate, 2–2.3 mm long, acute; keel narrow, entire. Petal blades obovate, ca. 2 mm long, yellow, erose at apex. Anthers oblong, deeply bifid and sagittate, ca. 0.5 mm long; filaments plane, ca. 0.5 mm long. Staminodia sparsely penicillate. Capsule slightly compressed dorsiventrally, obovoid, ca. 3 mm long; placentation basal. Seeds numerous, ellipsoid, 0.6–0.8 mm long, pale red-brown, longitudinally finely lined, translucent.

Distribution. Known only from grassy, rocky, acid savannas in Pará, Brazil.

Additional specimens examined. BRAZIL. PARÁ: Marabá, N$_5$, arredores do lago, canga, 14 May 1982, *R. S. Secco, C. Sperling, M. Condon, A. Mesquita, B. Gilberto R. & L. Marinho 155* (MG, NY, VDB); Marabá, Serra dos Carajás, N-4, proximo a transição para a mata, campo rupestre, solo de canga e na mata de terra firme, 20 Mar. 1984, *A. S. L. da Silva, N. A. Rosa, R. P. Bahia & M. R. Santos 1920* (MG, NY, VDB); Marabá, arredores estrada p/N$_1$ transição campo natural/veg. canga, 17 May 1982, *R. S. Secco, C. Sperling, M. Condon, A. Mesquita, B. Gilberto R. & Lucival Marinho 226.*

This little annual bears a strong resemblance to longer-spiked forms of *X. paraensis* Poeppig ex Kunth, but its leaves differ by

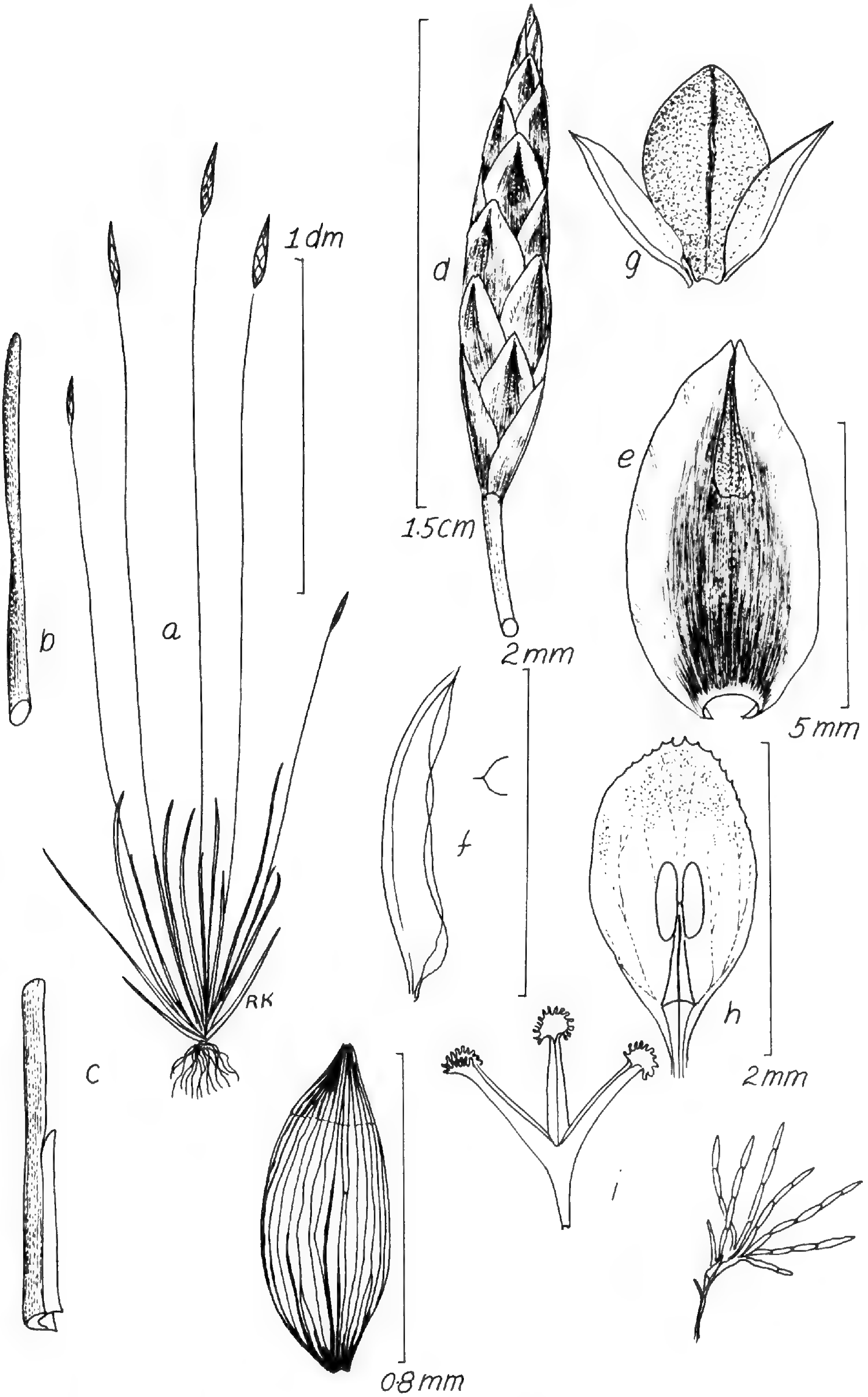


FIGURE 56. Xyris brachysepala (Sperling et al. 5641).—*a. Habit sketch.—b. Leaf apex.—c. Leaf blade-sheath junction.—d. Spike.—e. Fertile bract.—f. Lateral sepal.—g. Capsule, showing length relative to lateral sepals.—h. Petal blade, stamen.—i. Stylar apex.—j. Staminode.—k. Seed.*

being distinctly terete apically; the fertile bracts are larger but distinctly thinner with distinctive broad, pale thin borders and with narrower dorsal areas, these forming a carina subapically on the bract. The lateral sepals are much more reduced than is typical in most *Xyris*.

57. **Xyris paraensis** Poeppig ex Kunth, Enum. Pl. 4: 9. 1843. TYPE: Brazil. Pará: "Rio Para, *Poeppig, 1832*" (lectotype, B; phototype, US).

Three varieties are delimited by Smith & Downs (Arq. Bot. Estado São Paulo, nov. ser. 4(2): 28. 1966) for this complex whose greatest diversity appears to be in Pará, Brazil. The varieties *paraensis* and *longiceps* are thus far the only two collected within the area of my concentration, so, while the key below is to three, I am putting down full descriptions only of those two.

KEY TO VARIETIES OF *XYRIS PARAENSIS*

1a. Lateral sepals as viewed from the side broadly oblong and blunt; spikes predominantly ovoid to nearly round, mostly 5 mm long or less .... 57A. *X. paraensis* var. *paraensis*

1b. Lateral sepals as viewed from the side lanceolate and acute; spikes ellipsoid to cylindric, at maturity predominantly 1–2 cm long.

  2a. Spikes less than 5 mm thick, mostly cylindric, the bracts spiraled in 3–4 ranks .... 57B. *X. paraensis* var. *longiceps*

  2b. Spikes 5 mm thick, mostly ellipsoid, the bracts spiraled in 5–6 ranks .... 57C. *X. paraensis* var. *polystachya*

57A. **Xyris paraensis** var. **paraensis.** Figure 57A.

Cespitose or solitary, mostly low and slender, mostly annual plants 0.5–4 dm high, the roots fine, the stems short. Leaves erect to spreading flabellately, the principal leaves 2–15(–20) cm long, the sheaths eciliate, stramineous to brown or red-brown, narrowing gradually from base to blade, with or without a narrowly triangular ligule to 1 mm long; blades flattened, slightly if at all twisted, 1–2.5 mm wide, narrowly linear, tapering gradually to an acute, usually calloused apex, the margins thin, unbordered, usually smooth, the surface green to maroon, very finely nerved and smooth. Scape sheaths shorter than principal leaves, the base tubular, multicostate, keeled, distally open and with a prominent leaflike blade, or the blade short, erect, fleshy. Scapes straight or slightly flexuous, twisted, distally terete, 0.3–0.8 mm thick, mostly ecostate but finely striate, smooth. Spikes ovoid to subglobose, 0.3–0.5 mm long, mostly acute, the several to many bracts in a spiral, tightly imbricate, with strong, unicostate dorsal areas, the few sterile bracts grading slightly larger into the fertile bracts, these obovate, low-auriculate, ca. 2–4 mm long, the apex broadly to narrowly rounded, entire or erose, the backs rounded, convex, ecarinate. Lateral sepals free, inequilateral, 3–4 mm long, strongly curvate, broadly acute to obtuse, the wide keel coarsely and irregularly ciliate to ciliolate. Petal blades broadly to narrowly obovate, 2–4 mm long, yellow, the broadly rounded apex lacerate. Staminodia bibrachiate, the flat, narrow branches sparsely penicillate terminally. Anthers broadly oblong, 0.5–0.7 mm long, the parallel sacs separated by wide connective, the filaments 0.5–0.7 mm long. Capsules broadly obovoid, somewhat compressed dorsiventrally, ca. (1–)2 mm long, the placentation basal, the valves without septa. Seeds ellipsoid or fusiform on long funicles 0.5–0.9 mm long, apiculate, amber, longitudinally distinctly but finely ribbed.

Distribution. Sandy savannas of mostly white sand, locally abundant, rare in Belize; rare in southern Venezuela; frequent to common eastward across Guyana to French Guiana and contiguous northern Brazil.

Additional specimens examined. BELIZE: pure sand savanna, Hattieville, 7 May 1972, *Dwyer & Pippin 10981* (MO); wet sand, Manatee Lagoon, 5 Jan. 1906, *Peck 269* (GH); All Pines, *Schipp S-131* (BM, F, GH, MO, NY). BRAZIL. PARÁ: Mun. Itaituba, estrada Santarem–Cuiaba, BR 163, km 794, Serra do Cachimbo, *Amaral et al. 930* (INPA, NY, VDB); Campina do Itajura, Ilha de Colare, 28 Sep. 1954, *Black 54-1687a* (US, VDB); campina do Palha, Vigia, 10 Aug. 1954, *Black 54-16742* (US, VDB); Ilha de Colares, sítio Horizonte, Mun. Vigia, 29 Sep. 1954, *Black 54-16911* (US, VDB); vic. Cachoeira, BR 22, km 98, roadside, 24 Aug. 1964, *Prance & Silva 58840* (NY, VDB). TERR. RORAIMA: Serra da Lua foothills, 2°25–29′N, 69°11–14′W, 12 Jan. 1969,

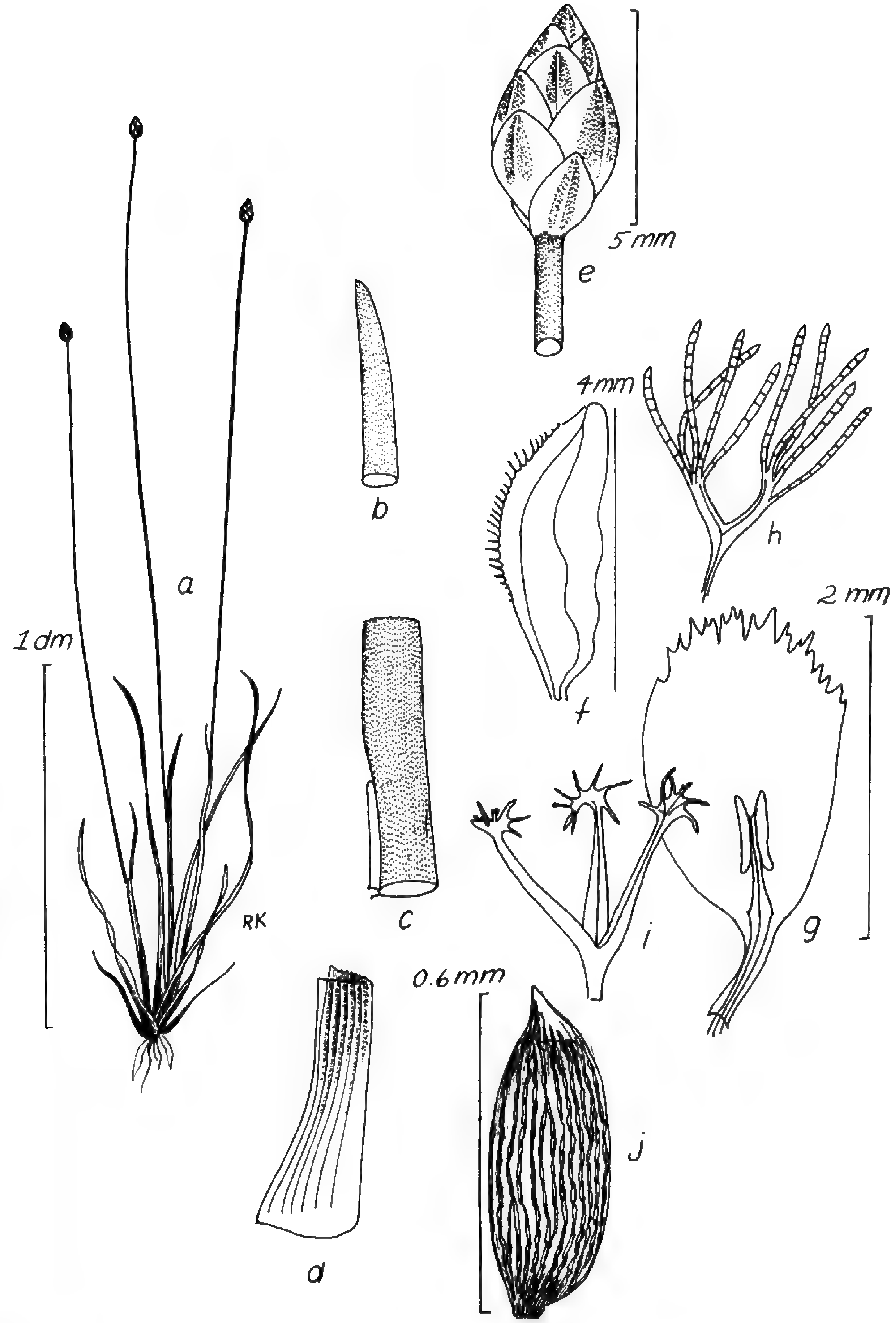


FIGURE 57A. Xyris paraensis *var.* paraensis (Black 54-16742).—*a. Habit sketch.—b. Leaf tip.—c. Leaf sheath-blade junction.—d. Leaf base.—e. Spike.—f. Lateral sepal.—g. Petal blade, stamen.—h. Staminode.—i. Stylar apex.—j. Seed.*

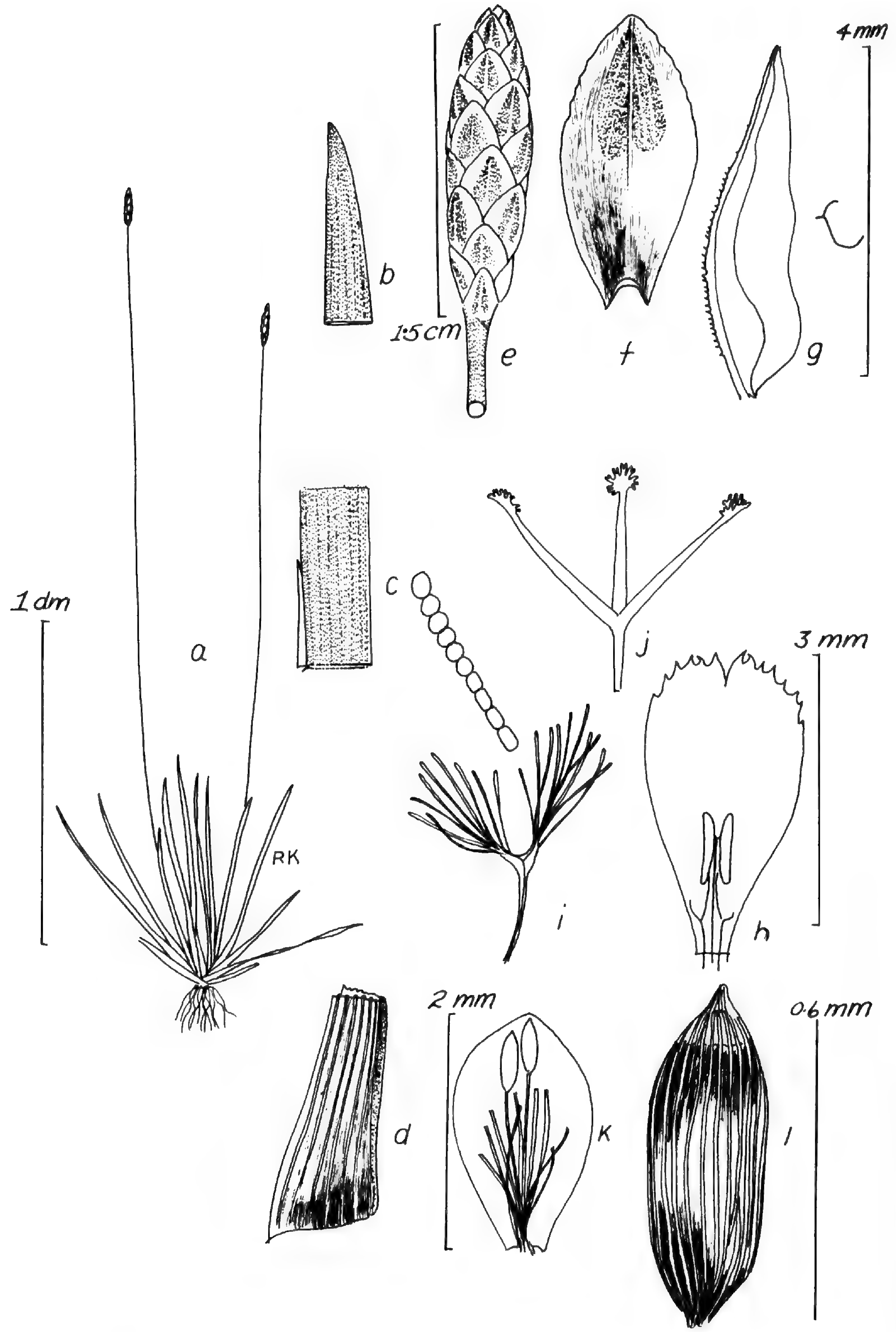


FIGURE 57B. Xyris paraensis *var.* longiceps *(*Huber 2581*)*.—*a. Habit sketch.—b. Leaf tip.—c. Leaf sheath-blade junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode, enlarged sector of beard hair.—j. Stylar apex.—k. Diagram of capsule and placenta.—l. Seed.*

Prance et al. 9208 (U). French Guiana: Savanes de Kourrou, transect no 12, *Institut Francais D'Amerique Tropicale* (U). Guyana: "English Guiana, *Schomburgk 98*" (two specimens, the left-hand one *X. savanensis* Miq.). Surinam: Lonbin savanna inter Zanderij I and Hannover, opn. 131, *van Donselaar 353* (U); Brokopondo 4 km E of village Brownsweg, 22 Dec. 1965, *van Donselaar 2841a* (U); Zanderij, sand savanna, *Florschutz 802* (U); Prope Jodensavanne (fluv. Suriname) tr. 10, p. 70, 8 Aug. 1956, *Heyligers 382* (U); Wilhelmina Gebergte, Zuid River, savanna S of Kayser Airstrip, 270 m, 26 Aug. 1963, *Irwin et al. 55233* (GH, K, NY, U, VDB); via secta ab Moengo tapoe ad Grote Zwiebelzwamp, big swaying swamp near km 18, 21 Oct. 1948, *Lanjouw & Lindeman 949* (U); Tibiti savanne, near km 3.2–4.0 second line, *Lanjouw & Lindeman 1789* (U); savanna 2 km N of river, 2 km W of Oost Rivier, 225 m, 11 July 1963, *Maguire et al. 54132* (NY, U, VDB); Center Sipaliwini savanna, ca. 2 km S of '4 Gebroeders Creek, *Oldenberger et al. 5954* (U); Forest of Zandery, 31 May 1916, *Samuels 433* (GH); Savanne ca. 2 km va. Bo. Lucie R., 9 Aug. 1963, *Schulz LBB 10358* (U); Nat. Res. "Brinckheuvel" (Saban-Pasi Savanne), *Teunissen & Wildschut 11522* (U). Venezuela. guarico: Morichal Hato Becevia 25 km sur de Calabozo, Nov. 1966, *L. Aristeguieta 6469* (VEN).

This variety is the most often misidentified as *X. savanensis*, which may produce smooth-leaved forms (var. *glabrata*). Careful examination should solve the problem in that *X. savanensis* produces no staminodial beard. If flowers are lacking, then seed characters help in that the shorter seed of *X. savanensis* has the typical truncate and apiculate apex. On the other hand, *X. mima* would pose a problem except for its uniquely comose seed tips.

57B. Xyris paraensis var. longiceps (Malme) Lyman B. Smith & Downs, Ark. Bot. Estad. São Paulo 4(2): 28. 1966. *Xyris longiceps* Malme, Rec. Trav. Bot. Neerl. 9: 131. 1912. TYPE: "in arenosis inundatis Para (Suriname), *Splitgerber 978*" (lectotype, U). Figure 57B.

Xyris leptostachya Malme, Rec. Trav. Bot. Neerl. 9: 132. 1912.

Leaf blades often longer and wider than in the typical variety, the leaf tips tending to be less thickened, sharper, the habit sometimes perennial or the plants harder-based, more strongly tufted. Spike outline narrower, mostly narrowly ellipsoid, or fusiform-cylindric, mostly 1–2 cm long, rarely wider than 0.4 cm. Lateral sepals predominantly lance-ovate, acute, the narrow keels rather uniformly ciliolate. Seeds mostly 0.5–0.6 mm long.

Distribution. Sandy savanna of mostly low-elevation, southeastern Colombia and eastward (occasionally) into Surinam (abundantly) and northern Brazil (Amapa, Pará).

Selected specimens examined. Colombia. amazonas: frequent in Araracuara savannas, Rio Caquetá, 400 m, 6 Sep. 1959, *Maguire et al. 44162* (NY). vaupés: Río Vaupés, cachivera de Yuruparí, 400 m, 24–26 Oct. 1952, *García-Barriga 14936* (NY); Río Kudujarí: Cerro Yapoboda, ca. 450 m, 5–6 Oct. 1951, *Schultes & Cabrera 14379-a* (GH); Río Negro, San Felipe & vic., *Schultes & Cabrera 18116* (GH); Circasia: savanna, ca. 800 ft., Nov. 1951, *Schultes & Cabrera 19647*. Surinam: Savanna Zanerij I, *Boldingh 3044* (U); zandsavanne bij Zanderij I, 11 Oct. 1958, *van Donselaar 377* (U); Zanderij I, 14 Sep. 1937, *Essed s.n.* (U); prope Jodensavanne (fluv. Suriname) in savannis arenosis, *Heyligers & Knoppe 325* (U); Mata, 15 km in dir. occid. a Zanderij, 27 Nov. 1960, *Kramer & Hekking 2239* (U); Zanderij I, open wet sand savanna, 4 Nov. 1948, *Lanjouw & Lindeman 162* (U, VEN); E of Kopie Peninica R. distr. Commewijne, 16 July 1953, *Lindeman 4407* (U); iter secundum surinamense, July–Sep. 1926, *Pulle 58a* (U). Venezuela. t. f. amazonas: alrededores del Campamento Asisa, margenes del Río Asisa, trib. del Río Parú, 8 May 1973, *Hoyos & Morillo 126* (US, VEN); alrededores de Puerto Ayacucho, 26 Jan. 1978, *Huber & Cerda 1445* (US, VEN); Aeropuerto de Maroa, white sand, 25 Aug. 1978, *Huber 2581* (US, VEN); ca. 30 km al N Puerto Ayacucho, ca. 80 m, 7 Nov. 1979, *Huber 4696* (US); Alto Ventuari, Jan. 1959, *Infante 44016* (VEN); Río Ventuari, Río Parú, etc. Sarranía Parú Expedition, 200 m, 15 Feb. 1949, *Phelps & Hitchcock 461* (NY, US, VEN); Maroa, 23 July 1982, *Stergios & Aymard 4014* (PORT, VDB); Esmeralda Savanna and SE base Cerro Duida, 200 m, 22 Aug. 1944, *Steyermark 57827* (F); Maroa, 80 m, airstrip, 7 Oct. 1983, *Steyermark 129426* (VDB, VEN); Esmeralda, ca. 325 ft., 1 Nov. 1928, *Tate 301* (NY). apure: betw. Río Cinaruco near mouth of Caño San Miguel and southern part of the Galera de Cinaruco, 29–30 Apr. 1977, *Davidse & Gonzalez 12348A* (US, VEN); E side of Galeras de Cinaruco, 6 km N of southernmost tip along Quebrada El Porvenir, ca. 53 airline km NE of Puerto Paez, 21 Feb. 1979, *Davidse & Gonzalez 15571* (MO). bolívar: sabanas e orillas del Río Hacha, ca. 300 m, subiendo el río desde el Salto Hacha, 200–500 m, 16–17 Feb. 1964, *Agostini 266a* (US); sandstone outcrops by Ven 10, ca. 800 m, N of Río Yuruani Ferry, Puente Kumerepa, 19 Dec. 1984, *Kral 72190* (MYF, VDB, VEN, and to be distributed); along Río Karuai, NW of Sta. Teresita de Kavanayen, 1,220 m, *Steyermark 60823A* (US).

The petiolelike constriction of old bracts in this and in var. *polystachya* is created by infolding of the auriclelike bract base. The closest affinity of this variety, other than to var. *polystachya*, is to *Xyris cuatrecasana*, which may turn out to be merely a part of the latter.

58. Xyris mima Lyman B. Smith & Downs, Proc. Biol. Soc. Wash. 73: 250, fig. 4. 1960. TYPE: Brazil. Pará: campo arenoso artificial, Missão Nova, Rio Cururu, região do Alto Rio Tapajos, 12 July 1959, *Egler & Raimundo 791* (holotype, US). Figure 58A, B.

Xyris trisperma Kral & Lyman B. Smith, Phytologia 53: 433–434, fig. 1a–i. 1983. TYPE: Venezuela. Bolívar: cumbre de Cerro Guaiquinima, Salto del Río Szczerbanari (Río Carapo), 1–2 km río arriba del Salto Szczerbanari, 750 m, 20–25 Jan. 1977, *J. A. Steyermark et al. 113149* (holotype, VEN; isotypes, US, VDB).

Solitary or cespitose, slender, mostly low annual (0.5–)1–3 dm high, the stems contracted. Leaves erect or spreading flabellately, 0.5–2.5 dm long; sheaths entire, strongly keeled, less than ½ as long as blades, gradually narrowing from the dilated base to the blade, there producing a narrowly triangular erect ligule to 0.5 mm long or eligulate, the surfaces tuberculate-rugose (rarely smooth); blades narrowly linear to linear-gladiate, strongly flattened, sometimes slightly twisted, apically incurved-acute, the margins tuberculate-scabrid (rarely entire), the surfaces verrucose-scabrid (rarely smooth), strongly nerved, deep reddish green to maroon. Scape sheaths slightly to much shorter than principal leaves, reddish brown below, multicostate, tubular, twisted, opening distally, strongly keeled, producing a short blade. Scapes straight or slightly flexuous, twisted, papillate or rugoscabrid, dull green, subterete to slightly compressed distally, thus oval or elliptic in cross section, bicostate, the costae strong, usually strongly tuberculate-scabrid or papillate. Spikes ovoid to short-cylindric or narrowly ellipsoid, 3–15 mm long, mostly acute, of few–several tightly spirally imbricate bracts with narrow but distinct, usually greenish dorsal areas, the sterile bracts mostly 4–6, the lowest the smallest, slightly shorter than the fertile bracts, ovate, keeled or carinate, grading into the fertile bracts, these mostly broadly ovate to broadly obovate, 4–4.5 mm long, the apex broadly rounded, sometimes emarginate, the margins entire, the backs ecarinate, convex. Lateral sepals free, slightly inequilateral, oblong-curvate, ca. 3–3.5 mm long, the broad, thin keel ciliate mostly from just below middle to the blunt apex. Petal blades broadly obovate, ca. 4 mm long, yellow, the broadly rounded apex lacerodentate. Staminodia bibrachiate, the narrow, flat branches penicillate-ciliate distally with clavate hairs. Anthers broadly oblong, ca. 0.5 mm long, shallowly bifid, deeply sagittate, on filaments ca. 0.6–0.7 mm long. Capsules broadly obovoid, planoconvex, ca. 2.5 mm long, the placentation basal, the valves lacking septa. Seeds numerous, mostly ellipsoid to fusiform, ca. 1 mm long, pale amber, the tip with a cone of pale bristles, the body finely longitudinally lined.

Distribution. Low, mostly white-sand savanna, Amazonian Brazil and contiguous Venezuela (Bolívar), locally abundant. Known in 1960 but only from the type collection.

Selected specimens examined. BRAZIL. AMAZONAS: Transamazon Highway, 9 km W of Rio dos Pombos, ca. 1.5 km E of Igarapé dos Oombos and ca. 64 km E of the Aripuanã, 19 June 1979, *Cleofé Calderón et al. 2577* (INPA, US, VDB); base of Serra Araca, 0–3 km south of Central Massif, 3 km E of Rio Jauari, 7 Feb. 1984, *Prance et al. 28870* (INPA, NY, US). MATO GROSSO: R. Juruena, Cachoeira São Simaõ, 21 May 1977, *Rosa & Santos 1959* (INPA, US, VDB). PARÁ: Mun. Itaituba, arredores da Base Aerea do Cachimbo, proximo ao destacamento km 6 da estrada que vai para o aeroporto km 794, 25 Apr. 1983, *Silva et al. 82* (INPA, NY, VDB). VENEZUELA. BOLÍVAR: topotype of *X. trisperma* Kral & Smith, 20–25 Jan. 1977, *Steyermark et al. 113222, 113445* (VDB, VEN).

This species very much resembles *X. savanensis* and *X. paraensis* var. *paraensis*. From the former it differs in its strongly bicostate scape, staminodia with beards, and longer and scaly-comose seeds. From the latter it usually differs in being much more scabrid of foliage and in its bicostate scape and longer, comose-tipped seeds.

In the Venezuelan locality the Steyermark discovery, found in a mixed population with *X. savanensis*, seemed to depart enough from

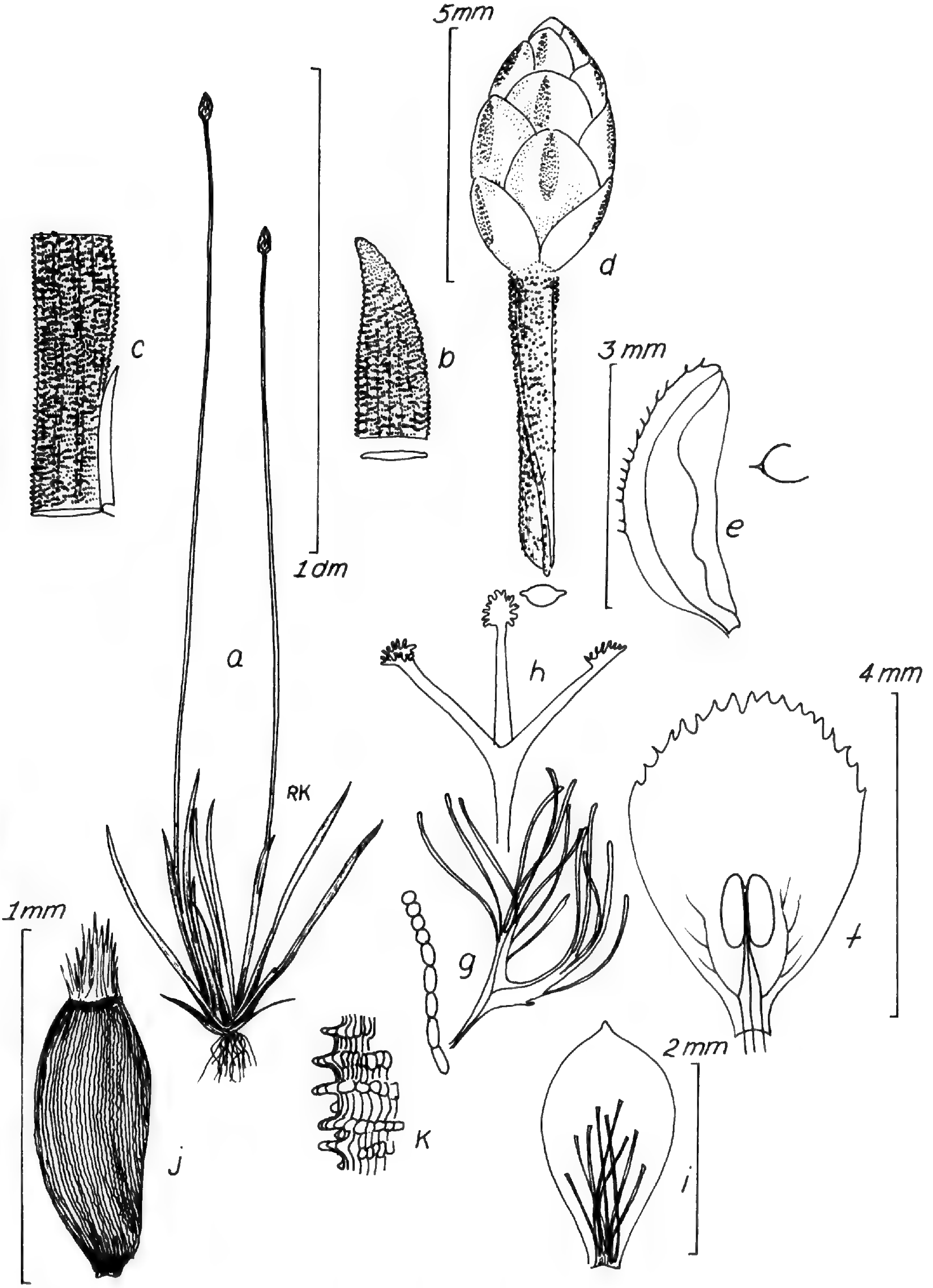


FIGURE 58A. Xyris mima (Steyermark & Dunsterville 113445).—*a. Habit sketch.—b. Leaf tip.—c. Leaf sheath–blade junction.—d. Spike, upper scape.—e. Lateral sepal.—f. Petal blade, stamen.—g. Staminode.—h. Stylar apex.—i. Capsule, two valves removed.—j. Seed.—k. Much-enlarged sector of leaf blade edge.*

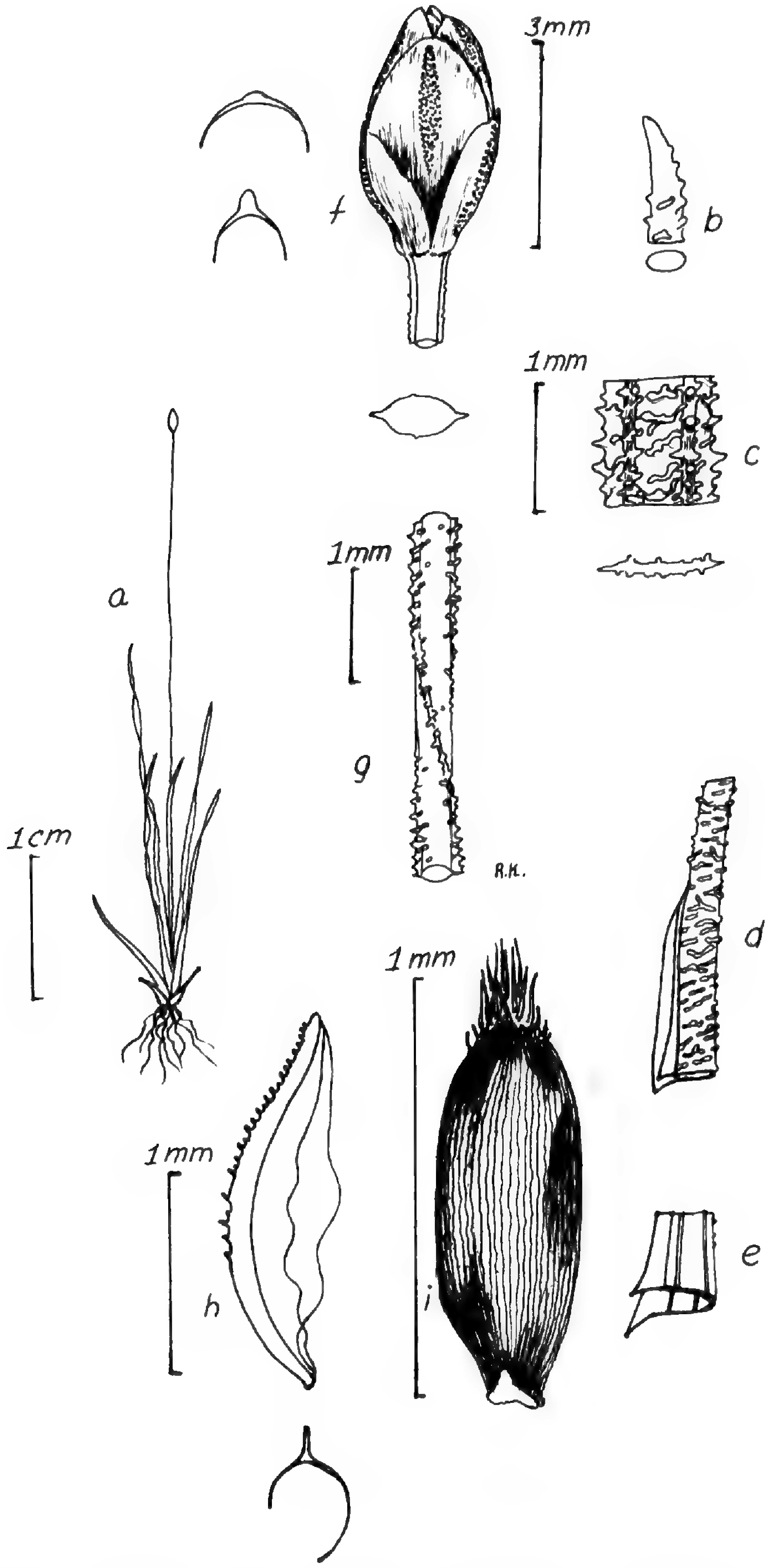


FIGURE 58B. Xyris mima *(from type of* X. trisperma*)*.—*a. Habit sketch.—b. Leaf tip.—c. Leaf blade, sector at midblade.—d. Leaf sheath–blade junction.—e. Leaf base.—f. Spike, upper scape.—g. Midscape sector.—h. Lateral sepal.—i. Seed.*

the original Smith and Downs description in regard to seed and sepal characters to warrant description. Cryptic species are not rare in *Xyris*, should be looked for, and at least for now deserve some place in the literature if only to acquaint readers with the "motion" in such a genus. However, it now appears, on consultation with a larger series of *X.*

mima, that *X. trisperma* fits within the former.

59. Xyris rubrolimbata Heimerl, Ann. k. k. Naturh. Hofmus. Wien 21: 70, pl. 4, figs. 4–6. 1906. TYPE: Colombia. Vaupés: moist sandy woods, Lomo, 100 km northwest of mouth of Casiquiare, Vaupés, Colombia, *Spruce 2994* (lectotype at W destroyed; isolectotype, K). Figure 59.

Low, cespitose, small but stiff annual mostly 0.5–1 dm high, the stems contracted, the roots capillary. Leaves spreading flabellately, 2–8 cm long, the sheaths from nearly as long as blades to longer, soft, strongly keeled, strongly nerved, entire, tapering gradually from the dilated base to the blades, there producing a narrowly triangular, erect, scarious ligule to 2 mm long; blades flattened, straight or rarely slightly twisted, linear-gladiate, narrowly acute, the margins cartilaginous-incrassate, usually forming a distinct, reddish brown band, the surfaces greenish gray or maroon, strongly and palely multinerved, smooth. Scape sheaths slightly shorter than principal leaves, tubular and twisted at base, striate, open toward apex, keeled, producing a short, flat, linear-triangular blade. Scapes straight or slightly flexuous, slightly twisted, terete distally, ca. 0.7 mm thick, greenish brown, striate, smooth. Spikes obovoid at maturity ca. 5 mm long, blunt, of several subdecussately arranged brown bracts with thin, usually fimbriolate margins and distinctly papillose dorsal areas; sterile bracts narrowly to broadly ovate, usually 4, the lowest pair ca. ½–⅔ as long as the spike, keeled, navicular; fertile bracts broadly obovoid, 3–3.5 mm long, the shallowly rounded or subtruncate apex aging erose, the backs slightly convex, the dorsal areas bisected by a single strong nerve. Lateral sepals strongly curvate, free, subequilateral, 2.5–3 mm long, blunt, yellow-brown, the firm, wide keel ciliolate-scabrid from ca. the middle to the apex. Petal blades obovate, ca. 3 mm long, the broadly rounded apex lacerate. Staminodia slightly bibrachiate, the broad, flat branches distally penicillate-ciliate. Capsule planoconvex, broadly obovoid, ca. 1.5 mm long, the placentation basal, the valves without septa. Seeds numerous, ellipsoid, 0.6–0.7 mm long, pale-apiculate, dark, translucent red-brown, longitudinally finely and spirally ribbed, the ribs finely beaded.

Distribution. Low Amazon caatinga, wet sand in southeastern Colombia and southwestern Venezuela, apparently rare.

Additional specimens examined. COLOMBIA. VAUPÉS: Río Guainía, Puerto Colombia (opposite Ven. Town of Maroa) and vic., ca. 800–850 ft., 31 Oct.–2 Nov. 1952, *Schultes et al. 18195* (GH). VENEZUELA. T. F. AMAZONAS: Río Negro at base of Cerro Cucuy, 2 Mar. 1944, *Baldwin 3212* (US); Maroa–Yavita rd., between Río Guianía and Caño Pimichin, at edge of bana (low Amazon caatinga) on wet white sand, 8 Oct. 1978, *Clark 6875* (NY); Maroa, 127 m, Guainía Alto Río Negro en malezas de terreno arenoso, 11 Feb. 1942, *Ll. Williams 14280* (F, US, VEN).

This little but uniformly distinctive annual xyris is so small as to be overlooked easily. It should be looked for in areas of Amazonian Brazil in places along the upper Rio Negro.

60. Xyris cuatrecasana Idrobo & Lyman B. Smith, Caldasia VI(29): 244–245, fig. 30a–d. 1954. TYPE: Colombia. Vaupés: Comisaria del Vaupés. Circasia; margenes del Vaupés, sobre granitos, 200 m, 9 Oct. 1939, *J. Cuatrecasas 7155* (holotype, COL; isotype, F). Figure 60.

Solitary or cespitose, soft-based annual to 3.5 dm high, the stem contracted. Leaves erect or slightly spreading flabellately, 8–12 cm long; sheaths ca. ½ or less as long as blades, entire, dull at base, pale red-brown or stramineous, tapering gradually to blade, there with a scarious, erect, narrow, acute ligule to 2 mm, the blades flat, ensiform-linear, 1.5–2.5 mm wide, tapering to narrowly acute apex, the margins subentire, the surfaces smooth and finely multinerved, green with strong maroon tints. Scape sheaths loose, shorter than leaves, carinate, short-bladed. Scapes lineal, straight or flexuous, slightly twisted, distally terete, ca. 1 mm thick, finely striate, ecostate, smooth. Spike ovoid-ellipsoid, ca. 1 cm long, acute, the numerous bracts tightly spirally

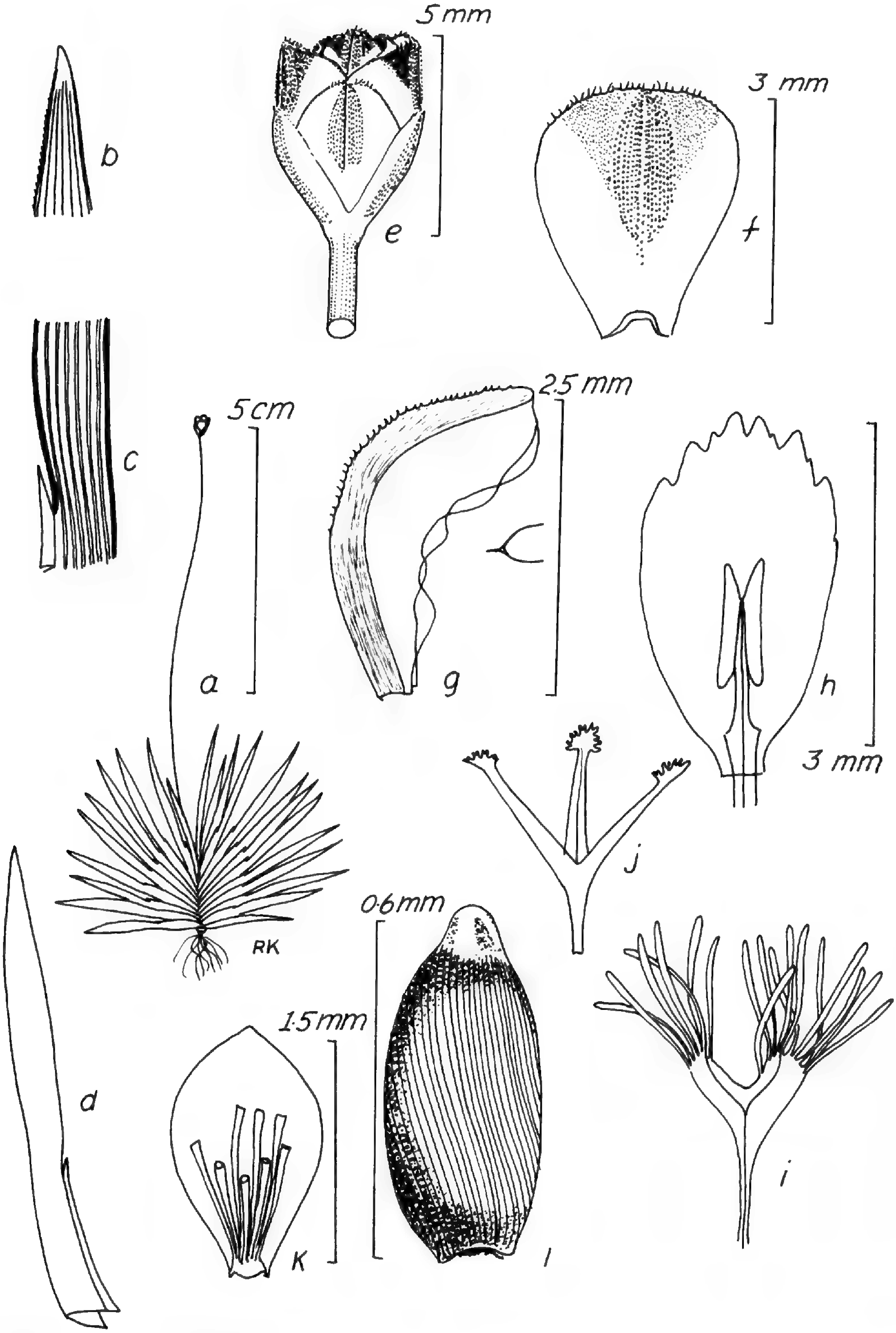


FIGURE 59. Xyris rubrolimbata (J. T. Baldwin 3212).—*a. Habit sketch.—b. Leaf apex.—c. Leaf blade-sheath junction.—d. Leaf, outlined.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode.—j. Stylar apex.—k. Capsule, two valves removed to show placentation.—l. Seed.*

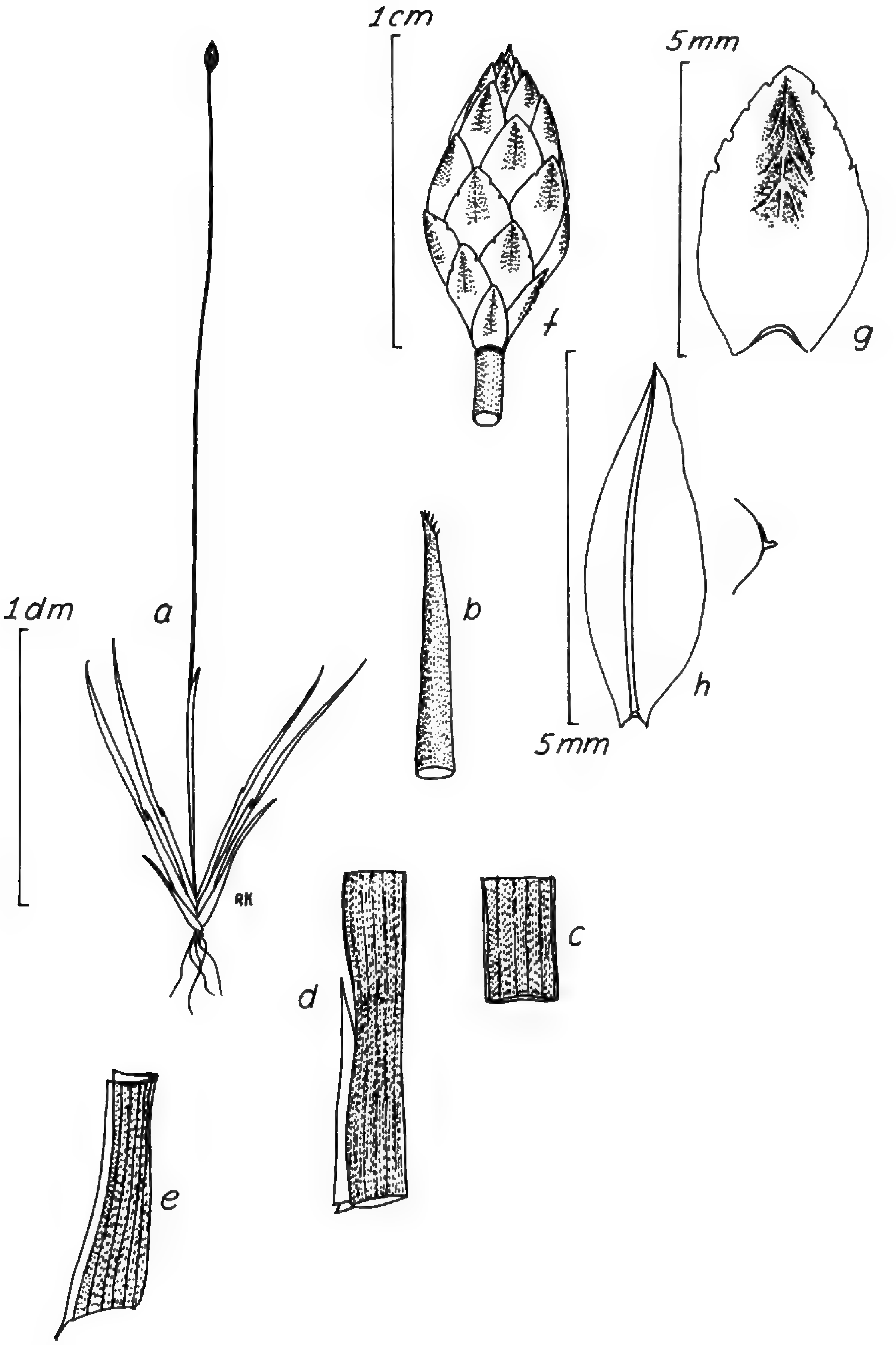


FIGURE 60. Xyris cuatrecasana *(from the isotype).—a. Habit sketch.—b. Leaf apex.—c. Sector of blade at midblade.—d. Leaf sheath–blade junction.—e. Leaf base.—f. Spike and upper scape.—g. Fertile bract.—h. Lateral sepal.*

imbricate, thin, the sterile bracts several, smaller than the fertile bracts and grading into them, these ovate, ca. 5 mm long, acute, ecarinate, with strong, dark, lanceolate, venose dorsal areas and scarious, subentire to erose edges. Lateral sepals free, subequilateral, ca. as long as bracts, very thin, lanceolate, narrowly acute, the firm, narrow keel subentire. Corolla, staminodes, and stamens not seen. Immature capsule ellipsoid, ca. 4

mm long, the valves eseptate, the placentation basal. Immature seeds ellipsoid, ca. 1 mm long.

Distribution. Known only from the type.

This is perhaps not distinguishable from *Xyris paraensis* and except for the equilateral sepals could be considered a disjunct collection of var. *polystachya* of that species. However, until more information (seeds, flowers) becomes available, it seems best to retain the taxon.

61. Xyris pectinata Kral, Lyman B. Smith & Wanderley, sp. nov. TYPE: Brazil. Amazonas: Estrada Transamazônica–Capim, campina aberta, terreno arenoso, Proj. RADAM, 1 June 1976, *T. R. Bahia 35* (holotype, INPA; isotypes, US, VDB). Figure 61.

Herba perennis densicaespitosa, tenella, glabra; radices graciles. Folia linearia, 4–6 cm longa, erecta vel leviter expansa, vaginis scaporum longiora. Laminae planae vel leviter tortae, 0.9–1.2 mm latae, vaginis 3–5-plo longiores, longitudine distincte multinervosae, ferrugineae vel olivaceae; apices contracti, incurvato-acuti; margines incrassati, minute ciliati; vaginae carinatae, carinibus persaepe minute rufociliatis, incrassatis, lateribus valde longitudine multicostatae, pallide vel intense ferrugineae, marginibus in laminas gradatim convergentibus, ad apicem ligulam acutam 0.5 mm longam fascientes, infime gradatim dilatatae. Vaginae scaporum laxae, plerumque apertae, tortae, basin versus nitidae, a medio carinatae, laminis aut similibus laminis foliorum aut brevibus. Scapi subteretes, filiformes, plus minusve spiraliter torti, 1.2–2 dm alti, ca. 0.4–0.5 mm crassi, olivacei, distaliter acute bicostati, costis laevibus. Spicae subglobosae vel late obovoideae, 4.5–6 mm longae, pluriflorae, breviter attenuatae; bracteae steriles 2(–4), paro infimo oblongo, 2–2.5 mm longo, areis dorsalibus linearibus bracteam aequantibus; bracteae fertiles arcte spiraliter imbricatae, late ovatae, obovatae, suborbiculatae, aut reniformes, ca. 3 mm longae, convexae et leviter carinatae, obtusae vel subtruncatae, ad apicem utrinque erosae et ciliatae, scariosae, minute tuberculato-rugulosae, a medio ad basim multo crassiores, nitidae, brunneolae, marginibus effuse et pectinate rigofimbriatis; area dorsali ovata, ca. 2–2.5 mm longa, glauca. Sepala lateralia ca. ½ connata, ca. 2 mm longa, inaequilateralia, lobis acutis scariosis, ala carinali angusta, integra. Laminae petalorum anguste obovatae, ca. 1.5 mm longae, ad apicem rotundatae, laceratae, luteolae. Staminodia aliquantum redacta, bibrachiata, brachiis ad apicem breviplumosis, pilis moniliformibus. Antherae oblongae, ca. 0.3–0.4 mm longae, loculis parallelis distinctis; filamenta ca. 0.5 mm longa. Capsula dorsali-ventraliter compressa, oblongo-cylindrica, tenuissima, 1.2–1.3 mm longa; placenta basalis. Semen solitarium, lenticulariter oblongo-ellipsoideum, 1–1.2 mm longum, translucidum, pallide luteo-brunneolum, longitudine subtiliter striatum.

Delicate, smooth, cespitose perennial; roots slender. Leaves linear, 4–6 cm long, erect or somewhat spreading, longer than the scape sheaths; blades 3–5 times longer than the sheaths, plane or slightly twisted, 0.9–1.2 mm wide, longitudinally distinctly multinerved, strongly flattened, ferrugineous to olive green; apices contracted, incurved-acute; margins thickened, minutely ciliate; sheaths carinate, with carinae minutely red-ciliate, incrassate, the sides strongly longitudinally nerved, pale to deep red-brown, the margins gradually converging into the blade, at apex producing an acute ligule 0.5 mm long, gradually dilating below. Sheaths of scales lax, mostly open, twisted, shining toward the base, carinate at the middle, with blades either similar to those of principal leaves or shorter. Scapes subterete, filiform, ± spirally twisted, 1.2–2 dm high, ca. 0.4–0.5 mm thick, olivaceous, sharply costate distally, the costae smooth. Spikes subglobose to broadly obovoid or short-cylindric, 4.5–6 mm long, several-flowered, short-attenuate; sterile bracts 2 (–4), the lowest pair oblong, 2–2.5 mm long, with dorsal areas linear and equal to them in length; fertile bracts tightly spirally imbricate, broadly ovate, obovate, suborbicular, or reniform, ca. 3 mm long, convex and slightly carinate, obtuse to subtruncate at apex on either side, erose, scarious, minutely rugulose-tuberculate, much thicker from the middle to the base, shining, brownish, with margins effusely and pectinately rigidly fimbriate; dorsal area ovate, ca. 2–2.5 mm long, gray-green. Lateral sepals ca. ½ connate, ca. 2 mm long, inequilateral, the lobes acute, scarious, the carinal keel narrow, entire. Petal blades narrowly obovate, ca. 1.5 mm long, apically rounded, lacerate, yellow. Staminodia somewhat reduced, bibrachiate, the branches at apex short-plumose with moniliform hairs. Anthers oblong, ca. 0.3–0.4 mm long, the locules parallel, distinct; filaments ca. 0.5 mm long. Capsule dorsiventrally compressed, oblong-cylindric, very thin, 1.2–1.3 mm long;

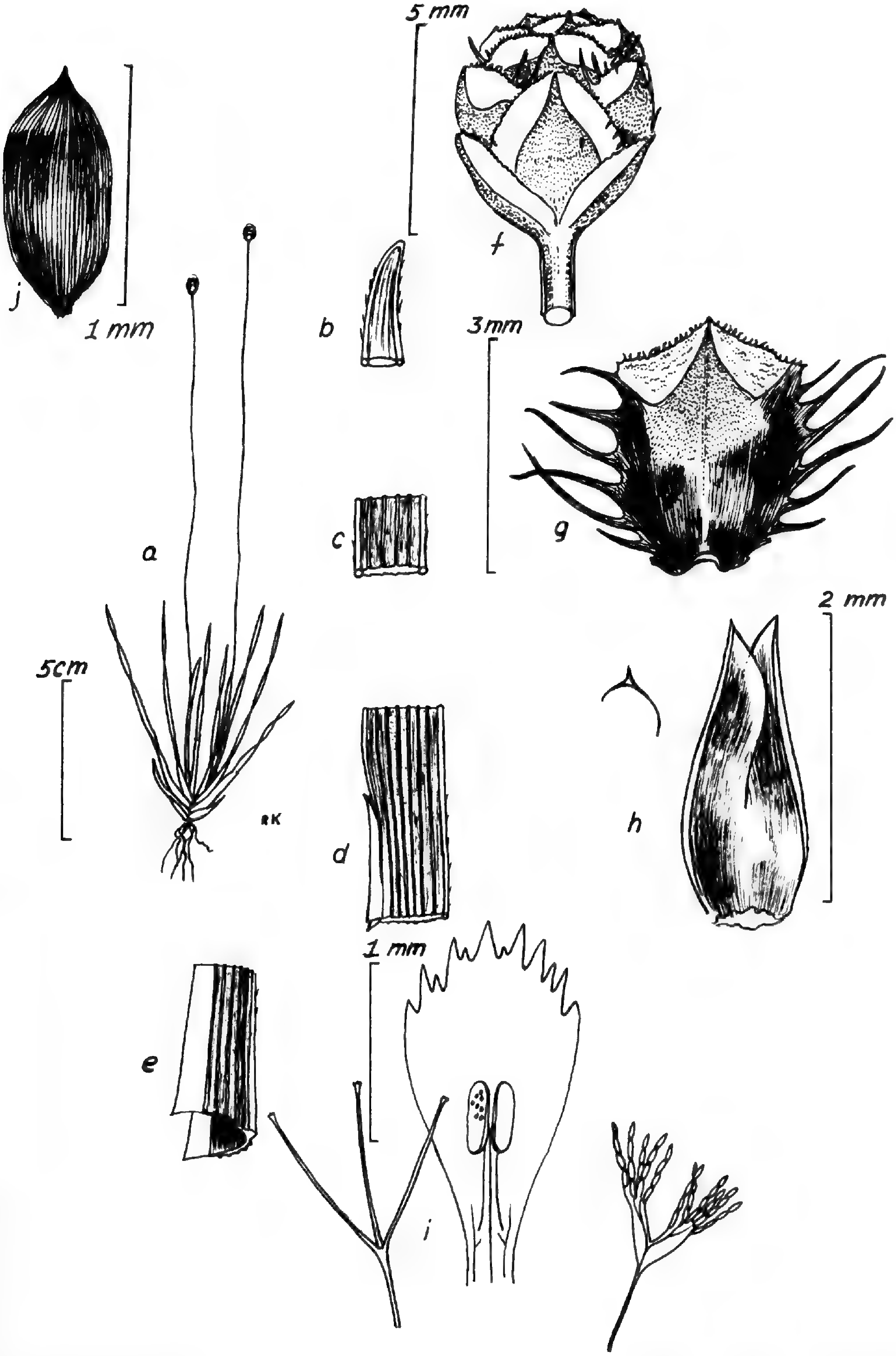


FIGURE 61. Xyris pectinata (T. R. Bahia 35).—*a. Habit sketch.—b. Leaf tip.—c. Sector of midblade.—d. Blade-sheath junction.—e. Leaf base.—f. Spike.—g. Fertile bract.—h. Lateral sepals.—i. Stylar apex, petal blade, stamen, staminodial apex.—j. Seed.*

placenta basal. Seed solitary, lenticularly oblong-ellipsoid, 1–1.2 mm long, filling capsule, translucent, pale yellow-brown, finely longitudinally striate.

Additional specimens examined. BRAZIL. AMAZONAS: Transamazona Highway, 53 km W of Aripuaná River; "campina" region, common in open campina of white sandy soil, 27 June 1979, *C. E. Calderón, O. P. Monteiro & J. Guedes 2696* (INPA, US, VDB); Município de Borba, acima de Terra Preta, campina do Rio Surubím, afluente do Rio Abacaxis, 4°29'S, 58°33'W. Campina aberta, areia branca. Erva de 10 cm de altura; flores amarelas, 4 July 1983, *C. A. Cid 4026* (INPA, NY, VDB).

This species is easily distinguished by its fringe of strong though slenderly tapering rigid bristles on the margins of the fertile bracts, nearly separate anther locules, and reduced staminodial condition. It is unusual in its particularly small and thin-walled capsule, this tightly filled by a single large seed.

62. **Xyris savanensis** Miq., Linn. 18: 605. 1844. TYPE: "Surinam, Berlyn, *Focke 1022*" (holotype, U). Figure 62.

Solitary or cespitose, soft-based annual 1–5 dm high; stem contracted. Leaves spreading flabellately to erect, (2–)5–20(–25) cm long; sheaths ½ or less as long as blades, entire, red-brown to tan or brown, papillose-rugulose, narrowing gradually from wide base to blade, there with an erect, narrowly triangular ligule to 0.5 mm long, or eligulate; blades flat, slightly twisted, gladiate-linear, 1–5 mm wide, narrowing gradually above middle to a narrowly acute apex, the margins slightly thickened or not thickened, papillose to scabrid, surfaces mostly rugose-scabrid. Scape sheath shorter than leaves, multicostate and tubular, keeled, open and short-bladed above. Scapes straight or flexuous, twisted, terete or subterete distally, 0.5–1 mm thick, ecostate to tricostate or striate, the costae and surfaces scabridulous or papillose (rarely nearly smooth). Spikes ovoid to cylindric, ellipsoid or subglobose, 0.3–0.7(–1) cm long, with many spirally imbricate bracts, these tan or reddish brown with darker green or maroon dorsal areas; sterile bracts smaller than fertile bracts, grading into them, the fertile bracts broadly obovate to suborbicular, 3–5 mm long, the apex broadly rounded, entire, backs strongly convex-rounded, ecarinate. Lateral sepals free, very inequilateral, elliptic, ca. 3 mm long, acute to obtuse, the strong, curvate keel irregularly ciliate and/or ciliolate. Petal blades broadly obovate, yellow, 2–2.5 mm long. Staminodia bibrachiate, the lance-linear branches beardless. Anthers oblong, ca. 0.5 mm long, deeply emarginate and sagittate on filaments about as long. Capsule broadly obovoid, 1.5–2.5 mm long, placentation basal. Seeds numerous, ellipsoid or ovoid, 0.4–0.5 mm long, apically truncate and minutely apiculate, the body pale yellow-brown or red-brown, translucent, faintly 20–24-ribbed and indistinctly cross-lined.

Distribution. South America, from the Andean foothills eastward, mostly at low to medium elevations, south into Argentina. Records of this species from Mesoamerica have all turned out to be *X. paraensis.* It is so commonly collected that even a partial citation of records (as in the case of the equally common *X. jupicai, X. laxifolia, X. fallax*) is better done separately.

It is not surprising that a widespread, common, and weedy xyris would show considerable variation in habit and in character of indumentum, pigmentation, and other features. Thus two additional varieties, *X. savanensis* var. *glabrata* Seubert, (Fl. Bras. 3(1): 217. 1855) and var. *procera* (Malme) Malme (Ark. Bot. 13(3): 53. 1913), have been described along with some forms. The former variety, as the name suggests, has totally smooth foliage, while the latter assumes (sometimes?) a perennial habit. The species nearest it taxonomically is *X. paraensis*, and here would be a great difficulty were it not for a pair of characters that, regardless of variety, appear to hold throughout the range. All specimens of *X. savanensis* lack bearded staminodes; all have seed uniformly truncate at apex, there with a short but distinguishable apiculus.

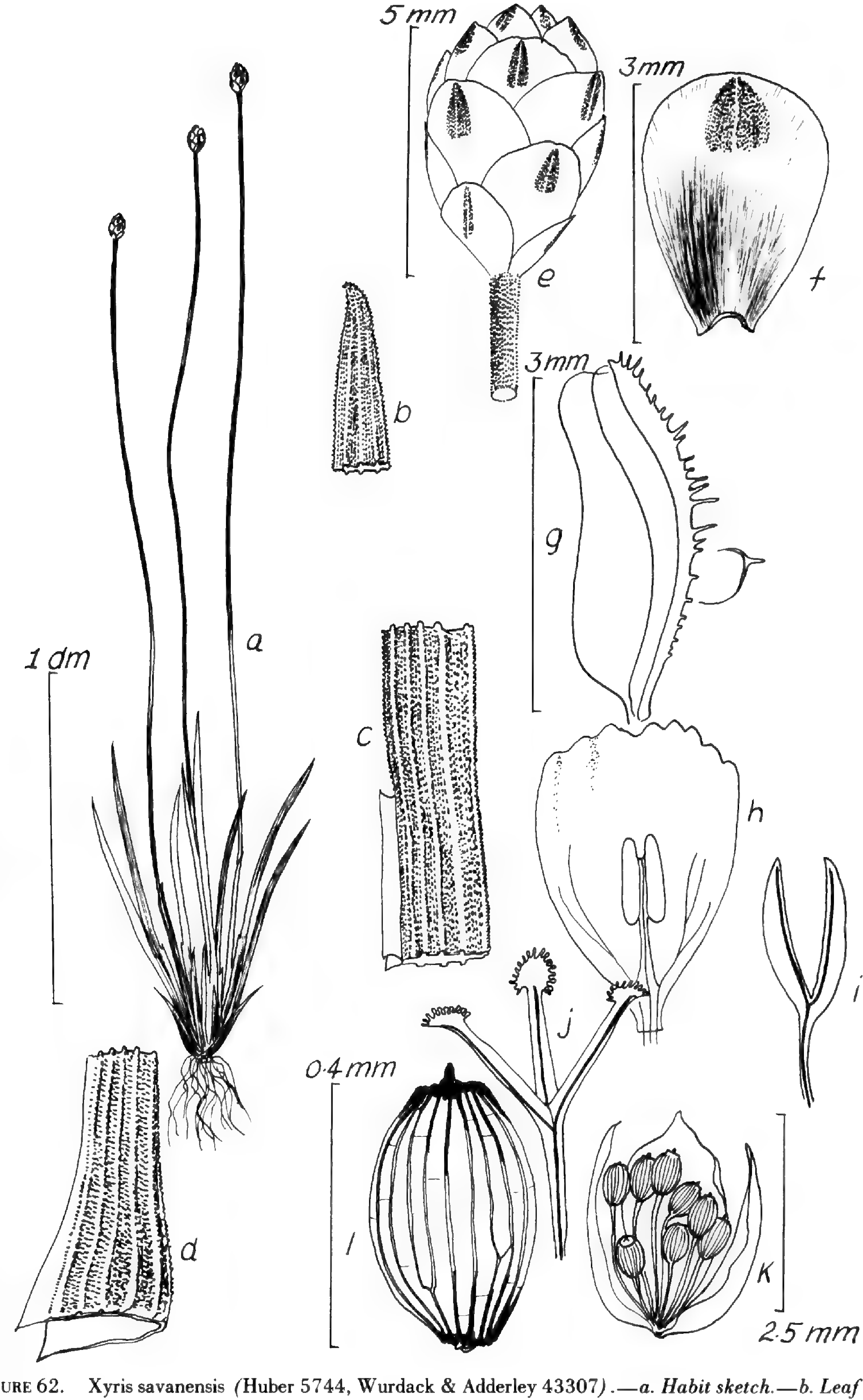


FIGURE 62. Xyris savanensis (Huber 5744, Wurdack & Adderley 43307).—*a. Habit sketch.—b. Leaf apex.—c. Leaf at junction of sheath and blade.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode.—j. Stylar apex.—k. Dehiscing capsule.—l. Seed.*

63. Xyris surinamensis Sprengel, Tent. Suppl. Syst. Veg. Linn. 2. 1828. TYPE: "Suriname, *Weigelt*, 1827" fide J. Lanjouw, Rec. Trav. Bot. Neerl. 34. 1937. Possibly (fide Lanjouw) based on same material as *X. eriophylla* Reichenb., but still a problem, the marked type not found. Figure 63A, B.

X. eriophylla Reichenb., Pl. Excic. Weigelt, 1827 (?). TYPE: Surinam, Leg. & Exc. *Weigelt 1827* (?lectotype at Delessert Herbarium; isolectotype, MO; phototype, GH).

Cespitose, hard-based, often bulbous, stocky perennial 2.5–4 dm high. Leaves often nearly as long as scapes, ascending or slightly spreading, 1.5–3 dm long; sheaths long-ciliate, usually with brownish hairs, the dilated base ecarinate, red to purple or deep brown, rugose, gradually narrowing to leaf blade, mostly eligulate; blades linear, flattened, 2–4 mm wide, often twisted, dull green, abruptly blunt-tipped or incurved-acute to incurved-narrowly rounded, the margins mostly pale, incrassate, ciliate or scabrociliate, rarely papillate; surfaces rugulose, strongly nerved, the strongest nerves often pale-incrassate, often hirtellous or scabridulous. Scape sheaths highly variable, keeled, from much shorter than leaves and elaminar to nearly as long and similar in blade. Scapes flexuous, twisted, flattened, distally 2–3 mm wide with strong costae comprising edges, often with one or both costae pale pilose-ciliate or scabrid, the sides pale yellow-green, strongly rugose, sometimes with additional lower costae. Spikes subglobose or broadly turbinate, 0.8–1 cm long, of many spirally imbricate or subdecussate, stiff, dull brown or red-brown, ciliolate or entire bracts with large, ovate dorsal areas. Sterile bracts ovate-triangular, slightly keeled, lower bracts much smaller than the fertile bracts and grading into them, the fertile bracts oblong to obovate, 6–8 mm long, slightly carinate, apically obtuse-angled or narrowly rounded, the dorsal area of lower ones venose and sometimes white pilose. Lateral sepals free, subequilateral to inequilateral, lance-linear, curvate, 5–7 mm long, acute, the firm keel lacerate, villosulous or ciliolate from middle to apex. Petal blades broadly obovate, 5–6 mm long, yellow, the broadly rounded apex erose-denticulate. Staminodia bibrachiate, the slender branches densely long penicillate-ciliate. Anthers oblong, ca. 2 mm long, deeply bifid and sagittate, on filaments ca. 1.5 mm long. Capsule narrowly to broadly obovoid, 4–5 mm long, the placentation appearing basal-central, but the valves dehiscing to reveal strong septa. Seeds few, cylindric-fusiform, ca. 1 mm long, pale amber, faintly longitudinally striate and cross-lined, often additionally with a few, conspicuous, irregular, dark red-brown ribs.

Distribution. Locally abundant in low- to high-elevation savanna from southeastern Colombia eastward across southern Venezuela into French Guiana, southward into Amazonas and Pará, Brazil.

Selected specimens examined. BRAZIL. AMAZONAS: Serra Aracá, 10 Feb. 1975, *Pires 15000* (MG, US, VDB); margens de um riacho da serra Aracá, 1 Nov. 1978, *Rosa & Lira 2343* (US). COLOMBIA. AMAZONAS: scrub savanna, Araracuará, Río Caquetá, 5 Sep. 1959, *Maguire et al. 44111* (NY, VEN). VAUPÉS: Cerro Yapobodá, 5 Oct. 1951, *Schultes & Cabrera 14234-A* (GH); Cerro Kanenda, ca. 800–900 ft., 10 Nov. 1952, *Schultes & Cabrera* (GH). GUYANA: Saesdyke, Nov. 1973, *Cooper 51* (U); N Rupununi, Apr. 1968, *Davis 773* (K); Wenamu Trail, Krabu Savanna, 28 Oct. 1966, *Forest Dept. Brit. Guiana Field No. R. B. 139*, Record No. *7972* (K); Rupununi Distr., Chaakoitou, near Mountain Point, 26 Oct. 1979, *Maas & Westra 4051* (K, U, US); Pakaraima Mts., Mt. Membaru, ca. 400 m, 12 Nov. 1979, *Maas & Westra 4342* (K, U, US); Pakaraima Mts., Kako Amerindian vill., 13 Nov. 1979, *Maas & Westra 4371* (U, US); same locality, Mt. Aymatoi, 1,150 m, 15 Oct. 1981, *Maas et al. 5691* (NY, U, VDB); Kopinang Savanna, Kopinang Falls, 2,700 ft., 30 Aug. 1961, *Maguire et al. 46015* (K); Kaietur Savanna, 1,100 ft., 7 Sep., *Sandwith 1420* (U); Kaietur Savanna, 30 Aug. 1933, *Tutin 659* (U). SURINAM: Zanderij, 21 Mar. 1959, *van Donselaar 479* (U); Zanderij, Kruid, 21 Dec. 1950, *Florschutz 737* (U); same locality, 22 July 1933, *Lanjouw 135* (U); Upper Commewijne River, W of Sapende, 14 July 1953, *Lindeman 4241* (C, U); Iter secundum surinamense, July–Sep. 1920, 28 July, *Pulle 45* (U); Nat. Res. Brinckheuvel (Saban Pasi Savanne), 2 Sep. 1967, *Wildschut & Teunissen 11602* (U). VENEZUELA. T. F. AMAZONAS: Serranía del Parú, 1,100 m, 3–4 Oct. 1979, *Huber 4287, 4323, 4331* (VEN), *4333* (US); sabana ubicada en la margen derecha (E) del bajo Río Pacimoni, *Huber & Medina 5871* (VEN, VDB); summit Cerro Guanay, 1,800 m, 2 Feb. 1951, *Maguire et al. 31701* (NY, VEN); Caño Hechimoni, 8 km above mouth Río Siapa, 9 Feb. 1954, *Maguire et al. 37637* (GH, NY, VEN); Esmeralda between Esmeralda Savana and

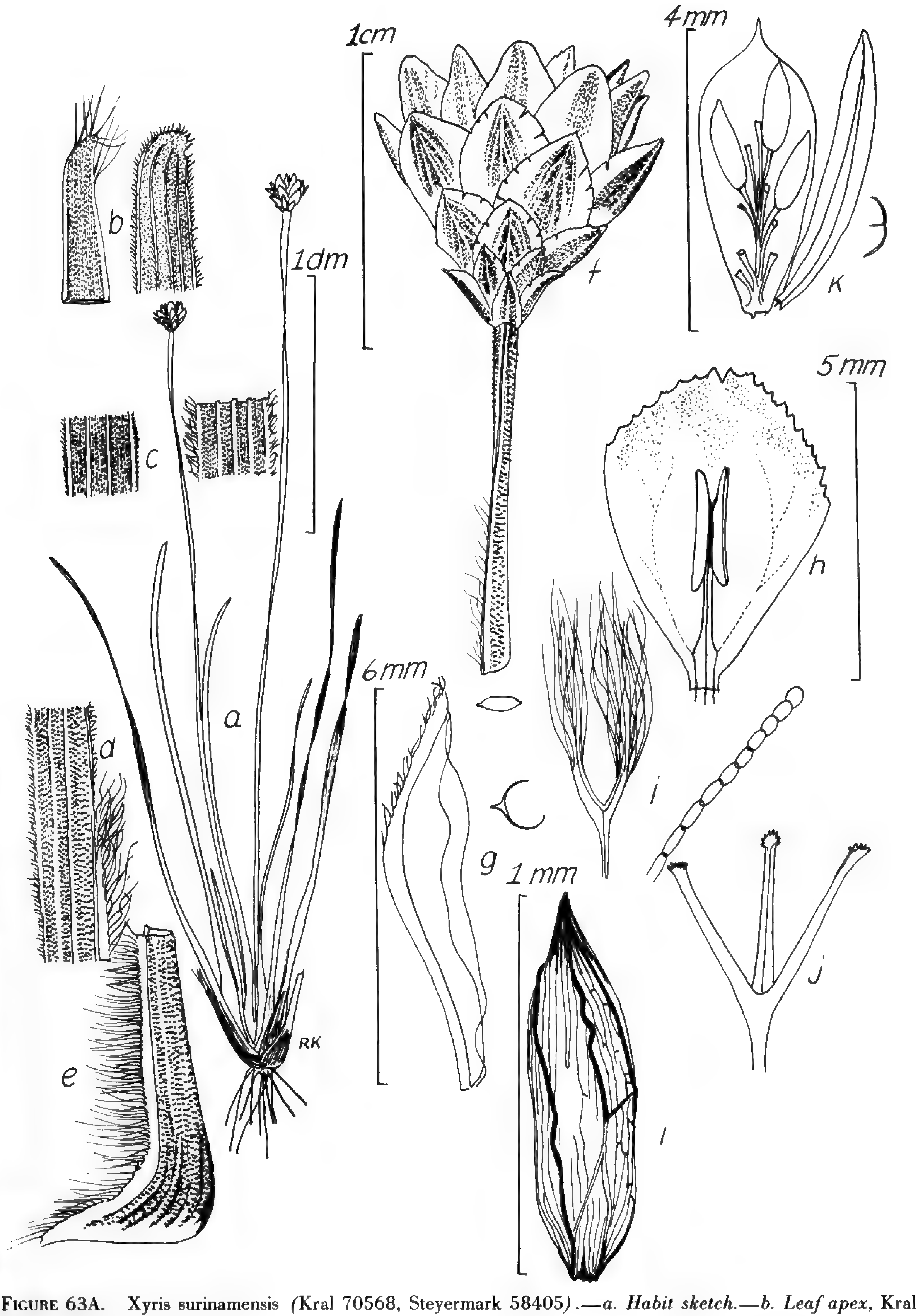


FIGURE 63A. Xyris surinamensis (Kral 70568, Steyermark 58405).—*a. Habit sketch.—b. Leaf apex,* Kral 70568 *at left,* Steyermark 58405 *at right.—c. Leaf at midblade,* Kral 70568 *at left,* Steyermark 58405 *at right.—d. Leaf at sheath apex.—e. Leaf base.—f. Spike.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode, enlarged apex of beard hair.—j. Stylar apex.—k. Capsule.—l. Seed.*

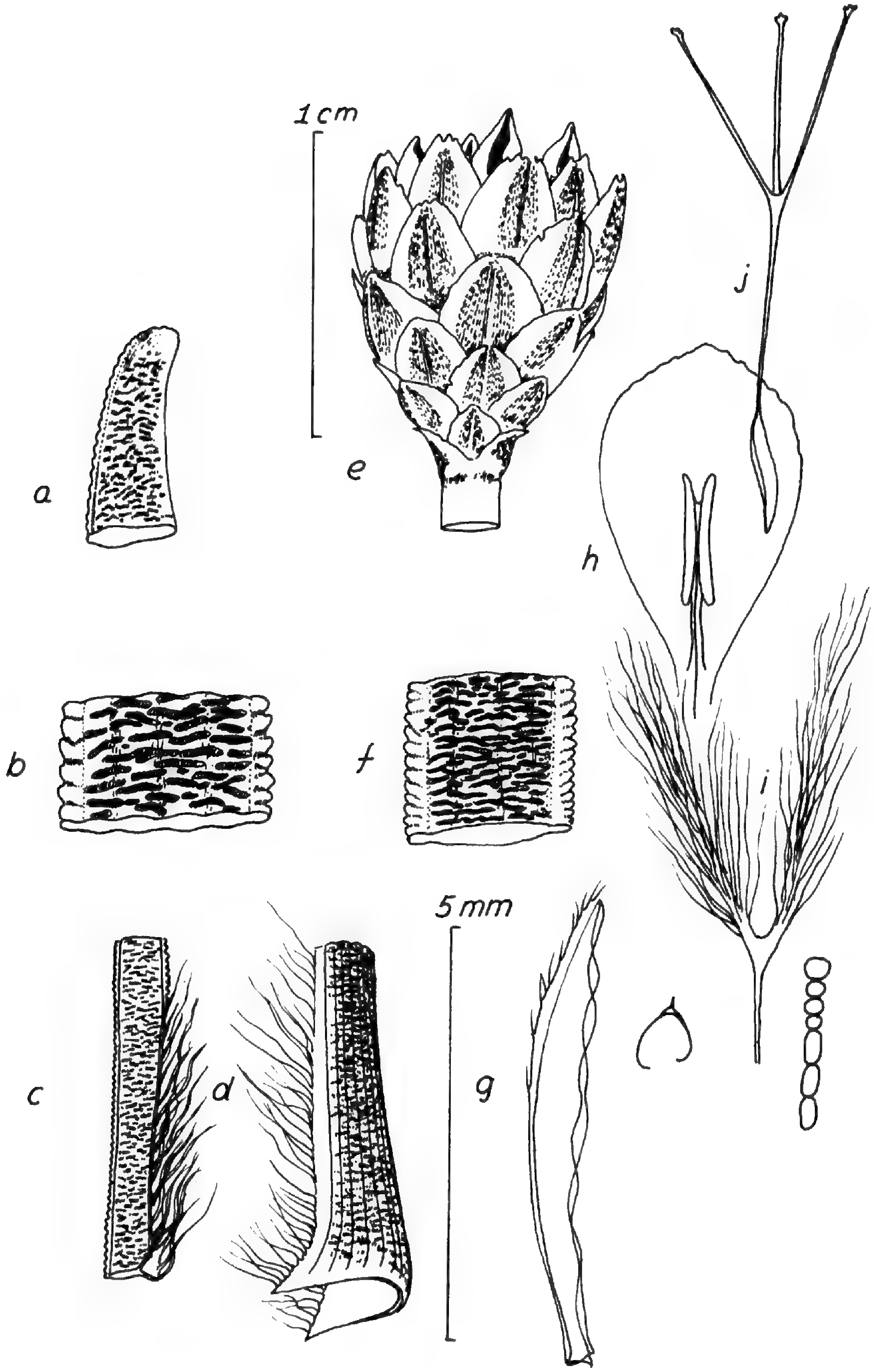


FIGURE 63B. Xyris surinamensis (Pires 15000).—*a. Leaf apex.—b. Sector of leaf midblade.—c. Leaf-sheath junction.—d. Leaf base.—e. Spike.—f. Sector of upper scape.—g. Lateral sepal.—h. Petal, stamen.—i. Staminode.—j. Stylar apex.*

Sabana Grande, NE of Esmeralda, 6 Sep. 1944, *Steyermark 58405* (F, NY); Grand Savanna, Esmeralda, ca. 325 ft., 1 Nov. 1928, *Tate 304* (C, NY). BOLÍVAR: cerca de San Rafael de Camoiran, ca. 1,240 m, 8 Jan. 1982, *Cordero y Utrera 5* (PORT); ca. 17 km al NE de Ikabaru, ca. 1,100 m, *Huber et al. 6723* (MYF, VDB, VEN); cerca de la ribera Norte del Río Carrao medio, ca. 8–10 km al NNE de la confluencia Carrao–Churun, 31 Aug. 1983, *Huber et al. 8270* (NY); al E del Churí-tepui en el Vallé del Río Karuay inferior, 18 Nov. 1984, *Huber*

9794 (MYF, VEN, VDB); ca. 5 km al norte del Poblado San Francisco de Yuruaní, 19 Jan. 1985, *Huber 9949* (MYF, VDB); el piedemonte septentrional del Cerro Zumbador, *Huber 10271* (MYF, VDB); ca. 35 km al W del caserio de Chiguao, 23 Mar. 1985, *Huber 10354* (MYF, VDB); 1.5 km E of Kavanayen in Gran Sabana, bog, 27 July 1983, *Kral 70536* (BM, F, L, MO, NY, SP, U, US, VDB, VEN, and others); Salto Yuruani, 28 July 1983, *Kral 70568* (BM, F, K, L, MO, NY, SP, U, US, VDB, VEN, and others); El Pauji, savanna E of town, 2 Nov. 1985, *Liesner 19357* (MO, VDB, VEN); savanna vic. Uriman, 300 m, 30 Apr. 1953, *Steyermark 75265* (C, F, NY, VEN).

As one might suspect from such a wide geographic distribution, the species is highly variable in stature, leaf dimensions, and in indumentum of scapes, leaves, and sepals. Its pale yellow blooms with broad petals expand in morning.

64. Xyris pratensis Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 34, fig. 19A–E. 1963. TYPE: Venezuela. T. F. Amazonas: pubescent, frequent in wet hummocks, Camp Savanna, Campo Grande, 1,500 m, Cerro Sipapo (Paraque), 10 Dec. 1948, *Maguire & Politi 27581* (holotype, NY; isotypes, GH, US). Figure 64.

Cespitose, slender, hard-based perennial 4–5.5 dm high, the stems short, ascending, covered by chaffy bases of old leaves. Leaves erect, 2–4 dm long; sheaths sparsely pilose-ciliate, as long as blades or longer, abruptly constricted above the dilated, deep red-brown base, then narrowing upward and keeled to blade, the margins intermittently pilose-ciliate; blades narrowly linear, flat, 2–3 mm wide, slightly narrowing above middle then abruptly incurved-acute or obliquely acute, the thickened tip often white bristly-ciliate, the margins thin, pale ciliate, the surfaces green with streaks of red, strongly multinerved. Scape sheaths somewhat shorter than leaves, above with strong blades like leaves but narrower. Scapes somewhat compressed distally, ca. 1–1.5 mm wide, elliptic in cross section, with the two costae making edges, strongly pale ciliate or with one costa smooth. Spikes ellipsoid, becoming obovoid, 8–10 mm long, the several bracts subdecussate, rather loosely imbricate, dark red-brown with distinct and usually paler dorsal areas, firm, the sterile bracts narrower and shorter than the fertile bracts, the lowermost keeled, sometimes pilosulous-ciliate, grading into fertile bracts, these oblong, bluntly acute or narrowly rounded, entire or apically villosulous, 6–7.5 mm long, the backs convex, ecarinate but with dorsal areas bisected by a strong costa. Lateral sepals equaling bracts or slightly longer, free, subequilateral, linear-oblanceolate, 7–8 mm long, acute, the dark, firm keel entire or above middle low-lacerate and also often minutely ciliate. Petal blades obovate, ca. 5.5 mm long, yellow, apically broadly acute. Staminodia bibrachiate, the flat branches densely penicillate-pilose. Anthers lance-oblong, deeply bifid, sagittate, 1.5 mm long, on filaments 1 mm long. Capsule ellipsoid, 3–3.5 mm long, placentation central, the valves with strong septa toward base, thus actually placentation axile there. Seeds several, narrowly ellipsoid, ca. 1 mm long, pale amber with a conic white apiculus, the body longitudinally finely but distinctly ribbed.

Distribution. High savanna, cerros Sipapo (Paraque) and Marahuaca, southern Territorio Federal Amazonas, Venezuela, infrequent.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: summit Cerro Marahuaca, 2,685 m, 15 Jan. 1981, *Maguire 65635* (NY, VDB); cumbre del Cerro Paraque, 1,600 m, alto Orinoco, *Phelps 20* (US); Cerro Sipapo, 17 Feb. 1981, *Steyermark 124532* (NY, VDB, VEN).

This species is very evidently closely related to *X. bicostata* Maguire & Lyman B. Smith of Cerro Huachamacari in Amazonas, which differs only in that the plants are (mostly) lower, with smaller and fewer-flowered spikes, and narrower scapes and leaves.

65A. Xyris bicostata Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 30, fig. 14A–F. 1963. TYPE: Venezuela. T. F. Amazonas: frequent on mossy rocky banks, dense woodlands along right fork of Caño de Dios, 1,800 m, Summit Camp, Cerro Huachamacari,

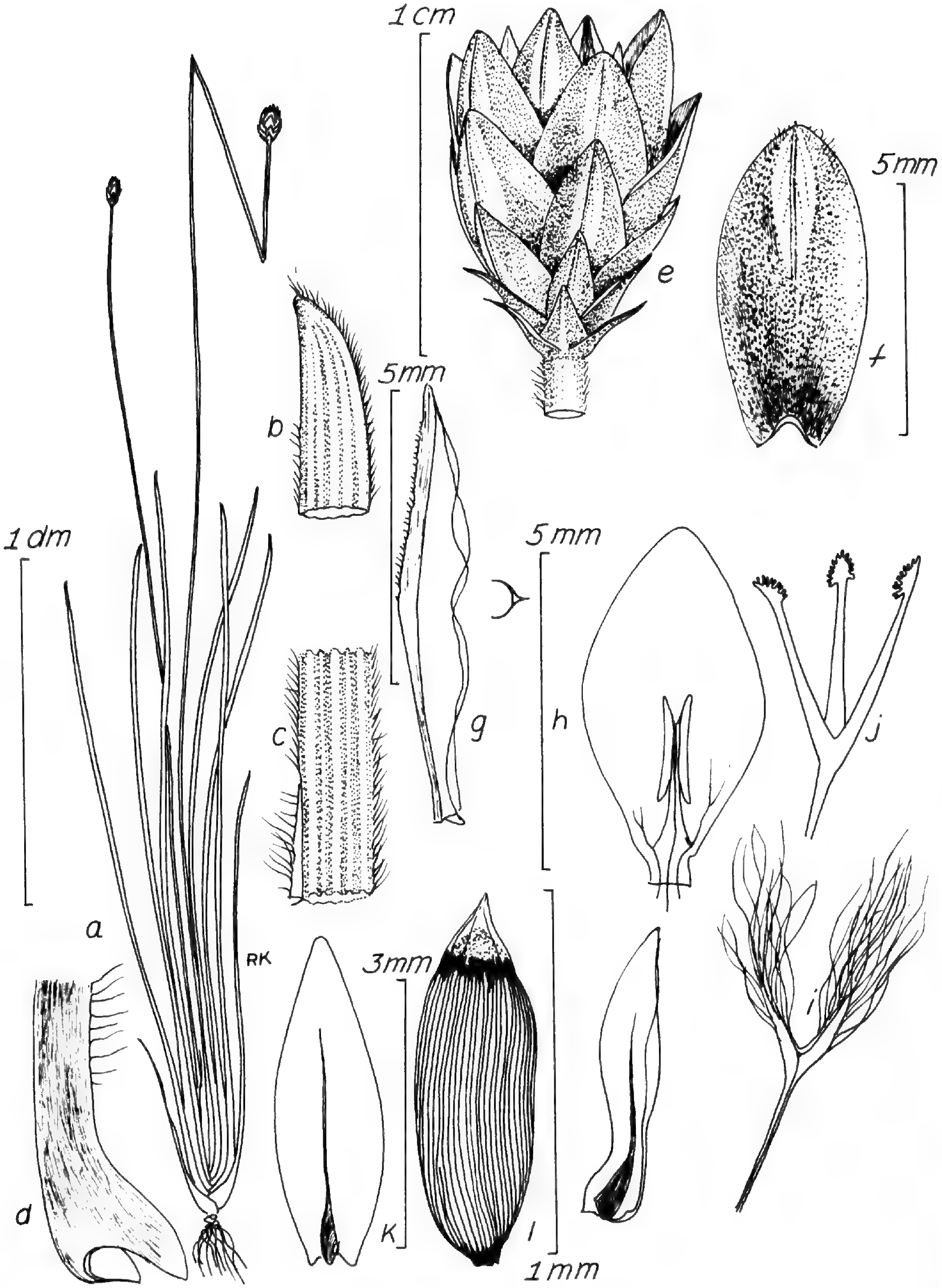


FIGURE 64. Xyris pratensis *(from the type).—a. Habit sketch.—b. Leaf tip.—c. Leaf sheath–blade junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode.—j. Stylar apex.—k. Capsule valve (two views, one on each side of seed sketch).—l. Seed.*

Río Cunucunuma, 13 Dec. 1960, *B. Maguire, R. Cowan & J. J. Wurdack 30169* (holotype, NY; isotypes, NY, US, VEN). Figure 65.

Cespitose slender perennial 2–3 dm high, the stems short, with base sometimes forming a short, stout rhizome. Leaves erect, 1–2 dm long; sheaths over ½ as long as blades, at very base red-brown ciliate, medially and distally pilose-ciliate with red-brown hairs, tapering gradually to blade, eligulate, the surfaces smooth or papillose-rugulose toward base; blades flat, narrowly linear, 0.8–1 mm wide, the apex abruptly conic-acute or terete-rounded, the margins finely ciliate to scabrociliate, the surfaces smooth and punctate, few-nerved, smooth or papillose toward base. Scape sheaths loose, as long as leaves, with long, strong blades. Scapes straight or slightly flexuous, lineal, 0.8–1 mm wide, oval distally in cross section, strongly bicostate, costae pale-ciliate or scabrociliate. Spikes narrowly obovoid, ellipsoid, aging obconic, 9–10 mm long, red-brown, few flowered; bracts subdecussate, the sterile bracts ca. 6, the lowest ones narrowly triangular, strongly keeled, grading into fertile bracts, these oblong or lance-ovate, 7.5–8 mm long, broadly acute or rounded, entire, carinate and keeled apically and with paler, linear-elliptic dorsal areas, often also with faint but evident arcuate lateral nerves. Lateral sepals free, subequilateral, ca. 6–7 mm long, lance-linear, narrowly acute, firm, pale red-brown, the narrow, firm keel entire. Petal blades narrowly obovate, ca. 6 mm long, yellow, the broadly acute apex irregularly dentate. Staminodia bibrachiate, the narrow flat branches penicillate pubescent toward and at apex. Anthers oblong, ca. 1.5 mm long, deeply bifid and auriculate, on filaments ca. 0.5 mm long. Capsule narrowly ellipsoid, ca. 4 mm long, the placentation appearing free-central, but capsule valves with shallow septa at base. Seeds numerous, ellipsoid, ca. 1 mm long, both ends acute, the body amber, finely longitudinally ribbed.

Distribution. A high-tepui endemic, thus far found on Cerro Marahuaca and on Cerro de La Neblina, along the Brazil–Venezuela border, as well as at the type locality, Cerro Huachamamacari. The specimens from Marahuaca and Neblina are uniformly different enough from the type to have been recognized as a species by Smith, who related them more to *X. tatei* Malme and named them *X. tillettii.* The material seems, however, to represent a varietal extreme of *X. bicostata,* particularly in its prominent, sharp and prominent, scabrociliate pairs of scape costae, and in its general spike and sepal dimensions. Yet the leaves are narrower than in the type, also slightly thicker and blunter, and the spike scales are less prominently keeled (though evidently costate) and are less spreading at maturity. Thus, the following is proposed:

65B. Xyris bicostata var. **tillettii** (Lyman B. Smith) Kral, stat. nov. *Xyris tillettii* Lyman B. Smith, Ernstia 9: 3–4. 1982. TYPE: Venezuela. T. F. Amazonas: Cerro Marahuaca, al NE de, y casi contigua con, Cerro Duida, este inmediatamente al N de La Esmeralda 3°10′N, 65°31′W, en el Río Orinoco, ca. 2,750 m, 2 & 9 Feb. 1975, *S. S. Tillett, P. Colvee et al. 752-332* (holotype, VEN; isotype, US).

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: plateau of Cerro de Marahuaca above Salto Los Monos on trib. headwaters of Río Iguapo, 3°37′N, 65°23′W, 2,555 m, 25 Feb. 1985, *Liesner 17962* (MO, VEN, VDB); Cerro Marahuaca, parte central de la Meseta Sur-este, 10–12 Oct. 1983, *Steyermark 129442* (VDB, VEN); Cerro de La Neblina, Planicie de Zuloaga, Río Titirico, 2,300 m, 10–15 Oct. 1970, *Steyermark 103845* (NY, VDB); Valle de Titirico N of Pico Phelps in Cerro Neblina, ca. 2,200 m, bog, 1 Dec. 1984, *Kral et al. 71920, Kral 71927* (NY, VDB, VEN, and to be distributed).

66. Xyris globosa Nilsson, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 24(14): 57, pl. 3. 1892. TYPE: Venezuela. T. F. Amazonas: "prope Esmeralda ad flumen orinoco, Dec. 1853, *R. Spruce 3244*" (lectotype, S; possible isolectotype, NY). Figure 66.

Solitary or cespitose, slender but stiffish, bulbous-based perennial 3–7 dm high, the

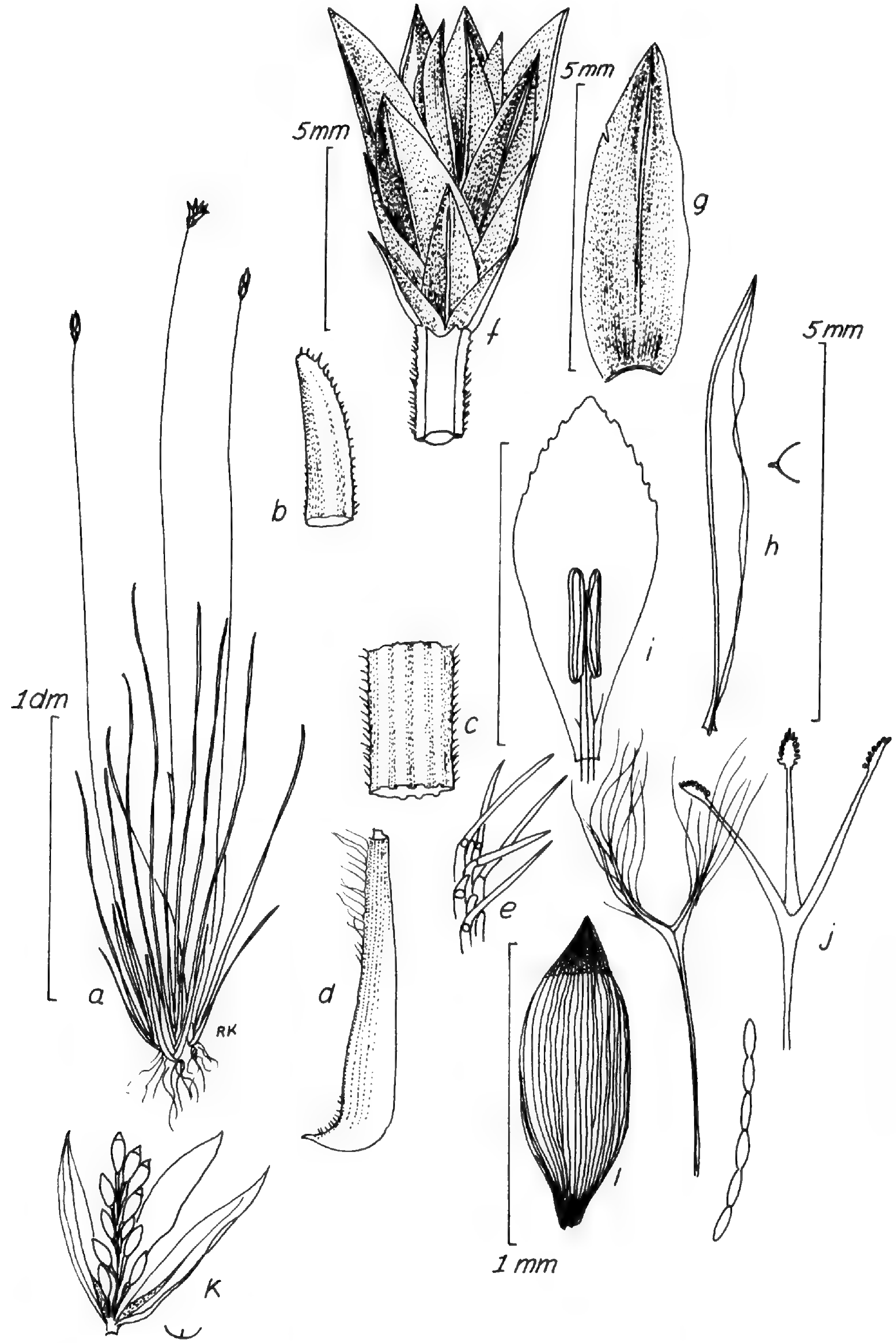


FIGURE 65. Xyris bicostata *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Leaf blade, midsector.—d. Leaf base.—e. Enlarged small sector of leaf blade edge.—f. Spike.—g. Fertile bract.—h. Lateral sepal.—i. Petal blade, stamen.—j. Staminode, enlarged sector of beard hair, stylar apex.—k. Dehisced capsule showing placentation and two septa.—l. Seed.*

stems contracted. Leaves erect, outermost scalelike, castaneous, the principal ones with sheath ⅛ or less the length of the blade, the base orbicular-dilated, villous-ciliate, castaneous, narrowing abruptly above, then tapering gradually into blade, this narrowly lineal, twisted, ca. 1 mm broad, slightly compressed with rounded-incrassate edges, the apex abruptly or narrowly conic, the surface smooth, longitudinally few ribbed, green. Scape sheaths much shorter than leaves, loosely convolute, multicostate, essentially bladeless. Scapes twisted, flexuous, terete, 0.7–1 mm thick, green, smooth, shallowly multiribbed or striate. Spikes broadly ovoid to subglobose or hemispherical, 5–10(–15) mm long, blunt, dull red-brown or tan, of many loosely and spirally imbricate bracts, these with pale-scarious borders, lacerate, white villous-ciliate, with distinct, narrow dorsal areas. Sterile bracts numerous, the lowest much the smallest, grading gradually to fertile bracts, these oblong to obovate, ca. 5(–7) mm long, broadly rounded, ecarinate or slightly carinate, the backs slightly convex-rounded. Lateral sepals free, subequilateral, linear-oblanceolate or oblong, ca. 5 mm long, obtuse, the sharp, alate keel pale-villous fimbriate or fimbriociliate with pale hairs from middle to apex. Petal blades narrowly obovate or elliptic, ca. 4.5–5.5 mm long, yellow, the apex broadly acute, the margins subentire. Staminodia bibrachiate, the broadly rectangular branches glabrous. Anthers narrowly oblong, deeply bifid and sagittate, ca. 1 mm long, on filaments ca. 0.7–1 mm long. Capsules deep brown, broadly obovoid, 2.5–3 mm long, the placentation basal-central, the valves lacking septa. Seeds numerous, oblong-ellipsoid, ca. 0.5–0.6 mm long, pale amber, apiculate, longitudinally with fine but distinct and anastomosing ribs.

Distribution. Mostly in low-elevation white-sand savanna in southwestern Venezuela (Territorio Federal Amazonas), particularly along the middle and upper Orinoco and tributaries; possibly in Colombia.

Selected specimens examined. VENEZUELA. T. F. AMAZONAS: La Esmeralda, Alto Orinoco, Jan.–Feb. 1969, *Farinas et al. 571* (VEN); Canaripo, bajo Río Ventuari, 11 Oct. 1977, *Huber 1064* (US); a unos 30 km al SE de la confluencia Orinoco–Ventuari, 30 Nov.–1 Dec. 1978, *Huber & Tillett 2819* (US); SSE de Sta. Barbara del Orinoco, ca. 100 m, 4 Dec. 1978, *Huber & Tillett 2852* (US); bajo Río Ventuari, ca. 10 km al E del Caserio de Carmelitas, 20 Feb. 1979, *Huber 3241* (US); W del Caño Pimichín un poco al sur del caserio Pimichín, 24 Feb. 1979, *Huber 3395* (US); also Caño Yagua, a unos 30 km al W de la Serranía El Tigre, 29 Feb. 1980, *Huber 4846* (VEN); 15 km N de Esmeralda, 8 Mar. 1980, *Huber 5059* (VEN); 20 km al NW Yavita, cabeceras Caño Pimichín, 11 Feb. 1981, *Huber & Medina 5948* (VDB, VEN); Savana el Venado, left bank Caño Pimichín above Pimichín, 23 Nov. 1953, *Maguire et al. 36360* (NY, US); Cerro Moriche, Río Ventuari, base Cerro Moriche, 17 Jan. 1951, *Maguire et al. 30992* (GH, NY, US, VEN); Cerro Moriche, cumbre, 4,500 ft., 15 Jan. 1951, *Maguire et al. 30936* (NY, US); Yapacana, Savanna III, 31 Dec. 1950, *Maguire et al. 30475* (NY, US, VEN); Cerro Moriche, 800 m, 14 Jan. 1951, *Maguire et al. 30897* (NY, US); Canaripo, 125 m, 28 Dec. 1976, *Steyermark & Redmond 112801* (MO, US, VDB, VEN); Cerro Yapacana, 8–9 Nov. 1979, *Thomas & Rogers 2610* (NY). BOLÍVAR: Cerro de Auyantepui, *Cardona 262* (US, VEN); morichal 2 km E of Río Orinoco between Río Horeda and Cerro Gavilan (Cerro Carighang), 100 m, 17 Dec. 1955, *Wurdack & Monachino 39952* (NY, US).

This, fuzzy-spiked plant, common in the Orinoco savannas, appears closest to *X. lacerata* Pohl and *X. lanulobractea* Steyerm., with the lacerate bract of the former but having villose-ciliate borders, and with the villose-ciliate border of the latter, yet with leaf bases villose-ciliate and more bulbous. It appears to be rare in low-altitude savanna in western Estado Bolívar. The leaf blades, if at all compressed, are thickened so that they have no sharp edge, something hard to reflect in key construction.

67. **Xyris arachnoidea** Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 28, fig. 12A–E. 1963. TYPE: Venezuela. T. F. Amazonas: flowers yellow, occasional, Savanna III, northwest base of Cerro Yapacana, 150 m, alto Río Orinoco, 17 Mar. 1953, *B. Maguire & J. J. Wurdack 34570* (holotype, NY; isotype, US). Figure 67.

Cespitose, hard- and fibrillose-based, subbulbous perennial 2.5–4 dm high, the stems contracted. Leaves erect, 1–2 dm long; sheaths dull brown, the very base abruptly

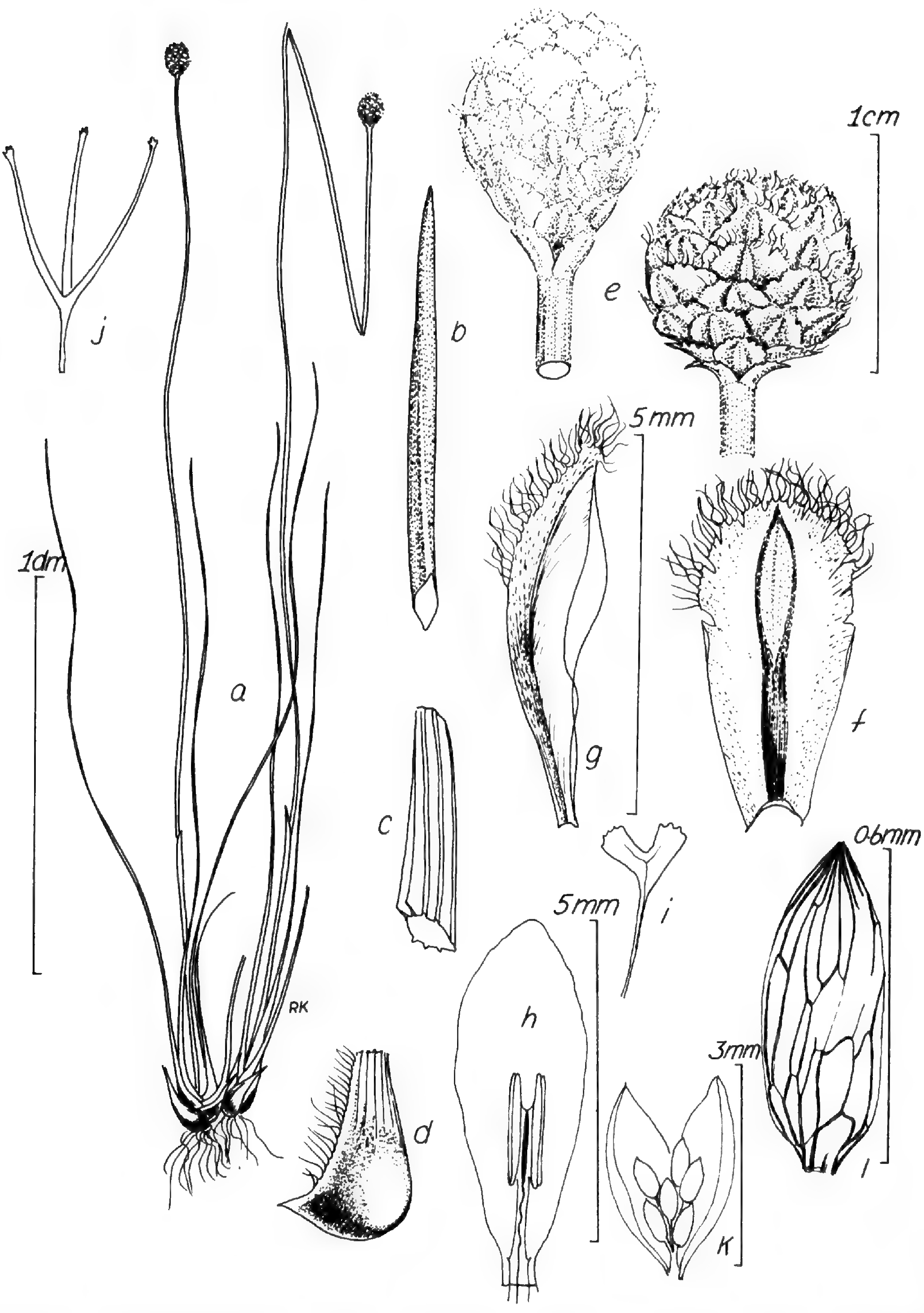


FIGURE 66. Xyris globosa (Huber 3395).—*a. Habit sketch.—b. Leaf tip.—c. Leaf at sheath–blade junction.—d. Leaf base.—e. Spikes, two types.—f. Fertile bract.—g. Lateral sepal.—h. Petal, stamen.—i. Staminode.—j. Stylar apex.—k. Capsule, one valve removed showing placentation.—l. Seed.*

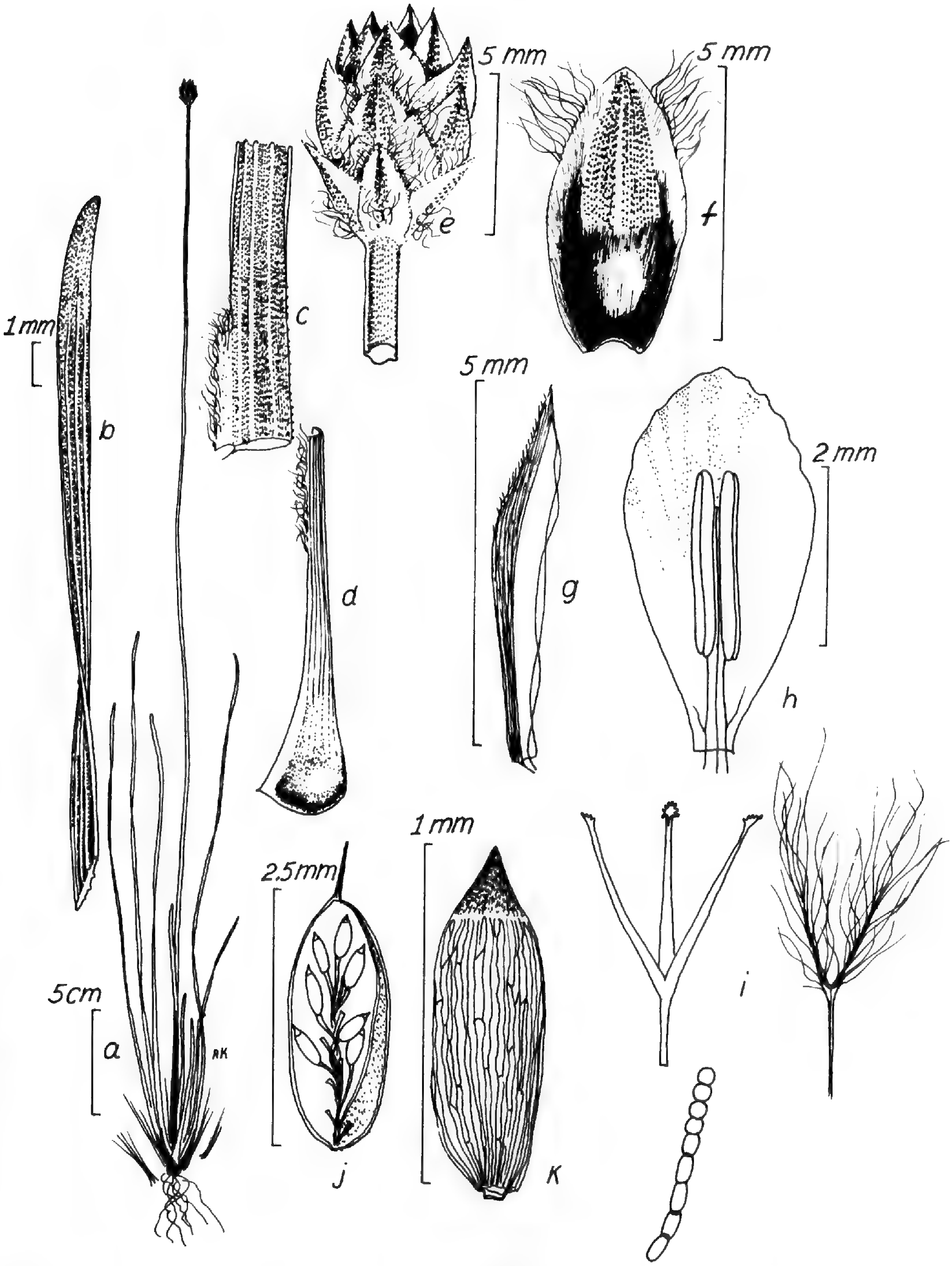


FIGURE 67. Xyris arachnoidea *(a–e from type, f–k from* Kral 70710*).—a. Habit sketch.—b. Leaf tip and upper blade.—c. Leaf sheath–blade junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade and stamen.—i. Staminode, style branches, enlarged staminodial hair.—j. Capsule, side view of one septum (shaded), placentation.—k. Seed.*

dilated, castaneous, above tapering gradually into blades and white-villous- or lanate-margined, the ligule concealed by cottony hairs; blades evenly linear, at least 5 times as long as sheaths, flattened, ca. 1 mm wide, abruptly narrowed to a callused, narrowly rounded apex, the margins entire or scabrid toward base, rather thick, sometimes pale and contrasting, sometimes with 1 edge double, the surfaces smooth or papillose-scabrid or rugulose toward base, sometimes with a few strong, yellowish nerves, otherwise dull green or maroon. Scape sheaths much shorter than leaves, thin, keeled and open, apically with short, erect, stiff blades. Scapes flexuous and twisted, apically subterete or oval in cross section, ca. 1 mm thick, 2–4-costate, the costae yellowish, low, smooth. Spikes ovoid, drying obovoid, 7–8 mm long, blunt, dull brown, of several spirally imbricate, firm but loose bracts, the sterile bracts narrowly to broadly triangular, grading slightly larger into fertile bracts, these ovate, 4–5 mm long, acute with margins (sometimes also backs) white villose and with strong, red-brown triangular dorsal areas. Lateral sepals free, subequilateral, curvate-lanceolate, 4.5–5 mm long, acuminate, lustrous red-brown, thin, the darker, wide, firm keel with a sparse fringe of villosulous or scalelike ascending hairs, villosulous at tip, aging subentire. Petal blades obovate, ca. 5 mm long, yellow, the narrowly rounded tip erose. Staminodia bibrachiate, the branches long, slender, long-penicillate from tip to base. Anthers oblong, ca. 2 mm long, ca. 2.5–3 mm long, the placentation free-central, the capsule valves septate. Seeds numerous, narrowly ellipsoid or cylindrical, ca. 1 mm long, apiculate, translucent pale brown with numerous, very fine, wavy, longitudinal ribs and some fine cross-lines.

Distribution. Locally abundant in sandy low-elevation savanna along the upper Orinoco, Territorio Federal Amazonas, Venezuela.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: SE bank of mid part of Caño Yagua at Cucurital de Yagua, ca. 120 m, *Davidse et al. 17403* (MO), *17435* (MO, US); Cerro Yapacana, 22 May 1981, *Guánchez 1164* (TFAV, VDB); el pie occidental del Cerro Yapacana, 14–28 Feb. 1978, *Huber 1617* (US); alrededores de Canaripo, 30 May 1978, *Huber 1914* (US, VEN); Savanna III, Cerro Yapacana, 3 June 1978, *Huber 2029* (VEN), *2040* (US); entre el medio Caño Yagua y el bosque al N del Cerro Cucurito, 18 Jan. 1979, *Huber 3136* (US); Caño Caname, ca. 18 km arriba (al E) de la boca, 29 May 1979, *Huber et al. 3749* (US); alto Caño Yagua, a unos 30 km al W de la Serranía El Tigre, 29 Feb. 1980, *Huber 4846a* (VEN); Savanna II, W base Cerro Yapacana, ca. 100 m, 10 Aug. 1983, *Kral & Huber 70710* (F, K, L, MO, NY, SP, US, VDB, VEN); Cerro Yapacana en la sabana grande el Caño Cotua, 7 May 1970, *Steyermark & Bunting 103243* (US, VEN).

This species is fairly common in the savannas around Cerro Yapacana and much resembles the more widespread and associated *X. subglabrata* Malme (*X. garcia-barrigae* Idr. & Smith). It differs, however, in having much more copious white villous or arachnoid pubescence on the bracts and in having distinctly flattened (rather than terete) leaf blades. The flowers are open in the morning, closed by mid afternoon.

68. Xyris malmeana Lyman B. Smith, Bol. Inspet. Fed. Obras Contra Secas, Rio 10: 126. 1939. TYPE: Brazil, Pará: open sandy soil 2 km S of Vigia, *Drouet 2136* (holotype, GH). Figure 68.

Xyris glabrata (Seub.) Griseb. sensu Griseb., Fl. Brit. W. Ind. 525 (Trinidad), not as to basionym *X. savanensis* Miq. var. *glabrata* Seub.

Slender, solitary or cespitose, glabrous perennial 4–6 dm high, the stems contracted. Leaves erect, 1–3 dm long; sheaths ciliate, pink to deep brown, the abruptly dilated base gradually narrowed, strongly ribbed and ecarinate into the blade, this flattened, narrowly linear, twisted, 1.5–3 mm wide, gradually narrowed above middle to a narrowly acuminate or subulate apex, the margins thin, smooth, the surfaces pale green, finely nerved. Scape sheaths much shorter than principal leaves, strongly ribbed, twisted, also keeled, with a cusplike blade apically. Scapes slenderly linear, straight or flexuous, twisted, subterete at apex, ca. 0.5 mm thick, with 3 or more low but sharp and distinct, smooth or papillose costae. Spikes broadly ellipsoid or ovoid, 5–8 mm long, acute, pale red-brown or dull brown, of several spirally imbricate, convex, ecarinate, entire to lacerate bracts with distinct dorsal areas, the sterile bracts slightly smaller than the fertile bracts, grading into them, the fertile bracts 4–6 mm long, broadly elliptic to obovate, broadly or narrowly rounded apically, sometimes the inner ones slightly keeled, all with a short, narrow,

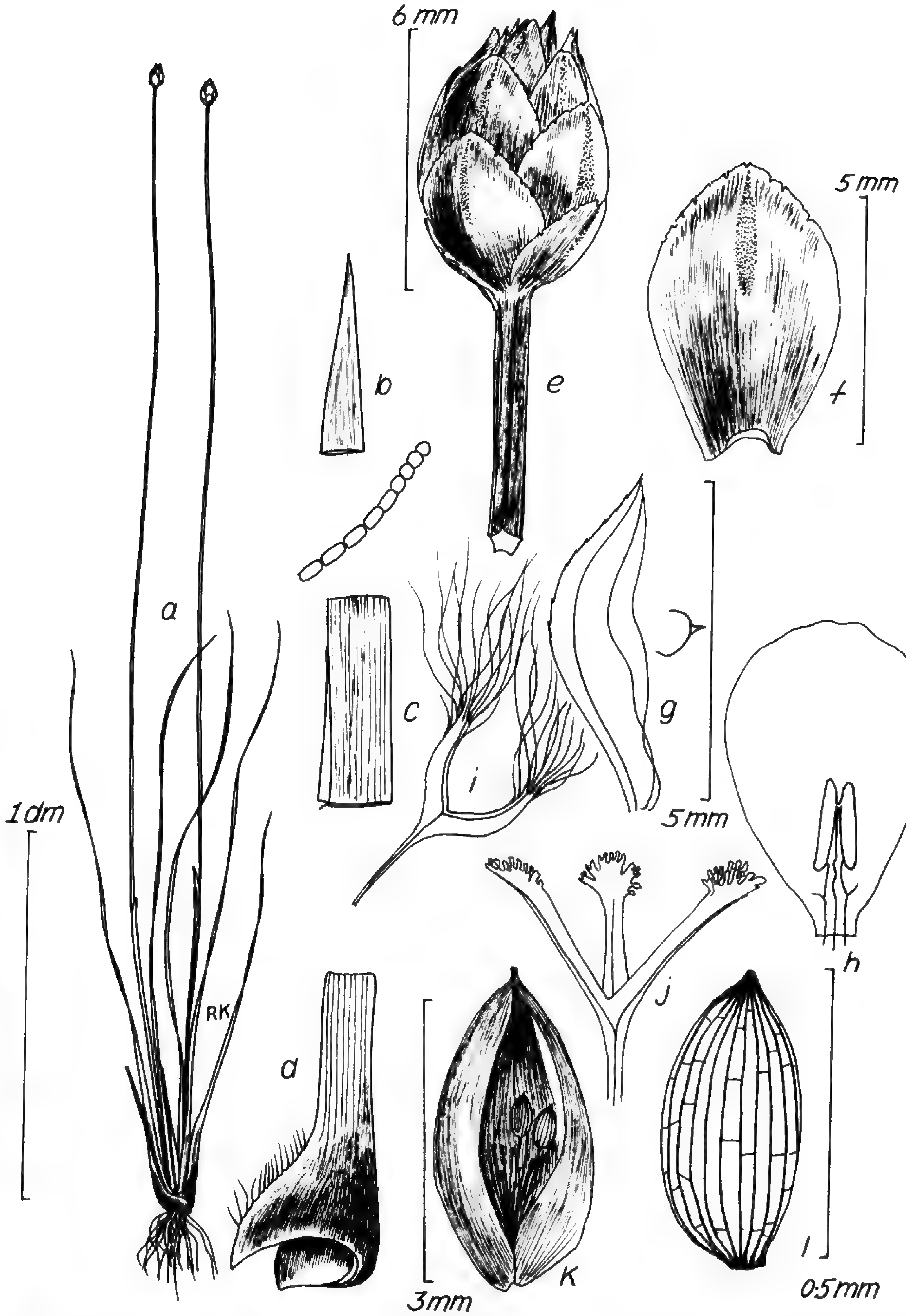


FIGURE 68. Xyris malmeana (Steyermark & Dunsterville 113285).—*a. Habit sketch.*—*b. Leaf tip.*—*c. Leaf sheath–blade junction.*—*d. Leaf base.*—*e. Spike.*—*f. Fertile bract.*—*g. Lateral sepal.*—*h. Petal blade, stamen.*—*i. Staminode.*—*j. Stylar apex.*—*k. Capsule.*—*l. Seed.*

usually greenish dorsal area. Lateral sepals free, slightly inequilateral, thin, elliptic-curvate, ca. 5 mm long, acute, the broad, firm keel lacerate-ciliolate from middle to apex, or nearly entire. Petal blades obovate, ca. 4 mm long, yellow, the broadly rounded apex subentire. Staminodia bibrachiate, the narrow, flat branches distally penicillate-ciliate. Anthers ca. 1 mm long, lance-oblong, deeply bifid and sagittate, on filaments 0.3–0.4 mm long. Capsule obovoid, firm-valved, 3.5–4 mm long, the placentation basal, the valves without septa. Seeds numerous, broadly ellipsoid, ca. 0.5 mm long, 2-apiculate, deep lustrous amber, finely ribbed longitudinally.

Distribution. Sandy, low- to high-elevation savanna, northern South America from Territorio Federal Amazonas, Venezuela, eastward to French Guiana and in contiguous northern Brazil in Amapá, Amazonas, Guapore, and Pará; Trinidad.

Selected specimens examined. BRAZIL. AMAPÁ: Camp 27.VI.1904, *A. Ducke s.n.* (MG, US). AMAZONAS: estrada Humaita–Lábrea, km 17, 10 June 1982, *Teixeira et al. 1059* (INPA, NY, VDB). GUAPORE: Porto Velho, *Cordeiro & Da Silva 272* (US). PARÁ: Vigia, campina do Palha, 10 Aug. 1954, *Black 54-16761* (US, VDB); Obidos, Jaramacaru River, 27 May 1957, *Egler 300* (US); Gurupa, campina da Gerenalda, *Pires & Silva 4712* (US, VDB). FRENCH GUIANA. Route de Simonmary, environs in 70 km, 7 June 1957 (*no collector name*—U). GUYANA: Rupununi Savanna, ca. 350 ft., 9 Aug. 1936, *Goodland 336* (US). SURINAM: Soesdyke, Oct. 1977, *Cooper 354* (U); Gros-savanna (prope km 103) opn. 309.8, Apr. 1959, *Van Donselaar 697* (U); Zanderij I, Aug. 1914, Essed (U); Jodensavanne (fluv. Suriname), *Heyligers 235* (U); near Singri Lanti 15 km W of Zanderij, 24 July 1976, *Jansma 13* (U); Tapfelberg, distr. Saramacca, *Kramer & Hekking 3275* (U); Tibiti savanne near km 5.8 in third line, 15 Jan. 1949, *Lanjouw & Lindeman 1850* (GH, U); savanna near Sapende, upper Commewijne River, 14 July 1953, *Lindeman 4233* (GH, U); Tapfelberg, savanna I, 3 Aug. 1944, *Maguire 24203* (NY, U); Sipaliwini savana area on Braz. Frontier, 255 m, 4 Sep. 1968, *Oldenburger et al. 58* (U); Nat. Res. "Brinckheuvel," 2 Sep. 1967, *Wildschut & Teunissen 11570* (U). TRINIDAD: Aripo Savanna, 21 Apr. 1920, *Britton et al. 1996* (GH, NY, US); Aripo-savanne, Manzanilla, 7 Feb. 1962, *Hekking 1347* (U). VENEZUELA. T. F. AMAZONAS: 20–25 km W de San Juan de Manapiare, 8 Oct. 1979, *Huber 4491* (US); Esmeralda, 9 Oct. 1928, *Luetzelburg 22498* (US). BOLÍVAR: SE base Auyan-tepui, 24 Nov. 1982, *Davidse & Huber 22565* (MO, VDB); 3 km S of El Pauji, 1,050 m, 19 Oct. 1985, *Holst & Liesner 2630* (MO, VDB, VEN); sabanas al SW de Kamarata, 23 Nov. 1982, *Huber et al. 6810* (MYF, VDB, VEN); Caserio de Kukenan, ESE de la punta SE del Churí-tepui, *Huber 9768* (MYF, VDB); flats above Río Yuruani at Salto Yuruani, 28 July 1983, *Kral 70572* (MO, NY, US, VDB, VEN); 1.3 km N of Río Yuruani Ferry, ca. 750 m, 29 July 1983, *Kral 70619* (NY, US, VDB, VEN); above Ven. 10, ca. 800 m, and N of Ferry, Puente Kumerepa, 17 Dec. 1984, *Kral 72189* (MYF, VDB, VEN—a large set to be distributed); cumbre de Cerro Guaiquinima, salto del Río Szczerbanari, 20–25 Jan. 1977, *Steyermark & Dunsterville 113285* (NY, US, VEN); Auyan-tepui, 1,100 m, Dec. 1937–Jan. 1938, *Tate 1316* (NY).

This species most resembles *X. lacerata* Pohl ex Seub. However, *Xyris malmeana* is usually lower, is more slender, and is less bulbous based. Its scapes are more sharply costate, its dorsal areas are narrower, and its lateral sepals are less ciliate.

69. Xyris araracuare Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 34, fig. 20A–F. 1963. TYPE: Colombia. Amazonas: frequent in scrub savanna, Araracuará, Río Caquetá, 5 Sep. 1959, *B. Maguire, C. K. Maguire & A. Fernandez 44132* (holotype, NY; isotype, US). Figure 69.

Slender, somewhat cespitose, bulbous-based perennial 2–3 dm high. Older leaves short, scalelike, covering "bulb." Main foliage leaves few, ascending, 10–20 cm long; sheaths ciliate, much shorter than blades, abruptly flaring at base, castaneous, ligule absent, tapering gradually above into blade, this green, subterete, fluted, lineal, twisted, 0.7–0.8 mm wide, smooth or scaberulous along lateral ribs, abruptly bluntly conic. Scape sheaths shorter than leaves, loose, blade short, cusplike. Scape straight or flexuous, twisted, terete and slightly grooved or fluted, punctate distally, proximally ribbed and scaberulous. Spike broadly obovoid, 7–8 mm long, blunt, many-flowered, pale dull brown, the bracts loosely spirally imbricate; sterile bracts mostly 6, broadly ovate or triangular, the lowest smallest, narrowly scarious-lacerate-bordered, grading gradually to fertile bracts, these ovate, ca. 5.5 mm long, the tips narrowly rounded, lacerate-bordered, the backs rounded with darker, lance to linear dorsal areas; innermost bracts more navicular, more acute, subentire,

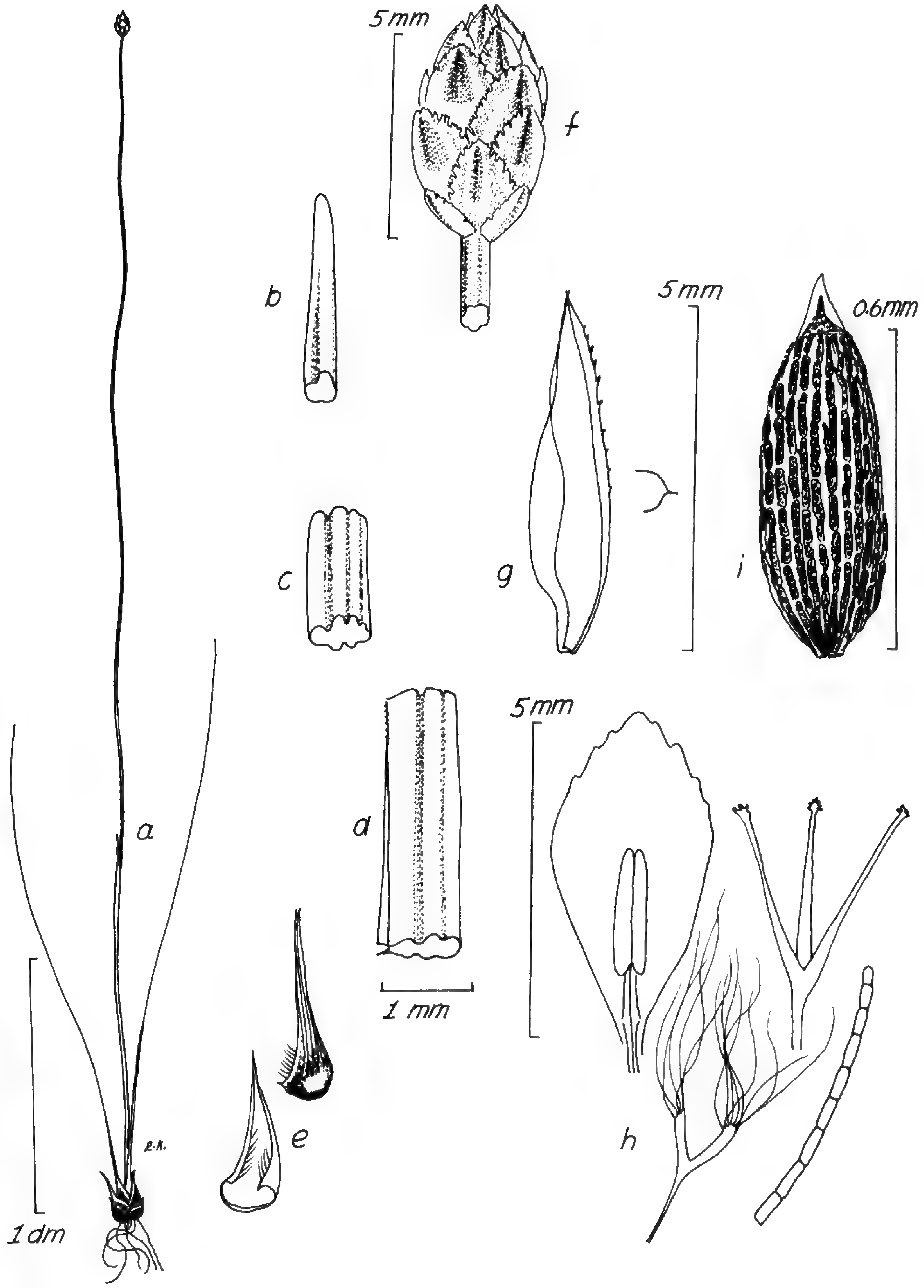


FIGURE 69. Xyris araracuare *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Sector of lead mid-blade.—d. Leaf at junction of sheath.—e. Two views of leaf base.—f. Spike.—g. Lateral sepal.—h. Petal blade, stamen, staminode, style branches, enlarged beard hair.—i. Seed.*

to 6 mm long. Lateral sepals free, subequilateral, elliptic-linear, ca. 4.5(–5.5) mm long, narrowly acute, pale brown except for darker, narrow, firm keel, this ciliate-scabrid from ca. middle to apex. Petal blades yellow, obovate, ca. 5 mm long, narrowly rounded apically, sparsely dentate. Staminodia bibrachiate, the branch apices sparsely long-penicillate. Anthers oblong, ca. 2 mm long, on filaments 0.5 mm long. Capsule narrowly obovoid, 2.5 mm long; placentation basal, funiculi long. Seeds numerous, narrowly lance-ovoid to ellipsoid, 0.6 mm long, translucent, longitudinally with several broad, wavy, distinct ribs.

Distribution. Sandy scrub savanna, known only from the type collection.

Evidently this species is very close to the widespread *X. lacerata* Pohl ex Seub., as the descriptions and illustrations show. It is best to include it now with that perspective until the entire genus is revised for South America.

70. Xyris lacerata Pohl ex Seub. in Martius, Fl. Bras. 3(1): 26, pl. 26. 1855. TYPE: Brazil: "Goias, *Pohl*" (isolectotype, BR; phototype, US no. *5752*). Figure 70.

Tall, bulbous-based, solitary or cespitose perennial 4–6 dm high, the stems contracted, the outer leaves scalelike, castaneous. Principal leaves 1.5–3 dm long, erect or ascending; sheaths less than ¼ length of blades, at base abruptly dilated, ciliate, cochleariform, usually castaneous, papillose-rugulose; above paler, entire, gradually tapering to blade, papillose-rugulose, eligulate; blades narrowly linear, flattened, or rarely thickened, subterete, twisted, 1.5–3 mm wide, acute to narrowly acuminate, often subulate, the edges thin or cartilaginous-incrassate, smooth or papillose, the surfaces dull green, smooth or papillose-rugulose, multinerved. Scape sheaths much shorter than leaves, tight, proximally twisted and multicostate, opening and keeled distally, producing a cusplike blade. Scapes twisted, straight or flexuous, terete distally, 0.5–1 mm thick, striate, ecostate or with 1 low costa, smooth to papillose. Spikes globose, broadly ovoid or hemispherical, 0.5–1 cm long, dull brown, of very many spirally imbricate, convex-rounded, lacerate and scarious-edged bracts having distinct, green to red-brown dorsal areas; sterile bracts several, distinctly smaller than and grading into fertile bracts, these oblong to obovate, 6–7 mm long, broadly rounded, ecarinate, and with broadly lacerate scarious borders (innermost fertile bracts narrower, frequently keeled). Lateral sepals free, slightly inequilateral, oblong-curvate, ca. 5.5–6 mm long, blunt, lustrous red-brown, the firm, narrow keel ciliolate from near base to tip. Petal blades obovate, 5.5–6 mm long, yellow, the rounded apex erose. Staminodia bibrachiate, the narrow flat branches long-penicillate from near base to tip. Anthers lance-oblong, ca. 2 mm long, shallowly bifid, deeply auriculate, on filaments ca. 0.5 mm long. Capsule narrowly ellipsoid, ca. 5 mm long, the placentation densely central, the valves lacking septa. Seeds numerous, broadly to narrowly ellipsoid or fusiform, 5–6 mm long, deep amber, 15–20-ribbed with much fainter crosslines.

Distribution. Sandy or sandy-silty or rocky campos and savannas, eastern Colombia eastward across southern Venezuela and probably into Guyana but with no official record; to the south, from the Andean foothills eastward from northern Brazil south into Argentina.

Selected specimens examined. Only northern records are listed. COLOMBIA. META: E of Río Zanza, 2 km above jct. with Río Cuejar, ca. 500 m, 22 Aug. 1950, *Idrobo & S. Smith 1544* (F); Villa Vicencio, 450 m, 26–31 Aug. 1917, *Pennell 1409* (NY); Savan. Boca de Monte, llanos de San Martín, *Smith & Idrobo 1391* (GH, NY); 2 km E Río Zanza, N end Cordillera Macarena, 22 Aug. 1950, *Smith & Idrobo 1543* (GH); Llanos Orientales, La Macarena (Parte Sur), Río Guayabero, sabanas, 235–700 m, Jan.–Mar. 1959, *García-Barriga & Mejia 17078* (NY). SANTANDER: Mesa de Los Santos, 1,500 m, *Killip & A. C. Smith 15139, 15190, 15280* (GH, NY). VAUPÉS: Mesa La Lindosa, ca. 15–20 km sur de San José del Guaviare, 13–15 Dec. 1950, *Idrobo & Schultes 674* (GH, U); lower Río Parana-pichuna, 10 Sep. 1976, *Zarucchi 2012* (GH). VENEZUELA. T. F. AMAZONAS: La Esmeralda, 15 July 1951, *Croizat 115* (NY, US); 15 km E Puerto Ayacucho, 30 Sep. 1960, *Foldats 3539* (NY, VEN); Aeropuerto de Puerto Ayacucho, 24 Aug. 1977,

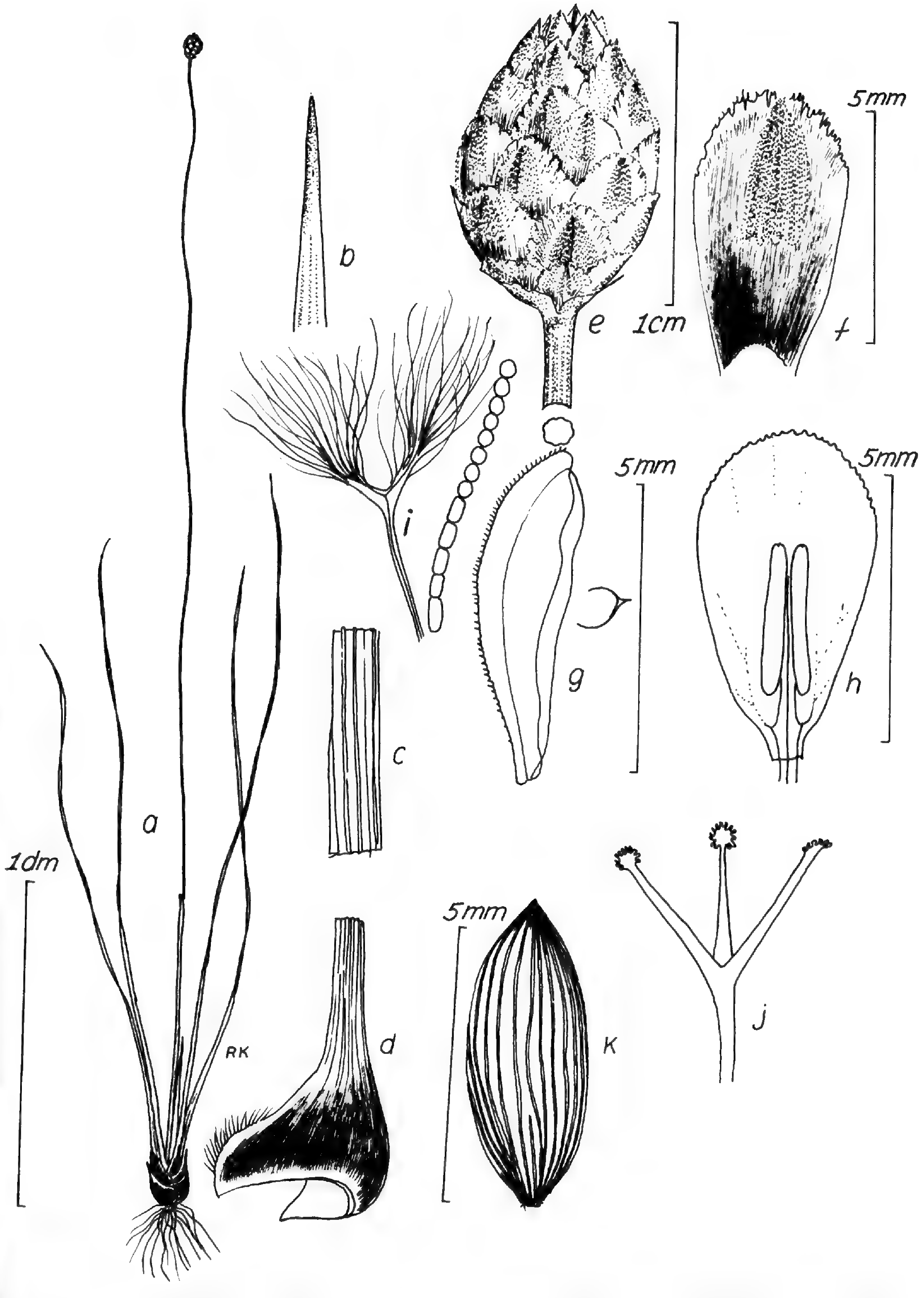


FIGURE 70. Xyris lacerata (Delascio et al. 11152).—*a. Habit sketch.—b. Leaf apex.—c. Leaf at sheath-blade junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode.—j. Stylar apex.—k. Seed.*

Huber 1000 (US, VEN); Cerro Morrocoy al Sur y La Serranía Colmena al Norte, 16 Oct. 1977, *Huber 1206* (VEN); cuenca del Río Manapiare, 150 m, 15 Aug. 1978, *Huber 2239* (US); alto Río Ventuari, sabana del Oso, 17 Aug. 1978, *Huber 2280* (US); sabanas de Rincones de Chacorro, 5 km NE de Galipero, ca. 80 m, 17 Aug. 1979, *Huber 4179* (US, VDB, VEN); sabanas de Santa Barbara, 19 July 1980 (VEN); ca. 30 km N of Puerto Ayacucho, *Kral et al. 70732* (NY, US, VDB, VEN); Puerto Ayacucho, S side, 22 Nov. 1984, *Kral & Boom 71781* (NY, VDB, VEN); Esmeralda Savanna, ca. Aug. 1928–Apr. 1929, *Tate 265* (F, NY). APURE: Estero la Yaguita, 23 Sep. 1979, *Garofalo 378* (US); Alto Apure, Gonzalez, Mar. 1975 (U, VEN); alrededores de Puerto Paez, sabana, 19 Mar. 1973, *Ramia & Montes 5159* (US); sabanas de El Rosero, July 1976, *Tejos s.n.* (US). BOLÍVAR: vic. Panare, 6 km from Maniapure toward Caicara, *Boom & Grillo 6290* (NY, VDB); alrededores de Puerto Nuevo, 14 Nov. 1982, *Guánchez & Huber 2469* (TFAV, VDB); 2 km S of Ciudad Piar, 300 m, 18 Oct. 1953, *Maguire et al. 35834* (GH, NY, US); 14 km SW of Caicara del Orinoco, 2 Sep. 1985, *Steyermark et al. 131112* (MO, VDB, VEN); E of Río Parguaza, 125 km N of Alcabala of Puerto Ayacucho, 8–11 Sep. 1985, *Steyermark et al. 131752* (MO, VDB, VEN); morichal just N of Río Chiguirete, 420 m, 11 Oct. 1954, *Wurdack & Guppy 20* (NY, US); 2 km E of Río Orinoco between Río Horeda and Cerro Gavilan, 17 Dec. 1955, *Wurdack & Monachino 39951* (NY, US). GUÁRICO: Parque Nacional Aguaro-Guáriquito: Morichal Charcote, Dec. 1981, *Delascio et al. 11152* (MO, VDB, VEN).

This common plant of low- to medium-elevation savanna bears a considerable resemblance to *X. tortula* C. Martius of the planalto of Brazil and may indeed intergrade with it. I have seen the phototype of *X. fallax*, the type supposedly still at M, and am surprised to see that it is comprised of two good specimens of *X. lacerata*.

71. Xyris oblata Kral & Lyman B. Smith, sp. nov. TYPE: Venezuela. T. F. Amazonas: en la sombrede arboles pequenos; fls. amarillas; en las sabanetas periodicamente enegadas cerca de la margem del Caño Temi, Yavita, 128 m, 31 Jan. 1942, *Llewelyn Williams 14121* (holotype, F; isotypes, F, US). Figure 71.

Planta solitaria vel caespitosa, tenuis, annua aut perennis, 3–4 dm alta, caulibus contractis. Folia principalia vulgo flabellate expansa, 1–2 dm longa; vaginae brunneociliatae, laminas ca. 2-plo breviora, brunneolae vel atroporphyreae, sursum in laminas gradatim contractae, eligulatae; laminae gladiatolineares, complanatae, 1–3.5 mm latae, a medio ad apicem gradatim contractae, ad apicem abrupte incurvatae vel erectae, acutae, leviter incrassatae; margines tenues, scabriduli; paginae leviter stratonervosae, marroninae, dense scabrido-rugosae. Vaginae scaporum foliis breviora, proxime contortae, carinatae et costatae, carinatis scabridis, ad apicem apertae, laminis curtis, ciliatis, erectis. Scapi recti vel flexuosi, torti, ad apicem teretes vel in sectione transversali ovales, papillati, ecostati, plani vel leviter striati. Spicae oblatae, ca. 5 mm altae, 6–7 mm latae, interdum proliferatae, brunneolae, bracteis numerosis integris, spiraliter imbricatis, area dorsalis distinctis; bracteae steriles plures, fertilibus leviter breviores et angustiores, fertiles gradatim profluentes; bracteae fertiles late obovatae, ca. 5 mm longae, subintegrae, ecarinatae, leviter convexae; area dorsalis ovata vel elliptica, pallide punctata. Sepala lateralia libera, inaequilatera, ca. 4 mm longa, obtusa, pallide spadiceae; ala carinali valde curvata, a medio ad apicem fimbriatolacerata. Lamina petalorum obovata, ca. 4.5 mm longa (est.), luteola. Staminodia bibrachiata, brachiis dense longipenicillatis. Antherae lanceolatae, 1.5 mm longae; filiis ca. 0.5 mm longis. Capsula ellipsoidea vel subrotunda, ca. 2.5 mm longa, planoconvexa, placentae axiales. Semina numerosa, ellipsoidea, ca. 0.8 mm longa, atrosuccinea, longitudine valde et anguste 28–30-costatae.

Solitary or cespitose, slender annual or short-lived perennial 3–4 dm high, the stems contracted. Leaves mostly spreading flabellately, 1–2 dm long; sheaths soft, ca. ½ as long as blades, carinate, brown ciliate, dull brown to deep red-brown, rugoscabrid, narrowed gradually to blades and eligulate; blades gladiate-linear, flat, 1–3.5 mm wide, tapering gradually from midblade to an erect or slightly incurved, bluntly acute, slightly thickened tip; margins thin, scabridulous; surfaces striate-ribbed, maroon, densely scabridulous-rugose. Scape sheath shorter than leaves, proximally twisted, carinate and costate, the keel scabrid, open at apex, with short, ciliate, erect blade. Scape straight or flexuous, twisted, distally terete or oval in cross section, papillate, ecostate, level or striate. Spikes depressed-globose, ca. 5 mm long, 6–7 mm broad, sometimes proliferous, dull brown, of many firm, entire, spirally imbricate bracts with distinct dorsal areas; sterile bracts several, the lowest narrower and slightly shorter than the fertile bracts, scabrid-ciliate, grading into fertile bracts; these obovate, ca. 5 mm long, broadly rounded, subentire, the backs shallowly convex, ecarinate, papillate, the dorsal area oval to elliptic, pale punctate. Lateral sepals free, inequilateral, ca. 4 mm long, obtuse, tan, the thin, strongly curvate keel fimbriolacerate from middle to apex. Petal blades obovate, ca. 4.5 mm long (estimate), yellow. Staminodia bibrachiate, the branches densely long-

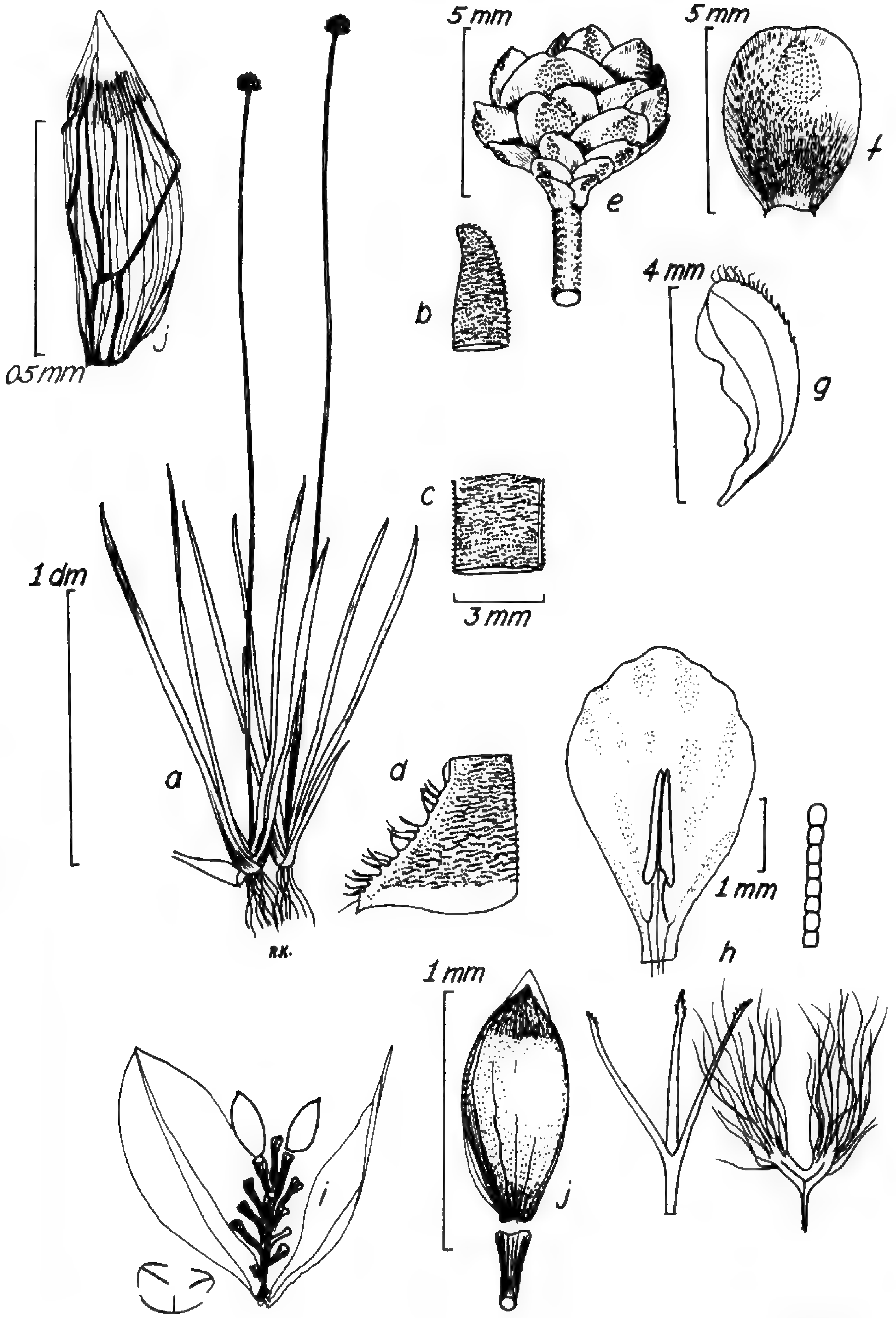


FIGURE 71. Xyris oblata *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Leaf at midblade.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen, staminode, beard hair, stylar apex.—i. Dehisced capsule, showing placentae, two valves, oblique view showing septum.—j. Bottom center, seed on funicle; upper left, detail.*

penicillate. Anthers lanceolate, ca. 1.5 mm long, planoconvex, the placentation axile at base. Seeds ellipsoid, ca. 0.8 mm long, dark amber, with 28–30 strong, narrow, irregular longitudinal ribs.

Distribution. So far known only from the type collection.

Material of this distinctive species in general character of leaves and aspect of plant much resembles some *X. savanensis.* It differs markedly in that the leaf sheaths are conspicuously ciliate, the spikes distinctively oblate, and the ornamentation of lateral sepals different. Also, the staminodial branches are densely long-penicillate, a character lacking in *X. savanensis.*

72. Xyris tenella Kunth, Enum. Pl. 4: 9. 1843. TYPE: Brazil. São Paulo: Sul do Estado, *Sellow s.n.* (lectotype, B; phototype, US). Figure 72.

Synonyms given below are only for Venezuelan material.

Xyris steyermarkii Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 30, fig. 15A–E. 1963. TYPE: Venezuela. Bolívar: Caño Mojado between base of upper falls and drop to escarpment, 1,985–1,910 m, summit, Chimantá Massif, Torono-tepui, 23 Feb. 1955, *J. A. Steyermark & J. J. Wurdack 1096* (holotype, NY; isotype, US).

Xyris yutajensis Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 36, fig. 19A–F. 1963. TYPE: Venezuela. T. F. Amazonas: small savanna and along left fork of Caño Yutaje, 1,250 m, Serranía Yutaje, Río Manapiare, 12 Feb. 1953, *B. Maguire & C. K. Maguire 35206* (holotype, NY; isotype, US).

Cespitose, delicate, low smooth annual, 0.5–2 dm high, the stems contracted. Leaves mostly erect, 2–8 cm long; sheaths soft, scarious, long-ciliate, stramineous or pale brown, less than ½ blade length, finely costate, evenly narrowed from dilated base to blade, eligulate; blades linear-filiform, slightly twisted, somewhat flattened, ca. 0.5 mm wide, narrowed at apex to an incurved-apiculate, callused tip; margins entire, smooth, or ciliolate; surfaces very finely nerved, green to maroon. Scape sheaths shorter than leaves, at base tubular, multicostate, brown, distally open and slightly dilated, keeled, with short, erect blades. Scapes filiform, terete, 0.3–0.4 mm thick, finely striate distally, sometimes unicostate with a low costa, or low-costate, costae papillate to finely scabrid. Spikes ellipsoid or lance-ovoid, drying narrowly obovoid, ca. 5–6 mm long, of a few thin, brown to tan bracts with prominent but narrow or streaklike dorsal areas; sterile bracts few, lance-ovate or oblong, navicular, smaller than the fertile bracts, grading into them; fertile bracts few, lanceolate, rounded-folded (navicular), ca. 5–5.5 mm long, acute, subentire or lacerate, the keel darker brown. Petal blades broadly obovate, 3 mm long, yellow, the broadly or narrowly rounded apex with sinuate-erose margin. Staminodia lacking or blade broadly bilobed, beardless (in the Guayanas). Anthers lance-oblong, ca. 1 mm long, deeply bifid and sagittate, on broad filaments 0.6–0.7 mm long. Capsule narrowly ovoid, ca. 3 mm long, acuminate, the placentation basal. Seeds ovoid to ellipsoid, ca. 0.5 mm long, deep amber, finely lined longitudinally.

Distribution. Low- to high-elevation savanna from southeastern Venezuela eastward to French Guiana; southward through the planalto of Brazil, thence south into Paraguay.

Selected specimens examined. Citations are selected from Venezuelan material only. VENEZUELA. T. F. AMAZONAS: below Salto Los Monos on trib. headwaters of Río Iguapo, 1,500–1,600 m, 11 Mar. 1985, *Liesner 18534* (MO, VDB); Cerro de Marahuaca, Río Yameduaka, 19 Feb. 1985, *Liesner 17711* (MO, VDB); Cerro Marahuaca, la meseta Sur-Este, 1,560 m, 13–14 Oct. 1983, *Steyermark 129599* (VDB, VEN). BOLÍVAR: Auyan-tepui, ca. 1,900 m, Apr. 1956, *Foldats 2642* (VEN); Cerro El Venado, ca. 20 km E de Canaima, *Huber et al. 8257* (NY); Auyan-tepui, sector SSE, 10 Dec. 1983, *Huber & Medina 8522*; Serranía Guanay, sect. nor-oriental, 20–28 Oct. 1985, *Huber 10966* (MYF, VDB, VEN); La Escalera, ca. 1,200 m, 22 July 1983, *Kral 70308* (VDB, VEN); top of La Escalera, ca. 1,200 m, 24 July 1983, *Kral 70327* (F, K, MO, NY, U, US, VDB, VEN); just S of La Escalera ca. 1,200 m, 24 July 1983, *Kral 70372* (VDB, VEN); 6.5 km N of Pioneer Monument by Ven. 10, ca. 1,200 m, 24 July 1983, *Kral 70396* (US, VDB, VEN); Salto Yuruaní, 1,000 m, 29 July 1983, *Kral 70614* (VDB, VEN); Auyantepui, *Panier & Schwabe 5/9* (VEN); Chimantá Massif, middle falls below Summit Camp, 1,925 m, 5 Feb. 1955, *Steyermark & Wurdack 468* (NY, US); between Luepa and Cerro Venamo, 1,300 m, 25 Apr. 1960, *Steyermark & Nilsson 770* (NY, US); Chimantá Massif, Torono-tepui, summit,

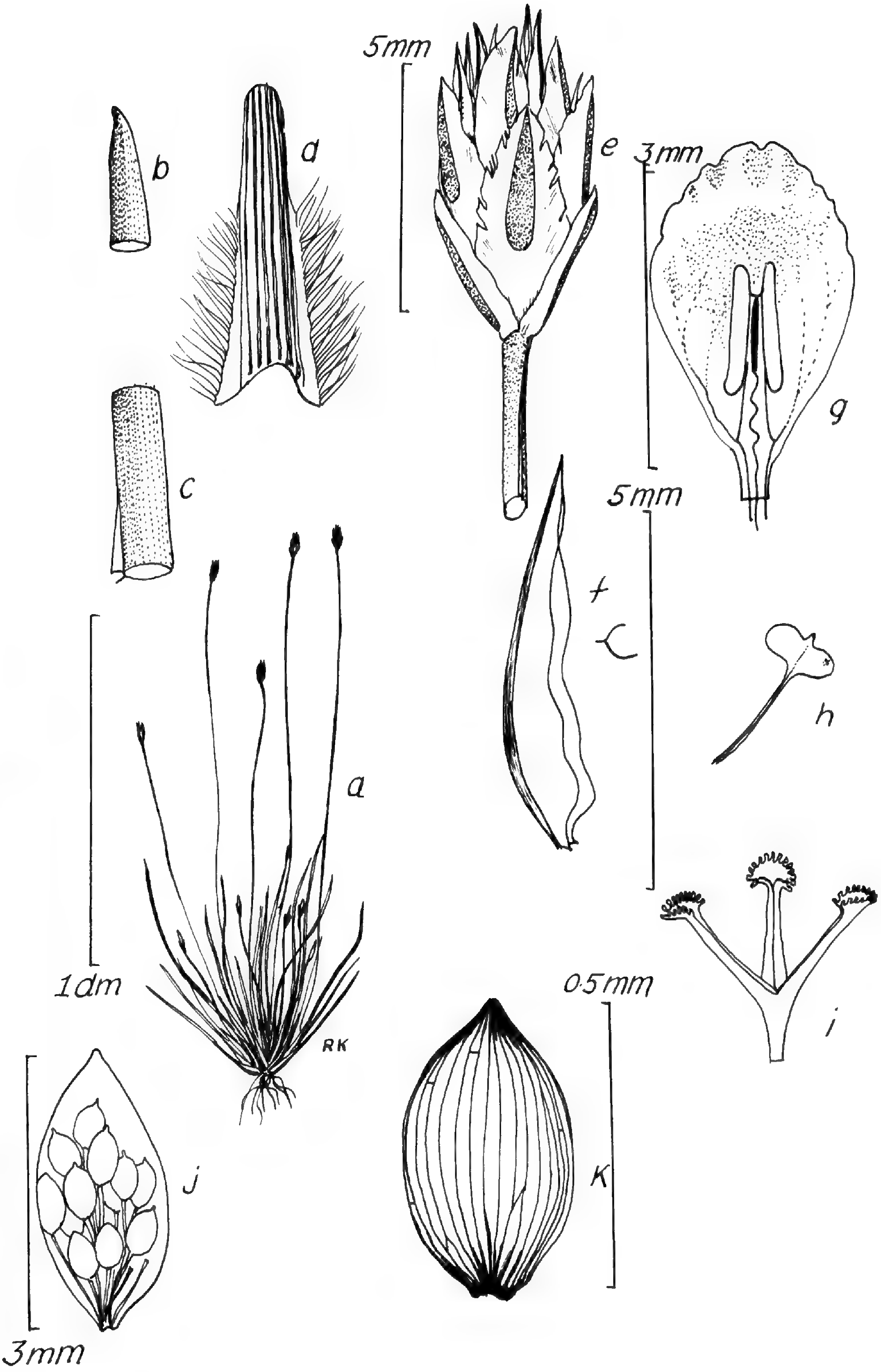


FIGURE 72. Xyris tenella (Kral 70372).—*a. Habit sketch.—b. Leaf apex.—c. Leaf blade–sheath junction.—d. Leaf base.—e. Spike.—f. Lateral sepal.—g. Petal blade, stamen.—h. Staminode.—i. Stylar apex.—j. Capsule, two valves removed, showing basal placentation.—k. Seed.*

Feb. 1955, *Steyermark & Wurdack 1096* (Type of *X. steyermarkii,* F, NY, US, VDB, VEN); Chimantá Massif, Torono-tepui South Caño, summit, 1,955 m, 23 Feb. 1955, *Steyermark & Wurdack 1122* (F, NY, US); Ptaritepui, entre "Drizzly Camp" y "Second Wall," 1,660–1,800 m, 11 May 1964, *Steyermark 93698* (F, MAC, NY, US, VDB, VEN); Meseta de Jaua, Cerro Jaua, 22–27 Mar. 1967, *Steyermark 97904* (F, K, NY, U, US, VDB); cumbre del Cerro Guaiquinima, sector suroeste-central, 26 May 1978, *Steyermark et al. 117480*; Cerro Marutani, 1,200 m, 2 Jan. 1981, *Steyermark 123895* (NY, US, VDB); parte superior del plato de Auyantepui, 2,300 m, Apr. 1956, *Vareschi & Foldats 4958* (NY, VEN).

Some insight into the *X. tenella* situation was given me by examination of a *Tate* specimen (*810*) from the gorge of Caño Negro, Savanna Hills, Mt. Duida. Malme, working when that part of Venezuela was hardly explored, did see this specimen, annotating it at first *X. tenella* Kunth var. *subtenella,* a taxon he later (Ark. Bot. 13(3): 44. 1913) changed to a form of the type variety. This led me to examine a rather large series of materials from Brazil and Paraguay. From these it appears that if transplants of *X. tenella* from Paraná or Mato Grosso were put in suitable habitat in Venezuela, such would be indistinguishable from forms named *X. steyermarkii* and *X. yutajensis.* The variety from French Guiana (var. *leprieurii* Malme, "Cajenne legit Le Prieur" isolectotype at L) is taller than the Venezuelan material, has flat, ciliolate-edged leaf blades, and narrowly ovoid spikes.

The dorsal area character in this species varies troublesomely. Sometimes it appears only on some bracts. In Brazil are specimens named other species that, if given the pencil-thin dorsal area, would again be placeable in *X. tenella.* The only constant, apart from the low and annual or short-lived perennial habit, seems to be the long brush of ciliae on the leaf-sheath edges. The dorsal area when present is very narrow, a ready means of distinguishing this from extremes of *X. guianensis,* which always has a broad dorsal area.

73. Xyris byssacea Kral, sp. nov. TYPE: Venezuela. T. F. Amazonas: Dpto. Río Negro, Valle de Titirico N of Pico Phelps in Cerro Neblina, ca. 0°56′N, 65°58′W, ca. 2,200 m; peat bog interspersed with shrub and low rocky but wet ridges, flowers opening in the A.M., 1 Dec. 1984, *R. Kral et al. 71926* (holotype, VEN; isotypes, MO, NY, US, VDB). Figure 73.

Planta perennis, densicaespitosa, glabra, delicatula. Caules breves; radices graciles. Folia principalia arcte disticha, suberecta, 8–15 cm longa, vaginis scaporum longiora; vaginae elongatae, laminis multi-plo longiores, byssaceociliatae, pallide brunneolae, nitidae, ad basin gradatim dilatatae, in laminas gradatim decrescentes, eligulatae; laminae compressae, 0.3–0.4 mm latae, leviter tortae, ferrugineae, nitidae, subcapillaceae, in apicem gradatim decrescentes, ad apicem conico-subulatae, plerumque setaceae. Scapi tenues, 20–30 cm longi, brunnei, apicem versus teretes, ecostati vel leviter striati, ca. 0.5 mm crassi. Spicae pauciflorae, ellipsoideae, tum curtocylindricae, pallide brunneolae, ca. 6 mm longae; bracteae leviter expanse, integrae, decussatae, area dorsali lineare, infimae 4 steriles, par inferiora lanceolata, ca. 3–4 mm longa, acuta, valde carinata, par intima ovata, ca. 4 mm longa, ad apicem curto-carinata, area dorsali redacto; bracteae fertiles 2–4, oblongae, 4.5–5 mm longae, subconduplicatae, anguste rotundatae, a medio ad apicem carinatae, area dorsali lineari. Sepala lateralia libera, inaequilateralia, anguste-elliptica, ca. 4.5–5 mm longa, acuta, leviter curvata, ala carinali angusta sed crassa, integra. Laminae petalorum anguste obovatae, luteolae, ca. 4 mm longae, integrae. Staminodia bibrachiata, brachiis anguste triangulatis, longipenicillatis. Antherae lanceolatae, vadose bifidae et sagittatae, ca. 1.5 mm longae, filiis ca. 0.5 mm longis. Capsula matura anguste ellipsoidea, ca. 3 mm longa; placenta basalis, funiculis elongatis. Semina ellipsoidea vel cylindrica, ca. 1 mm longa, translucentia, pallide ferrugineobrunneola, subtiliter longitudine spiraliter lineata.

Densely cespitose, smooth, delicate perennial. Stems short; roots slender. Principal leaves tightly distichous, suberect, 8–15 cm long, longer than the scape sheaths; sheaths elongate, many times longer than the blades, cobwebby-ciliate, pale brown, shining, gradually dilated toward base, gradually narrowing into blades, eligulate; blades flattened, subcapillary, 0.3–0.4 mm wide, slightly twisted, entire, red-brown, lustrous, gradually tapering, conic-subulate at apex, often setaceous. Scapes slender, 20–30 cm long, brown, terete toward apex, ecostate to slightly striate, ca. 0.5 mm thick. Spikes few-flowered, ellipsoid, later short-cylindric, pale brown, ca. 6 mm long; bracts spreading slightly, decussate, entire, the dorsal areas linear, the lowest 4 bracts sterile, the lowest pair lanceolate, ca. 3–4 mm long, acute, strongly carinate, the inner pair ovate, ca. 4 mm long, with a short carina

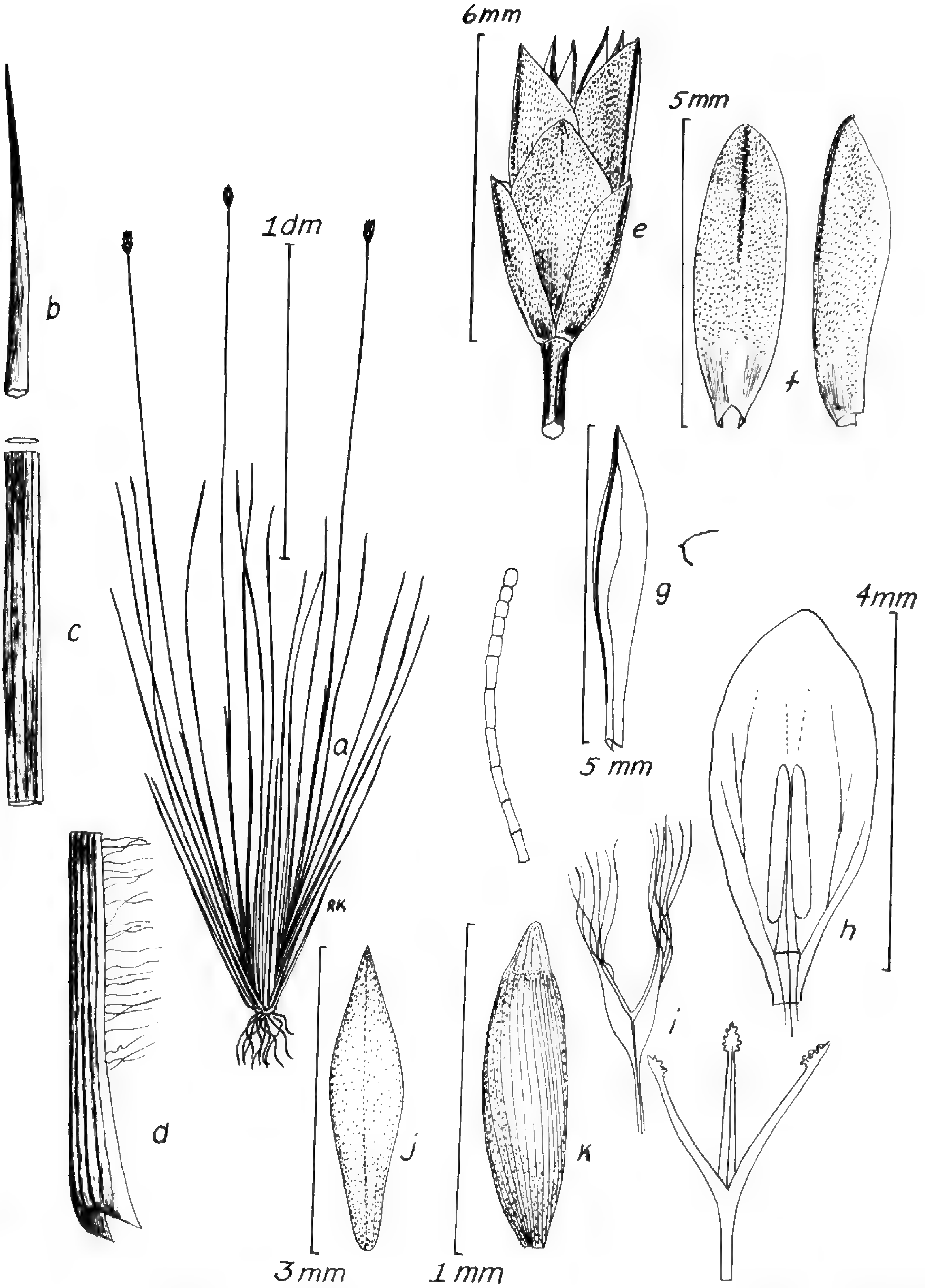


FIGURE 73. Xyris byssacea *(from an isotype)*.—*a. Habit sketch.*—*b. Leaf apex.*—*c. Sector of leaf at blade–sheath junction.*—*d. Leaf base.*—*e. Spike.*—*f. Two views of fertile bract.*—*g. Lateral sepal.*—*h. Petal blade, stamen.*—*i. Staminode, stylar apex.*—*j. Capsule.*—*k. Seed.*

at apex, the dorsal area reduced; fertile bracts 2–4, oblong, 4.5–5 mm long, subconduplicate, narrowly rounded, carinate from middle to apex, the dorsal area linear. Lateral sepals free, inequilateral, narrowly elliptic, ca. 4.5–5 mm long, acute, slightly curvate, the carinal keel narrow but thick, entire. Petal blades narrowly obovate, yellow, ca. 4 mm long, entire. Staminodia bibrachiate, the branches narrowly triangular, long-penicillate. Anthers lanceolate, shallowly bifid and sagittate, ca. 1.5 mm long, on filaments ca. 0.5 mm long. Capsule narrowly ellipsoid, ca. 3 mm long; placenta basal, the funicles elongate. Seeds ellipsoid to cylindric, ca. 1 mm long, translucent, pale red-brown, finely spirally lined longitudinally.

Distribution. Known only from the type area.

This species combines the slender habit of *X. delicatula* and *X. carinata* with the smooth, glassy-scaped character of *X. setigera*; yet the foliage is utterly smooth and the filiform, evenly tapering leaf blades entire. Notable are the spreading arachnoid-ciliate hairs of the sheath margins.

74. Xyris cryptantha Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 16, fig. 2A–E. 1963. TYPE: Venezuela. T. F. Amazonas: Ríos Pacimoni–Yatua–Casiquiare, fls. yellow, locally frequent, Sabana Pacimoni on rt. bank of Río Pacimoni, above mouth 50 km, 100 m, 2 Oct. 1957, *B. Maguire, J. J. Wurdack & C. K. Maguire 41677* (holotype, NY; isotypes, US, NY, VEN). Figure 74.

Mostly low, slender, tufted, fibrillose-based and short-lived perennial or annual 0.6–2.5 dm high, the stems contracted. Leaves erect, 0.5–2 dm long; sheaths floccose-ciliate or pilose-ciliate, less than ½ as long as blades, dilated at very base, broad, castaneous, tapering abruptly, then gradually to blades, eligulate, the blades filiform, subterete or slightly compressed but not sharp-edged, 0.7–1 mm thick, smooth and pale-puncticulate, conic-subulate or incurved-conic at apex. Scape sheaths much shorter than leaves, loosely tubular, with short, erect blades. Scapes linear-filiform, straight or flexuous, slightly twisted, smooth, maroon, pale-puncticulate (stomata), ca. 0.5 mm thick, distally terete, ecostate. Spikes obovoid, 5–9 mm long, reddish brown, few-flowered, the bracts distichous and loose, with large, distinct, pale brown dorsal areas, the sterile bracts ca. 4, the lowest pair distinctly longer than the fertile bracts, narrowly oblong-pandurate, with carinate, cucullate, acute tips arching over spike tip, often there connivent; fertile bracts oblong, 5.5–6 mm long, navicular, erect, the margins entire, scarious, lacerate, the tips rounded. Lateral sepals free, subequilateral, lance-linear, ca. 5.5 mm long, narrowly acute to acuminate, lustrous red-brown, the narrow, firm keel lacerate or friable-fimbriate above middle, later distantly ciliolate. Petal blades broadly obovate, ca. 5.5 mm long, yellow, the broadly rounded apex erose. Staminodia bibrachiate, the branches densely long-penicillate. Anthers ca. 1.5 mm long, deeply bifid at apex, auriculate at base, on filaments 1 mm long. Capsule narrowly ellipsoid-cylindric, 2.5–3 mm long, trilocular, the placentation thus axile, appearing free-central as valves detach. Seeds numerous on short funicles, ovoid or ellipsoid, ca. 0.5 mm long, pale red-brown, apiculate, longitudinally prominently but finely ribbed.

Distribution. Low, sandy savanna, locally abundant, southeastern Colombia, Territorio Federal Amazonas in Venezuela, and a disjunction in the Serra Araca, Amazonas, Brazil.

Additional specimens examined. BRAZIL. AMAZONAS: plateau of northern massif of Serra Aracá, 0°51–57′N, 63°21–22′W, 1,200 m, S side of North Mt., open plateau savanna, 11 Feb. 1984, *G. T. Prance et al. 28981* (INPA, NY). COLOMBIA. AMAZONAS: Puerto Huesito, sabanas del Alto de La Cruz; entre el Caño Chaquita (afluente del Atabapo) y en Caño Gente, 18–20 Aug. 1975, *H. García-Barriga 20890* (GH, US, VDB). VENEZUELA. T. F. AMAZONAS: la margen izquierda del Río Sipapo a unos 4–6 km aguas abajo de la boca del Río Guayapo, 8 Oct. 1983, *Guánchez & Varadarajan 2524, 2570* (TFAV, VDB); caño "Cabeza de Manteco" a 3–4 km de la boca, 100 m, al norte del medio Río Autana, 12 Nov. 1984, *Guánchez & Melgueiro 3543* (TFAV, VDB); sabanas en los alrededores de Guarinuma, 95 m, 25 Aug. 1978, *Huber 2656* (US, VDB); 2 km al W de San Antonio del Orinoco, 120 m, 20 July 1980, *Huber & Tillett 5423* (VDB, VEN); 5 km al S de la Laguna Yagua, 22 July 1980, *Huber & Tillett 5475* (VDB, VEN); ribera izquierda (Sur) bajo Río Siapa, poco distante de su desembocadura en el Río Casiquiare, 125 m, 7 Feb. 1981, *Huber & Medina 5799* (VDB, VEN); Sabana Pacimoni on rt. bank of Río Pacimoni, 50 km above mouth, 2 Oct. 1957, *Maguire & Wurdack 41667* (NY, US); Sabana El Venado on left bank of Caño Pimichín above Pimichín, 2 July 1959, *Wurdack & Adderley 43294* (NY, U, US, VEN).

This distinctive xyrid, in its low habit, slender foliage, small seeds, and general bract

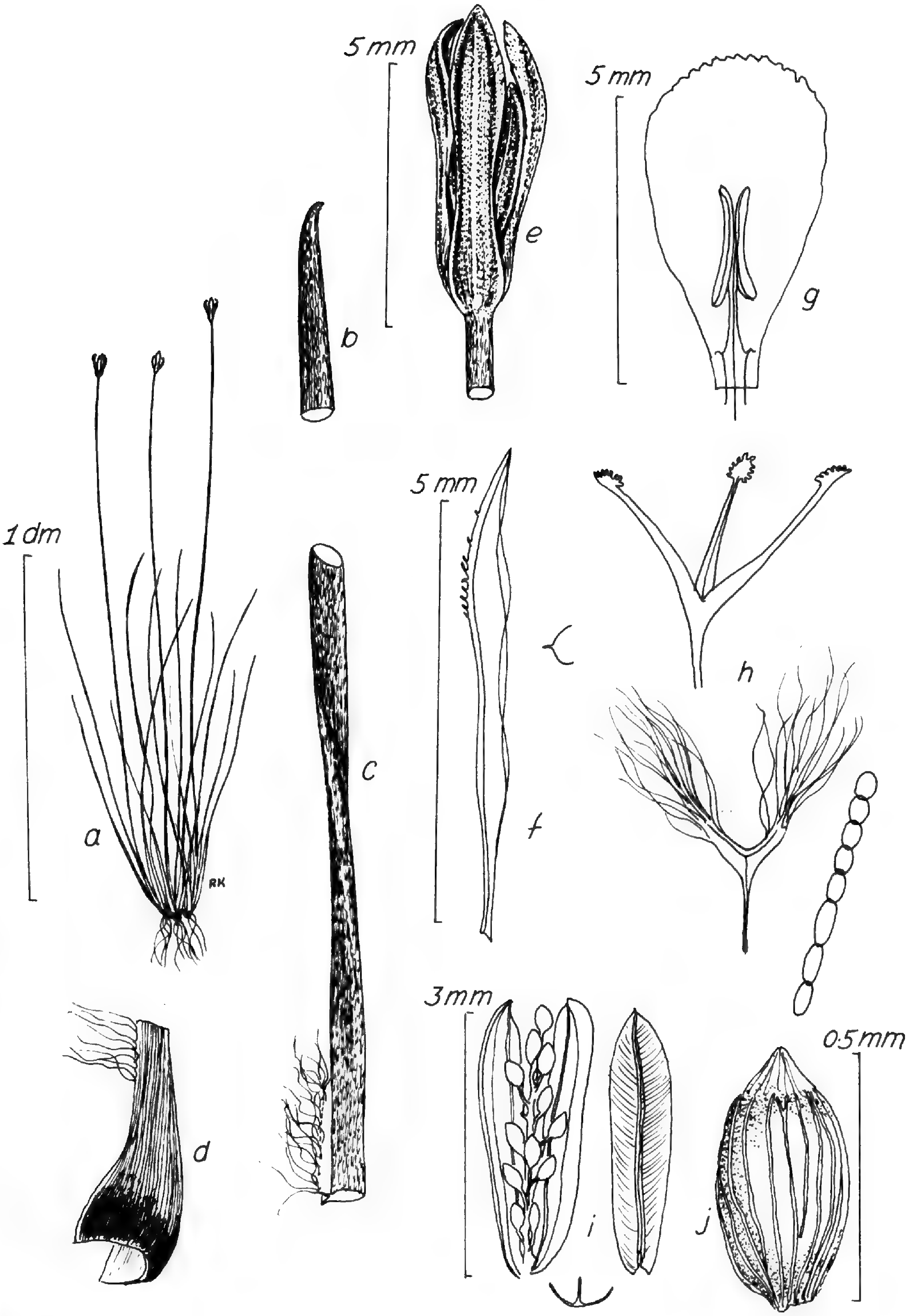


FIGURE 74. Xyris cryptantha (Huber & Tillett 5475).—*a. Habit sketch.—b. Leaf tip.—c. Leaf blade–sheath junction.—d. Leaf base.—e. Spike.—f. Lateral sepal.—g. Petal blade, stamen.—h. Stylar apex, staminode.—i. Capsule; at left with one valve removed; a valve at right.—j. Seed.*

characters definitely lies near *X. oxylepis*, a species with which it is associated in the white-sand savannas.

75. Xyris oxylepis Idrobo & Lyman B. Smith, Caldasia 6(29): 204, fig. 7a–c. 1954. TYPE: Colombia. Vaupés: "Río Kuduyari, cerro Yapoboda, sabanas sobre piedras areniscas," ca. 450 m, 5 Oct. 1951, *R. E. Schultes & I. Cabrera 14234-B* (holotype, COL; isotype, US). Figure 75A, B.

Xyris fusiformis Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 24, fig. 8A–E. 1963. TYPE: Venezuela. T. F. Amazonas: Sabana El Venado on left bank of Caño Pimichín, above Pimichín, 140 m, 10 Oct. 1957, Río Guainía, *B. Maguire et al. 41815* (holotype, NY; isotypes, GH, US).

Slender, low, wiry, cespitose perennial, the bases cloaked in fibrillose-chaffy remnants of old leaves, the stems contracted, the plants 1–3 dm high. Leaves mostly erect, quill-like, sometimes exceeding the scapes; sheaths less than ½ as long as blades, at base dull brown to castaneous, dilated, above brownish or red-brown, the edges villous-ciliate with brown hairs below, tapering gradually to blades and white-cottony-ciliate above, at junction with blade producing a broad, blunt ligule or essentially eligulate; blades subterete, usually with 4 or more rounded ribs and shallow sulci, sometimes with a strong ventral sulcus, narrowly linear, 0.5–0.7(–1) mm thick, apically conic-acute or narrowly triangular, smooth, the surfaces smooth or papillate, often white puncticulate. Scape sheaths much shorter than leaves, tubular and multicostate proximally, distally producing a short blade similar to leaves. Scapes twisted and flexuous, about as broad as leaves, terete distally, smooth, prominently multicostate, the ribs low, white puncticulate. Spikes narrowly ellipsoid or fusiform, aging cylindric, 7–10 mm long, acute, of a few, loosely imbricate, subdecussate, ecarinate bracts with strong dorsal areas; lower 4 bracts sterile, lance-ovate, 5–8 mm long, ½ or more as long as spike, broadly acute or narrowly rounded apically, scarious-edged, with large, elliptic, medially 1-nerved dorsal areas; fertile bracts 2–3, usually slightly longer and often with slightly narrower outline than sterile bracts, ca. 8 mm long, with similar dorsal areas. Lateral sepals free, equilateral, lance-linear to elliptic-linear, 6–7.5 mm long, acute, the narrow, firm keel entire or with scattered cilia above middle. Petal blades obovate, 5–6 mm long, yellow, the broadly or narrowly rounded apex erose or dentate-lacerate. Staminodia bibrachiate, the branches long-penicillate. Anthers oblong, ca. 2–2.5 mm long, nearly ½ bifid, deeply sagittate, on filaments 1.5–2 mm long. Capsule ellipsoid, ca. 3 mm long; valves with strong septa from base to tip, the placentation appearing axile. Seeds short-cylindrical, 0.7–0.8 mm long, pale amber, apiculate, finely anastomosing-ribbed longitudinally.

Distribution. Low-elevation sandy savanna, southeastern Colombia (rare) eastward into southwestern Venezuela, where locally abundant in the Orinoco savannas.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: Santa Cruz, margen del Río Atabapo, 4 Sep. 1960, *Foldats 3675* (US); Cerro Yapacana, Savanna III, 3 June 1978, *Huber 2036* (US); sabanas al SE de Carmelitas, 26 Aug. 1978, *Huber 2668* (US); Caño Yagua, 15 km río arriba desde la boca, 6 Dec. 1978, *Huber & Tillett 2906* (US); savanna III, 20–25 km al W de San Juan de Manapiare, *Huber 4588* (US); Estación de Piscicultura de Puerto Ayacucho, 75 m, *Maas & Huber 5164* (U, VDB); 30 km al N de Puerto Ayacucho, 5 km al NE de Galipero, 80 m, *Huber 5746* (US); same locality, 7 Nov. 1979, *Huber 4695* (US, VDB); 1 km N de la Laguna Yagua, 27 July 1980, *Huber & Tillett 5574* (US, VDB, VEN); 5 km NE de Galipero, 4 Nov. 1980, *Huber 5746* (US); Savanna I, W base Cerro Yapacana, 9 Aug. 1983, *Kral & Huber 70691* (F, K, L, MO, NY, SP, TFAV, US, VDB, VEN, and others); savannas II and III, 10 Aug. 1983, *Kral & Huber 70711* (US, NY, VDB, VEN); left bank of Caño Pimichín above Pimichín, 140 m, 23 Nov. 1953, *Maguire & Wurdack 36356* (NY, US); Yapacana savannas, 16 Sep. 1957, *Maguire et al. 41538* (NY, US); Cerro Yapacana, base, 8–9 Nov. 1979, *Thomas & Rogers 2590a* (NY).

The overlap of this Colombian rarity with the Venezuelan ecological and morphological equivalent, *X. fusiformis*, necessitates their combination even though ripe seeds are undescribed from Colombian material. In the savannas along the upper Orinoco it is a common sight, its pale yellow flowers unfolding in the afternoon. To illustrate reason for the

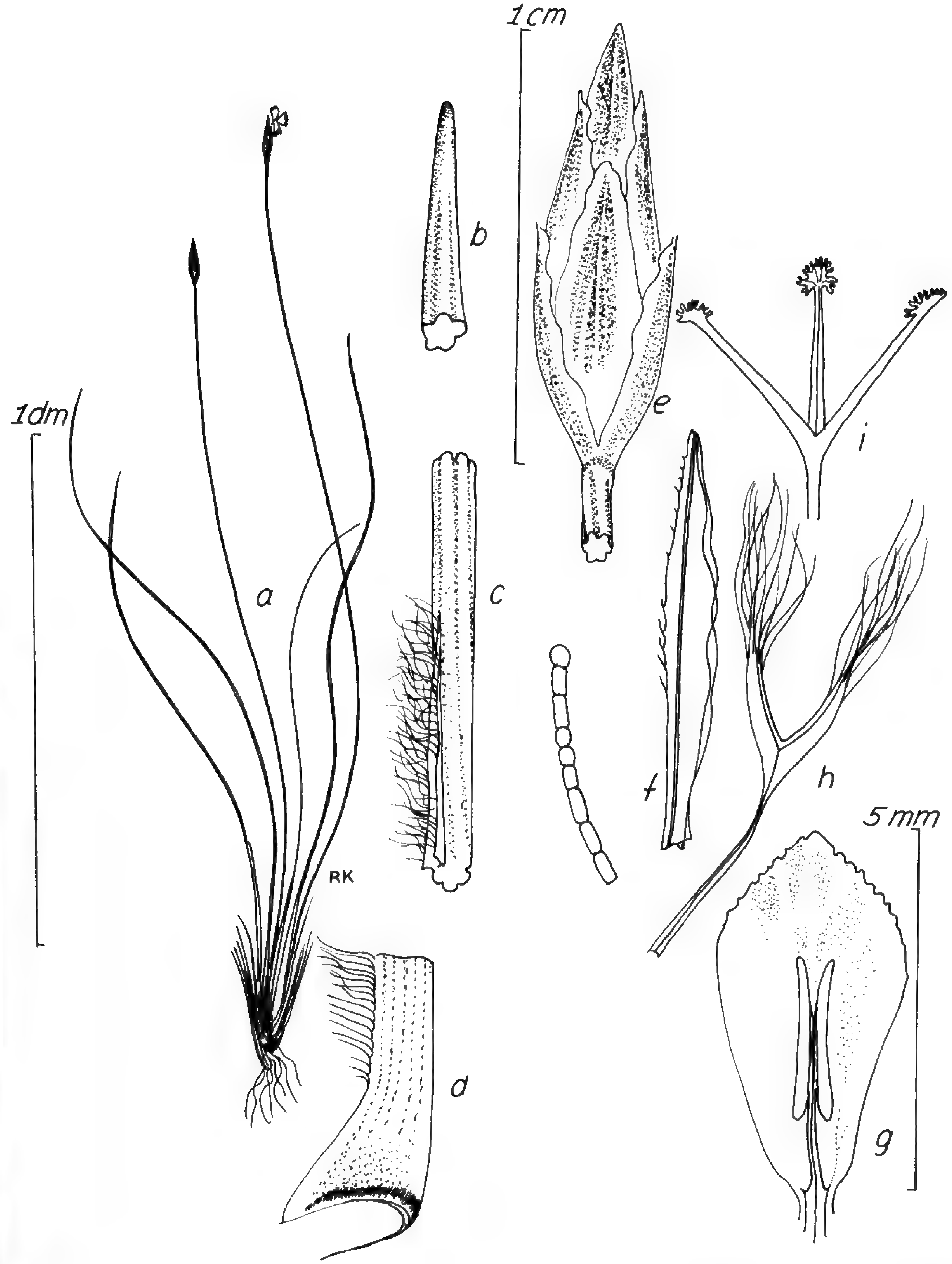


FIGURE 75A. Xyris oxylepis *(from the isotype).—a. Habit sketch.—b. Leaf apex.—c. Leaf blade-sheath junction.—d. Leaf base.—e. Spike.—f. Lateral sepal.—g. Petal blade, stamen.—h. Staminode.—i. Stylar apex.*

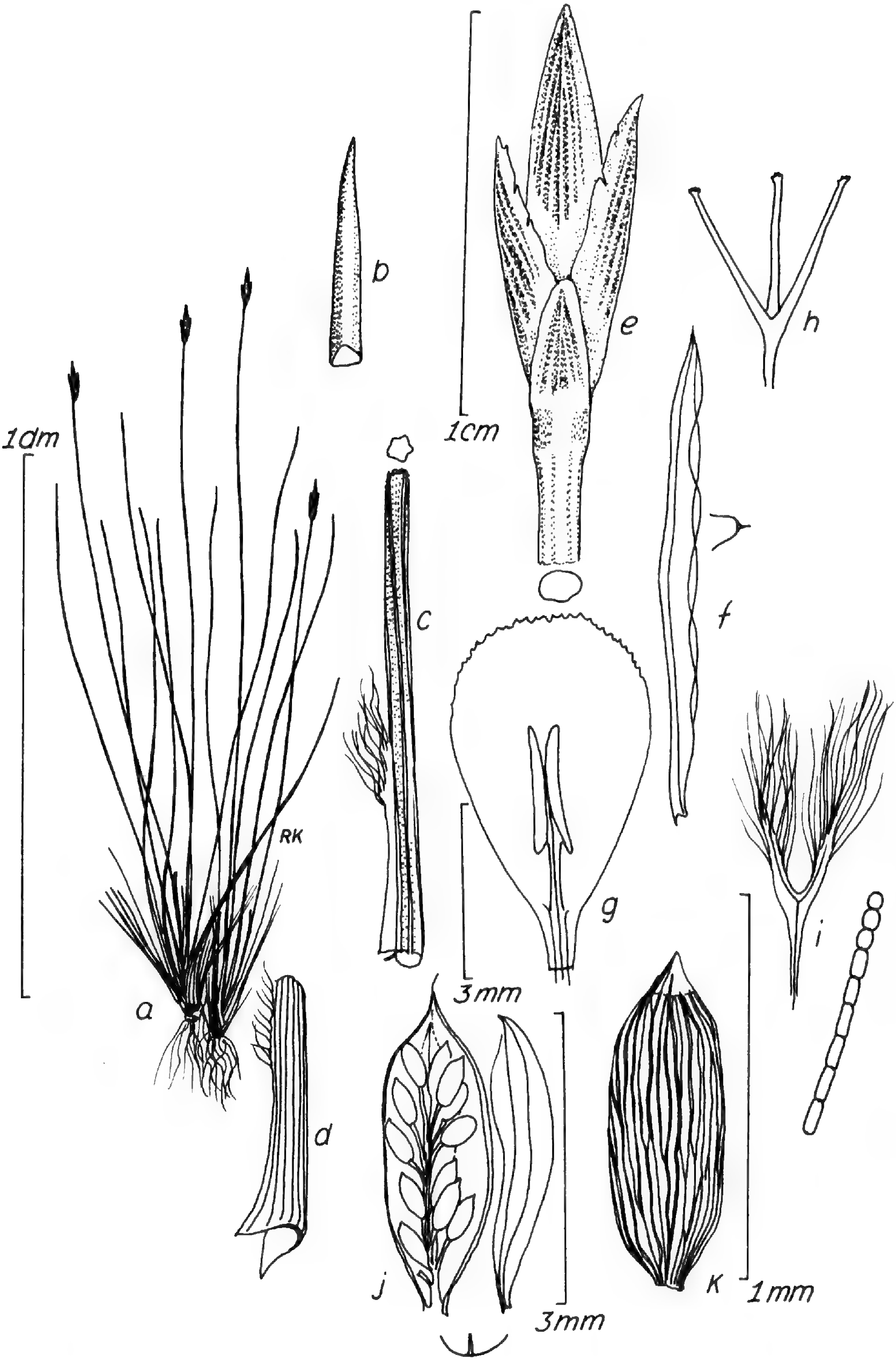


FIGURE 75B. Xyris oxylepis *(from type of* X. fusiformis *and from* Kral & Huber 70691*).—a. Habit sketch.—b. Leaf tip.—c. Leaf blade-sheath junction.—d. Leaf base.—e. Spike.—f. Lateral sepal.—g. Petal, stamen.—h. Stylar apex.—i. Staminode.—j. Capsule; at left with valve removed; at right a valve showing the septum.—k. Seed.*

combination of Colombian and Venezuelan material, Figures 75A (from the type of *X. oxylepis*) and 75B (from material of *X. fusiformis*) are presented.

76. Xyris wurdackii Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 24–25, fig. 9A–E. 1963. TYPE: Venezuela. T. F. Amazonas: Yavita–Pimichín trail near Pimichín, 140 m, Río Guainía, 22 Nov. 1953, *B. Maguire, J. J. Wurdack & G. S. Bunting 36366A* (holotype, NY; isotype, US). Figure 76A.

KEY TO THE SUBSPECIES OF *XYRIS WURDACKII*

1a. Most scapes overtopped by principal leaves; leaf blades and scapes prominently white puncticulate; fertile bracts pilose-ciliate at tips .... 76A. *X. wurdackii* subsp. *wurdackii*
1b. Most scapes overtopping principal leaves; leaf blades and scapes not noticeably white puncticulate; fertile bracts completely smooth .... 76B. *X. wurdackii* subsp. *caquetensis*

76A. Xyris wurdackii subsp. wurdackii.

Cespitose or solitary, perennial, sub-bulbous and fibrillose at base, the stems contracted. Leaves erect or ascending, few, the larger ones 1–3 dm long, twisted and flexuous, mostly overtopping scapes; sheaths less than ⅓ as long as blades, dilated at very base, dark brown or castaneous, gradually narrowing above, long-villous-ciliate, at bristly apex narrowing abruptly into blade, producing a broad, short, rounded-tipped ligule; blades linear, smooth, spirally fluted, terete, 1–1.5 mm thick, ventrally deeply sulcate and with numerous spiral lines of punctae, tapering shortly above middle to narrowly conic apices. Scape sheaths very short, mostly hidden in leaf sheaths, short-bladed. Scapes flexuous and twisted, 6–20 cm high, fluted and punctate as in leaf blades, proximally somewhat flattened, distally subterete with several low ridges, ca. as thick as leaf blades. Spikes obovoid, 7–10 mm long, the outer bracts subulate with raised midribs, nearly as long as or as long as the spike, the backs or at least the margins densely villous-tomentose with pale hairs, these often obscuring the bract outlines; bracts slightly widening inward in spike, the lowermost fertile ones the largest, lanceolate, 6–8 mm long, narrowly acute and at upper margins long-villous-pubescent, the convex backs castaneous and with large, lanceolate, pale-punctate dorsal areas, the margins strongly convolute apically. Lateral sepals lance-linear, free, equilateral, ca. 5 mm long, acuminate, the thin keel finely lacerate or flattened-villose toward apex. Petal blades broadly obovate, ca. 5 mm long, yellow, the narrowly rounded apex erose-crenulate. Staminodia bibrachiate, the narrow, flattened branches densely long-penicillate-ciliate. Anthers oblong-linear, ca. 1.5 mm long, on filaments ca. 1–1.5 mm long, deeply bifid, deeply sagittate. Capsule short-cylindric, ca. 3 mm long, the placental zone extending nearly to apex, the narrow valves with strong septa, thus placentation axile. Seeds numerous, ellipsoid, ca. 0.5 mm long, yellow-amber, multiribbed with narrow but distinct, often anastomosing, ridges longitudinally.

Distribution. Low-elevation savannas, southern Territorio Federal Amazonas, Venezuela.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: ca. a 5 km al W del bajo Río Temi, 100 m, 24 Feb. 1979, *Huber 3427* (US); 2–3 km al SE del bajo Río Guasacavi, 10 Mar. 1980, *Huber 5113* (US); 20 km al S del medio Caño Caname, ca. 100 m, 10 Mar. 1980, *Huber 5144* (US, VDB); 20 km al NW de Yavita, en las cabaceras del Caño Pimichín, 120 m, 11 Feb. 1980, *Huber & Medina 5949a* (VEN).

This subspecies appears to be fairly abundant in and around the type locality. It is very distinct in its combination of terete leaves and long, blonde or silvery, bristly and villose indumentum of spikes and edges of leaf sheaths.

76B. Xyris wurdackii subsp. **caquetensis** Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 24–25. 1963. TYPE: Colombia. Amazonas: frequent in scrub savanna, Araracuara, Río Caque-

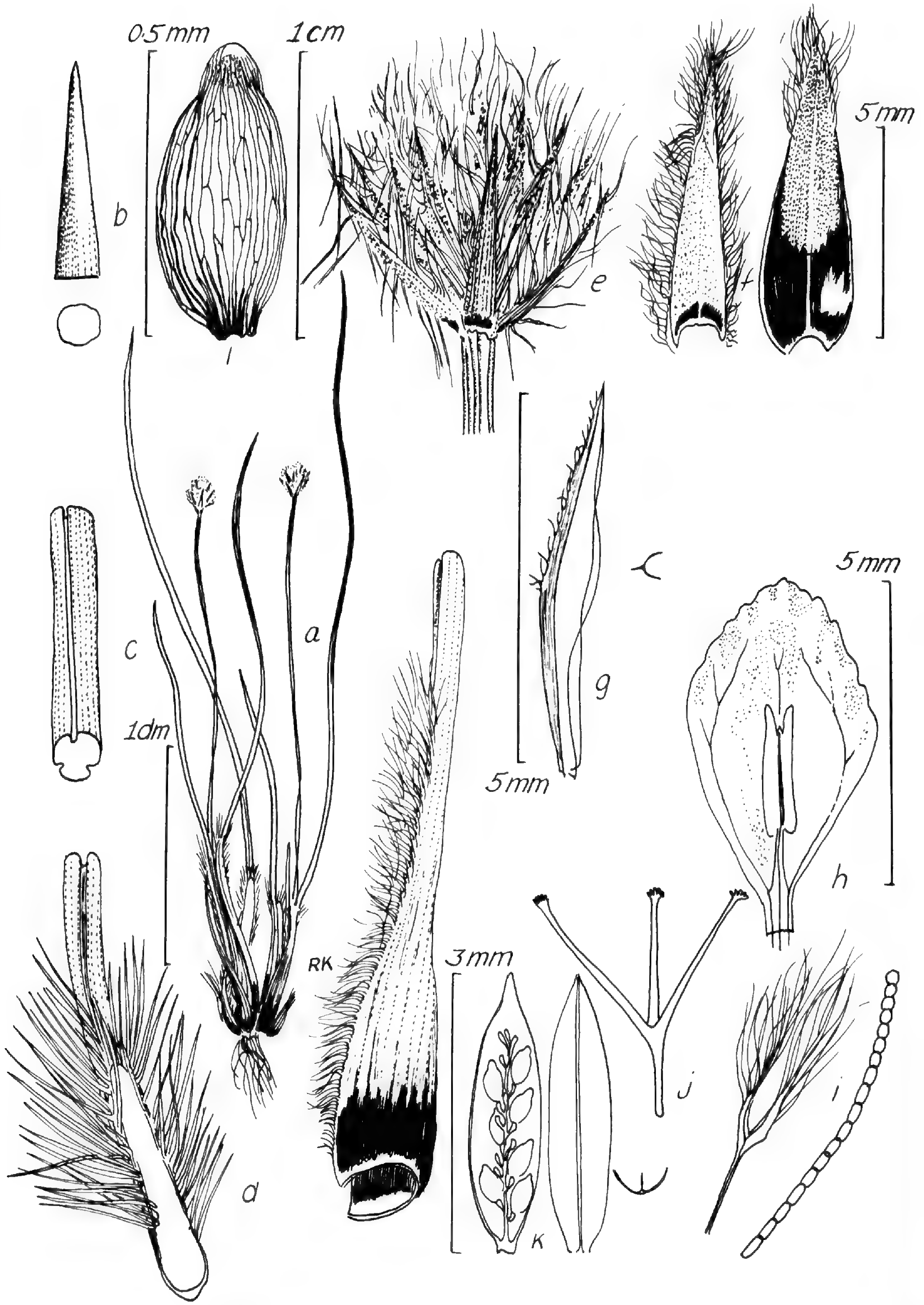


FIGURE 76A. Xyris wurdackii (Huber 5144).—*a. Habit sketch.—b. Leaf apex.—c. Leaf blade, ca. mid-blade.—d. Leaf base.—e. Spike.—f. Lowermost bract (left); lowermost fertile bract (right).—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode, enlarged beard hair.—j. Stylar apex.—k. Capsule through center longitudinally (left); one valve showing septum and cross section of same valve (right).—l. Seed.*

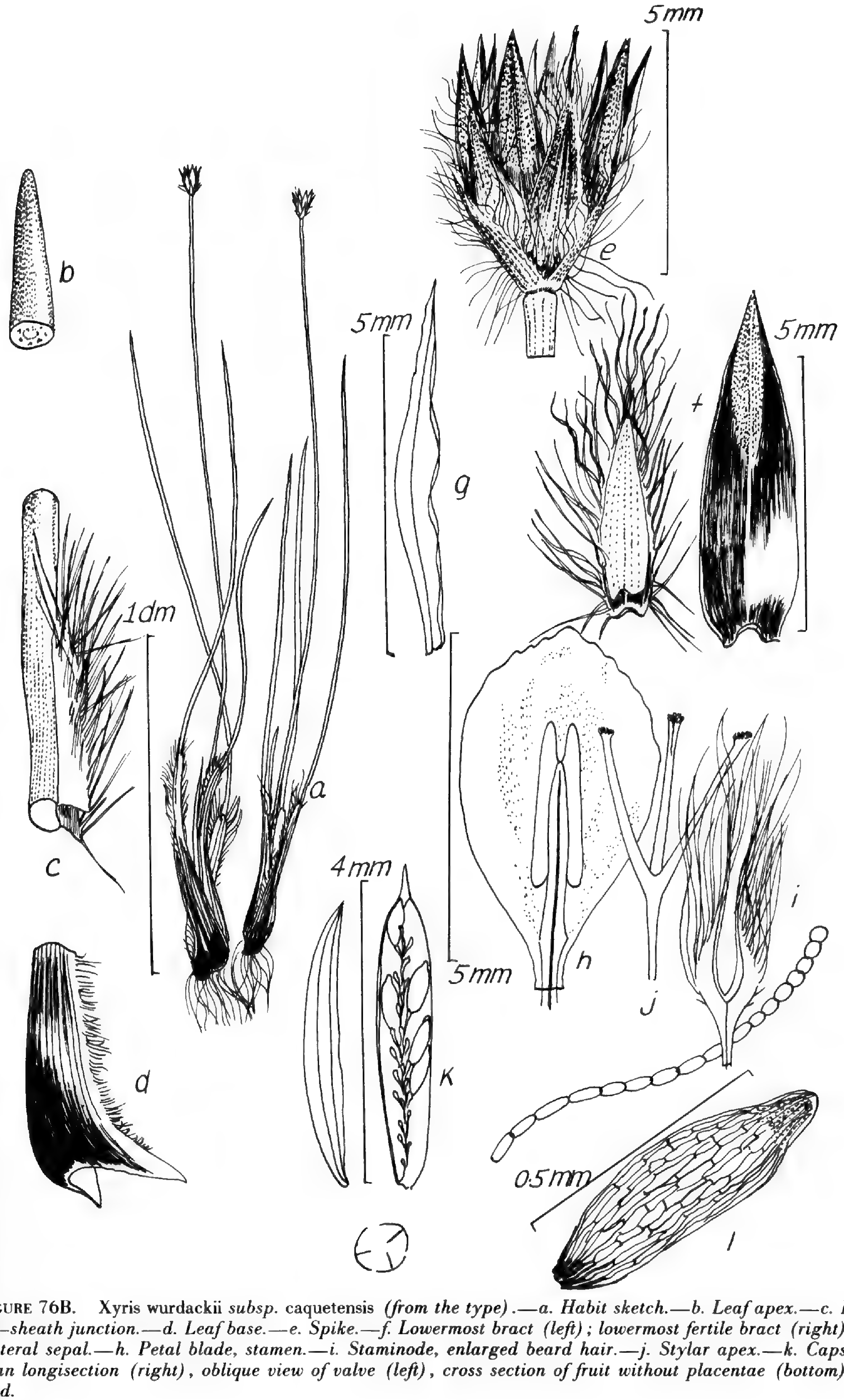


FIGURE 76B. Xyris wurdackii *subsp.* caquetensis *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Leaf blade–sheath junction.—d. Leaf base.—e. Spike.—f. Lowermost bract (left); lowermost fertile bract (right).—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode, enlarged beard hair.—j. Stylar apex.—k. Capsule; nedian longisection (right), oblique view of valve (left), cross section of fruit without placentae (bottom).—. Seed.*

ta, 5 Sep. 1959, *B. Maguire, C. K. Maguire & A. Fernandez 44129* (holotype, COL; isotypes, NY, US). Figure 76B.

This subspecies resembles the type subspecies, but most scapes overtop most leaves, and the leaf blades and scapes lack the prominent rows of pale punctae; the lowest sterile bracts are much shorter than spike and shorter than the outer fertile bracts; the inner sterile bracts are progressively less ciliate, becoming totally smooth; and the fertile bracts are entirely smooth. The capsule is narrowly cylindric and ca. 4 mm long; the seeds are slightly narrower and longer (0.5–0.6 mm); and the fine longitudinal ribs are more anastomosing.

Distribution. Known only from the type area.

Paratype. COLOMBIA. AMAZONAS: frequent in Aracuara Savannas, Río Caquetá, *Maguire et al. 44173* (NY).

This is another of the "close" vicariads involving the savannas of southern Colombia and Venezuela.

77. Xyris frequens Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 32–33, fig. 16A–E. 1963. TYPE: Venezuela. T. F. Amazonas: sabanita along Caño Pimichín on right bank 1 km above Pimichín, Río Guainía, 140 m, 24 Nov. 1953, *B. Maguire & J. J. Wurdack 36383* (holotype, NY; isotypes, NY, US). Figure 77.

Firm-based, cespitose perennial 2.5–3.5 dm high, the stems contracted. Leaves erect, the principal ones 1.5–3.5 dm long, the outer ones broad, short, bladeless brown scales; sheaths at intervals villous-ciliate, less than ¼ the length of the blades, pale red-brown, rugulose or nearly smooth, tapering gradually to green, rigid, flexuous or straight, terete or subterete blades 1 mm thick, apically blunt-conic, punctate, tipped (often) with a pale pilose coma, the surfaces smooth distally, proximally rugulose, strongly ribbed or ecostate. Scape sheaths shorter than leaves, open, producing elongate blades similar to leaves. Scapes flexuous and twisted, somewhat compressed, oval in cross section, smooth or finely rugulose. Spikes broadly ellipsoid, drying turbinate, 1–1.4 cm long, bracts several, in several ranks, loosely subdecussate, reddish brown with strong, paler dorsal areas, aging excurvate; sterile bracts several, broadly triangular to ovate, ecarinate, often villous-tufted apically at base, the lowest bracts much smaller than and grading into the fertile bracts, these broadly oblong, rounded-folded, 8–10 mm long, narrowly rounded or acute apically, subentire or erose, when young often villous-ciliate apically and red-bordered, the dorsal areas with a strong midnerve, often with several subparallel laterals. Lateral sepals free, equilateral, lance-linear, ca. 5 mm long, acuminate, the dark, wide, firm keel entire or apically ascending-ciliolate or villous-fimbriolate and coarsely serrate toward base. Petal blades elliptic, ca. 5 mm long, broadly acute and wavy-margined, yellow. Staminodia narrowly bibrachiate, the slender branches penicillate-pilose. Anthers narrowly oblong, 2.5 mm long, deeply bifid, deeply sagittate, on filaments ca. 1 mm long. Capsule ellipsoid-cylindric, ca. 5 mm long, the placentation appearing free-central from base to apex, but each valve detaching with a wide septum, thus placentation actually axile. Seeds numerous on short funiculi, narrowly ellipsoid, 1.5–1.6 mm long, including a pale, conic apiculus, the body finely striate, pale brown, overlain by a coarse, irregularly anastomosing reticulum of dark brown ridges.

Distribution. So far known only from savannas along the Caño Pimichín and those below Cerro Yapacana, Territorio Federal Amazonas, Venezuela. Other than the type, the only records appear to be the following.

Additional specimens examined. VENEZUELA. T. F. AMAZONAS: Savanna III, NW base of Cerro Yapacana, 150 m, 17 Mar. 1953, *B. Maguire & J. J. Wurdack 34572* (NY); Savanna III, Yapacana savannas, 10 Aug. 1983, *Kral & Huber 70706* (MO, NY, US, VDB, VEN).

This species most resembles the more widespread *X. surinamensis* but tends to have

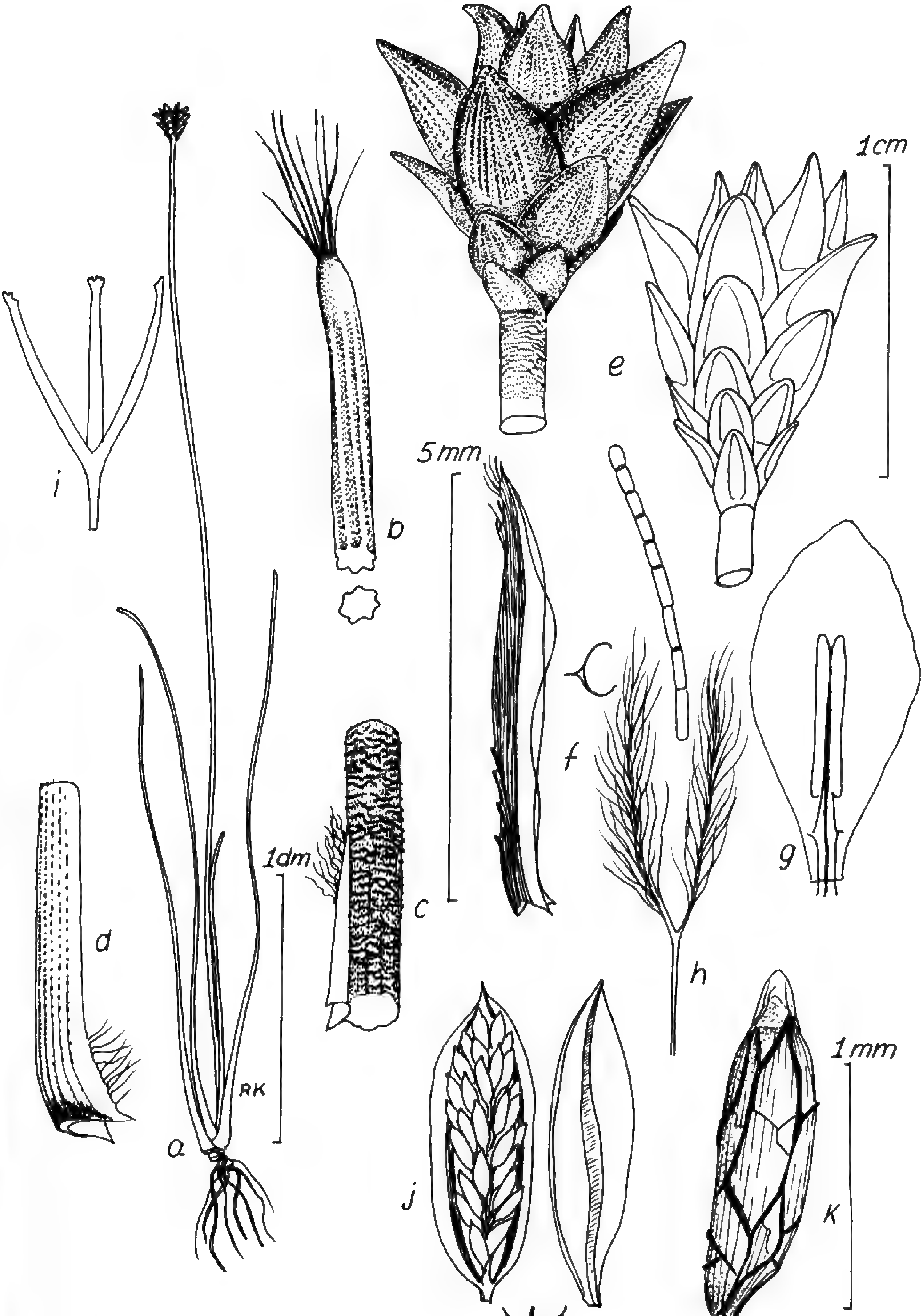


FIGURE 77. Xyris frequens *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Leaf at blade-sheath unction.—d. Leaf base.—e. Spike (at left in fruit, at right dried spike at anthesis).—f. Lateral sepal.—g. Petal, stamen.—h. Staminode.—i. Stylar apex.—j. Capsule, one valve removed; one valve, inner view.—k. Seed.*

more terete scape and leaf blade and a taller habit. Tips of most principal leaves have conspicuous tufts of pale, bristly trichomes.

78. Xyris subglabrata Malme, Bull. Torrey Bot. Club 48: 322. 1931. TYPE: Venezuela. T. F. Amazonas: Grand Savanna, section 1, in swampy ground, petals crimped, orange-yellow. Esmeralda, ca. 325 ft., 1 Nov. 1928, *G. H. H. Tate 303* (holotype, NY; phototype, F). Figure 78.

Xyris garcia-barrigae Idrobo & Lyman B. Smith, Caldasia 6: 204, fig. 8. 1954. TYPE: Colombia. Amazonas: Sabana de la Angostura, ca. 400 m, Río Caqueta, Araracuara, 21 Dec. 1951, *H. García-Barriga & R. E. Schultes 14168* (holotype, COL; isotypes, NY, US).

Cespitose, hard- and fibrillose-based perennial 1–3.5 dm high, the stems short, up from a stocky, horizontal or ascending rhizome. Leaves erect or ascending (0.7)1–2 dm long; sheaths with margins arachnoid or cottony, or pilose-ciliate, abruptly dilated at very base, reddish brown or castaneous, red-brown above, strongly papillose-rugose or nearly smooth, narrowing gradually to blades, ligulate or eligulate, the scarious edges often densely cottony; leaf blades lineal, terete-fluted, often sulcate and few-ribbed ventrally, 0.5–1 mm thick, dull green or maroon tinted, tapering to narrowly conic tips, these sometimes pilose-tufted, the surfaces smooth or papillose-rugulose toward base. Scape sheaths roughly equal to leaves and appearing like them. Scapes straight or flexuous, pale red-brown, slightly twisted, subterete distally, 0.7–1 mm thick, ecostate or striate, sometimes sulcate, papillose or smooth. Spikes ovoid to broadly ellipsoid, globose or obovoid, ca. 5–7 mm long, dark brown with several firm, spirally imbricate bracts having strong dorsal areas, also often with tips and base of bracts bearing white-villous patches; the lowest sterile bracts less than ½ length of the fertile ones, ovate, ecarinate; fertile bracts broadly obovate, ca. 5–6 mm long, convex-rounded-backed, the apices broadly rounded, entire, the dorsal areas broadly triangular with strong mid and lateral nerves. Lateral sepals free, slightly inequilateral, lanceolate, ca. 4.5–5 mm long, acute, deep lustrous yellow-brown, the firm keel villosulous or ciliate above middle. Petal blades broadly obovate, 4 mm long, yellow, the broadly rounded apices erose-denticulate. Staminodia bibrachiate, the narrow branches long-penicillate. Anthers oblong, ca. 2 mm long, deeply bifid and auriculate, extrorse, on stout filaments ca. 1 mm long. Capsule narrowly obovoid, somewhat compressed dorsiventrally, ca. 3 mm long, placentation appearing free-central, but valves with complete septa toward capsule base. Seeds oblong-short-cylindric or narrowly ovoid, ca. 0.6–0.7 mm long, apiculate, dark amber, finely lined and very finely cross-lined longitudinally.

Distribution. Mostly low-elevation, white-sand savanna, southeastern Colombia, southwestern Venezuela, and contiguous Amazonas, Brazil.

Additional specimens examined. BRAZIL. AMAZONAS: base of Serra Araca, 0–3 km S of central massif, 3 km E of Rio Jauari, 0°49′N, 63°19′W, 8 Feb. 1984, *G. T. Prance et al. 28885* (INPA, NY, VDB); plateau of northern massif of Serra Araca, 1,200 m, south side of North Mountain, open plateau savanna, 0°51′N, 63°21–22′W, 11 Feb. 1984, *G. T. Prance et al. 28979* (INPA, NY, VDB). COLOMBIA. VAUPÉS: Río Kuduyari, Cerro Yapaboda, ca. 450 m, 5 Oct. 1951, *Schultes & Cabrera 14234* (GH); same locality, 17 Nov. 1953, *Schultes et al. 18495* (GH); Río Paraná, Pichuna, trib. of Río Vaupés, ca. 700 ft., June 1953, *Schultes & Cabrera 19924, 19947* (GH); Cerro Yapoboda, ca. 900–1,000 ft., Apr. 1953, *Schultes & Cabrera 20055* (GH). VENEZUELA. T. F. AMAZONAS: sabana al pie del Duida, Jan.–Feb. 1969, *Farinias et al.* (NY, US); Sta. Cruz, margen del Río Atabapo, 4 Sep. 1960, *Foldats 3691* (NY, US, VEN); same locality, 9 Sep. 1960, *Foldats 3826* (NY, US, VEN); transecta, margen derecha del caño "Cabez de Manteco" afluente del Río Autana, a 2–3 km de la desembocadura, 12 Nov. 1984, *Melgueiro & Guánchez 17* (TFAV, VDB); transecto desde comunidad indigena de la etnia Piaroa, Río Autana en raudal "seguera," 90–110 m, 6 Nov. 1984, *Guánchez & Melgueiro 3306* (TFAV, VDB); 2–3 km SE del bajo Rio Guasacavi, 10 Mar. 1980, *Huber s.n.* (VEN); savana del bajo Río Ventuari, 20 km E la confluencia con el Río Orinoco, 11 Oct. 1977, *Huber 1062* (US, VEN); alrededores de Canaripo, Río Ventuari, 30 May 1978, *Huber 1913* (US, VEN); Savanna III, Cerro Yapacana, 100 m, 3 June 1978, *Huber 2053* (NY, US); Santa Barbara, 23 Aug. 1978, *Huber s.n.* (US, VDB); sabana, Caño Yagua, 24 Aug. 1978, *Huber 2557* (US); a unos 30 km al SE de la confl. Orinoco–Ventuari, 30 Nov.–1 Dec. 1978, *Hube* *& Tillett 2779* (US); sabana ubicada en la ribera NE de Caño Caname, 100 m, 30 June 1979, *Huber 4047* (VEN);

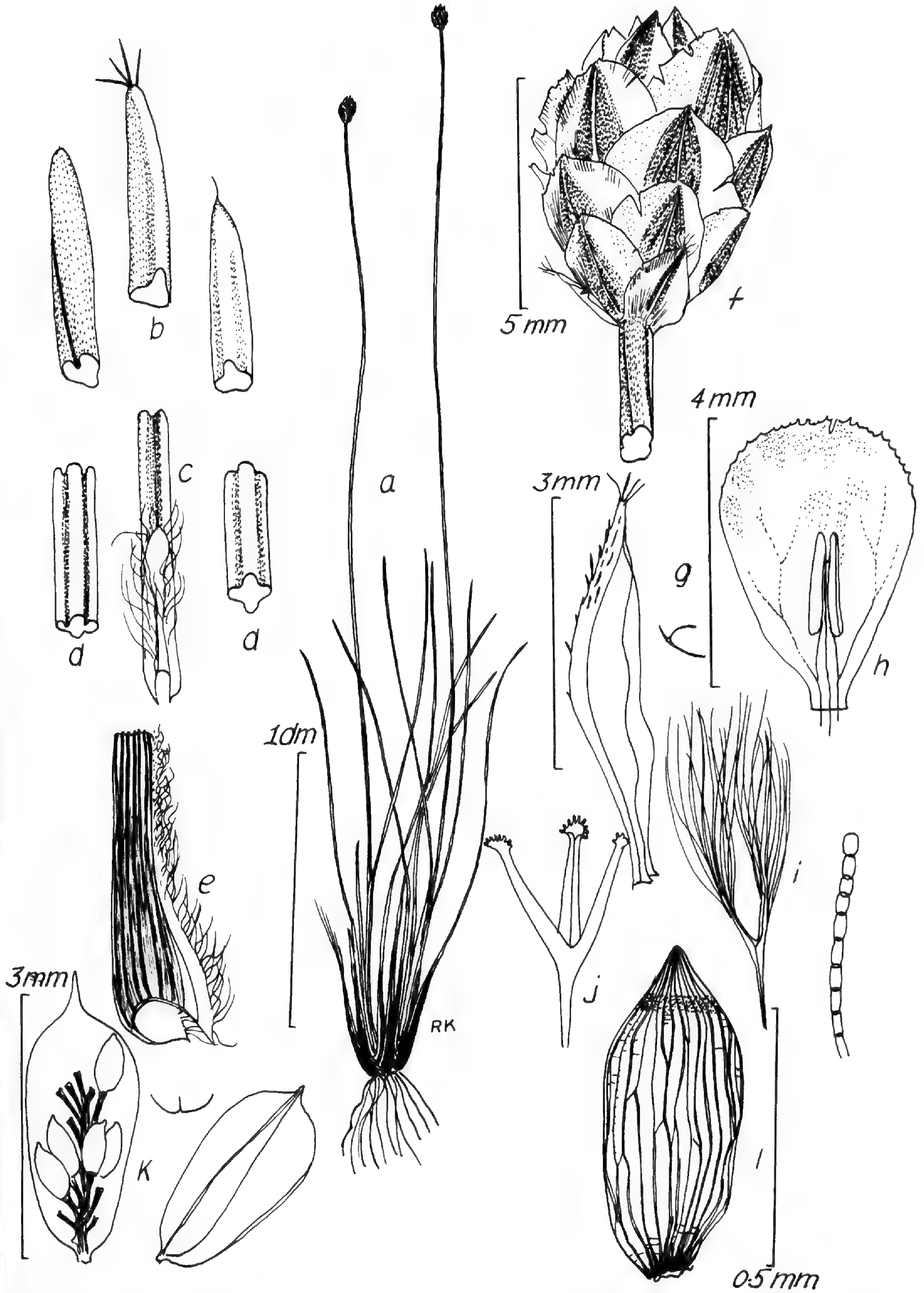


FIGURE 78. Xyris subglabrata (Kral 70692, 70709).—*a. Habit sketch.—b. Three types of leaf apices.—c. Leaf sheath–blade junction.—d. Two sorts of blade sectors.—e. Leaf base.—f. Spike.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode, enlarged beard hair apex.—j. Stylar apex.—k. Capsule; at left with two valves removed to show placentation, at right a single valve showing septum.—l. Seed.*

2 km S del medio Río Puruname, al SE del Caserío de Puruname, 100 m, *Huber & Tillet 5454* (US, VDB); 20 km NW Yavita, cabeceras Caño Pimichín, 120 m, 11 Feb. 1981, *Huber & Medina 5949* (VDB, VEN); km 11 de la Carretera San Carlos–Solano, 120 m, 16 Sep. 1980, *Huber et al. 5673* (VEN); Savanna I, Cerro Yapacana, 10 Aug. 1983, *Kral & Huber 70692* (BM, F, K, L, MO, NY, SP, TFAV, U, US, VDB, VEN, and others); Savanna II, 10 Aug. 1983, *Kral & Huber 70709* (BM, F, K, L, MO, NY, SP, TFAV, U, US, VDB, VEN, and others); Cerro Moriche, Río Ventuari, 4,500 ft., 15 Jan. 1951, *Maguire et al. 30936A* (NY, US, VEN); Bana 12 km N San Carlos, 100–120 m, 6 Feb. 1977, *Morillo & Villa 5395* (VEN); "Bana de Mary," 10 km San Carlos de Río Negro a Solano, 27 Aug. 1982, *Ruiz et al. 4025* (MY); between Esmeralda Savana and SE base of Cerro Duida, 200 m, 22 Aug. 1944, *Steyermark 57826* (F, NY); Cerro Yapacana, 7 May 1970, *Steyermark & Bunting 103253* (US, VDB, VEN); Canaripo, 28 Dec. 1976, *Steyermark & Redmond 112806* (MO, US, VDB, VEN); same locality, 2 Mar. 1977, *Steyermark et al. 113824* (MO, US, VDB, VEN); Sabana de Moyo, rt. bank of Orinoco, 31 July 1959, *Wurdack & Adderley 43711* (NY, US, VEN). BOLÍVAR: Dist. Piar, llanura del Río Ambutuir medio, ca. 20 km al NE de Uriman, 600 m, 8 Dec. 1983, *Huber 8473* (NY).

This plant, along with *X. setigera* Oliver, often has the corolla attacked by a fungus, the spore masses lending an orange quality to the flower. This color is sometimes recorded on labels, but I have not seen any *Xyris* with healthy orange corollas. Consultation of the type material of *X. garcia-barrigae* and of other material so identified will show no significant differences from the earlier-named *X. subglabrata*.

79. Xyris lithophila Kral & Lyman B. Smith, sp. nov. TYPE: Venezuela. Bolívar: Dist. Roscio, arbustales, sabana rocosa y vegetación ribereña en los alrededores del Salto "La Milagrosa," ca. 15 km al SW de S. Ignacio de Yuruaní. Formando pequeñas colonias sobre rocas en el lecho del río, 4°55′N, 61°14′W, 1,000 m, 22 June 1983, *O. Huber & Clara Alarcon 7568* (holotype, VEN; isotypes, MYF, VDB). Figure 79.

Planta perennis, caespitosa, gracilis. Radices graciles. Caules breves. Folia principalia erecta, subtorta, flexuosa, 0.8–2 dm longa, leviter papilloso-rugulosa, vaginis scaporum longiora; laminae 2–3-plo vagines longiores, filiformes, leviter compressae vel subteretes, 0.5–0.8 mm latae, longitudine leviter nervosae, nitidae, pallide olivaceae vel spadiceae; apices peranguste conicae aut subulatae; vaginae ecarinatae, pallide ferrugineae, ad basin leviter dilatatae, multicostatae, brunneolae, multicostatae, in laminas gradatim decrescentes, aciebus dense longivillosis, trichomatibus pallidis. Vaginae scaporum multicostatae, tubulosae, apicem versus apertae, laminis brevibus. Scapi 2–3.5 dm alti, glabri, leviter torti, nitidi, leviter papillosi, olivacei, ad apicem tereti, leviter striati. Spicae pauciflorae, ellipticae vel obovoideae, 7–9 mm longae, obtusae. Bracteae erectae, laxe spiraliter imbricatae, ecarinatae sed mediane conspicue constatae, integrae, pallide brunneolae, basin versus atrocastaneae; bracteae steriles 4, pari infimo late oblongo, ca. 4–5 mm longo, rotundato, ½–⅔-plo spica longiori; bracteae fertiles late oblongae vel anguste obovatae, ca. 6–6.5 mm longae, rotundatae, area dorsali anguste triangulata, atroferruginea. Sepala lateralia libera, subaequilatera, oblanceolata, 5.5–6 mm longa, leviter curvata, acuta; ala carinali lata a medio ad apicem lacerato-vel-fimbriato-ciliata. Laminae petalorum late obovatae, 4.5–5 mm longae, luteolae, ad late rotundatum apicem erosae. Staminodia bibrachiata, brachiis a basi ad apicem longipenicillatis. Antherae anguste oblongae, ca. 2 mm longae, profunde bifidae et sagittatae, filis ca. 1.5 mm longis. Capsula matura non visa sed quasi maturas capsulas et seminas vidi: sic, fructificatio cylindrica, ca. 3 mm longa et placenta centralis, valvis capsulae profunde septatis a basi ad apicem; semina numerosa ellipsoidea, ca. 0.7 mm longa, translucida, longitudine leviter multilineata.

Slender, tufted perennial; roots slender; stems short. Main foliage leaves erect, slightly twisted and flexuous, 0.8–2 dm long, lightly papillose-rugulose, longer than the scape sheaths; blades 2–3 times longer than the sheaths, filiform, slightly compressed or subterete, 0.5–0.8 mm wide, longitudinally finely nerved, shining, pale olive green to brownish; tips narrowly conic or subulate; sheaths ecarinate, pale reddish brown, slightly dilated at base, multicostate, brownish, gradually narrowing into blades, the margins densely long-villous, the trichomes pale. Scape sheaths multicostate, tubular, opening toward apex, short-bladed. Scapes 2–3.5 dm high, smooth, slightly twisted, shining, lightly papillose, olivaceous, terete toward apex, finely striate. Spikes few-flowered, elliptic to obovoid, 7–9 mm long, obtuse. Bracts erect, loosely spirally imbricate, ecarinate but with conspicuous midrib, entire, pale brown, deep castaneous toward base. Lateral sepals free, subequilateral, oblanceolate, 5.5–6 mm long, slightly curvate, acute; keel broad, lacerate- to fimbriate-ciliate from middle to apex. Petal blades broadly obovate, 4.5–5 mm long, yellow, the broadly rounded apex erose. Staminodia bibrachiate, the branches long-penicillate from

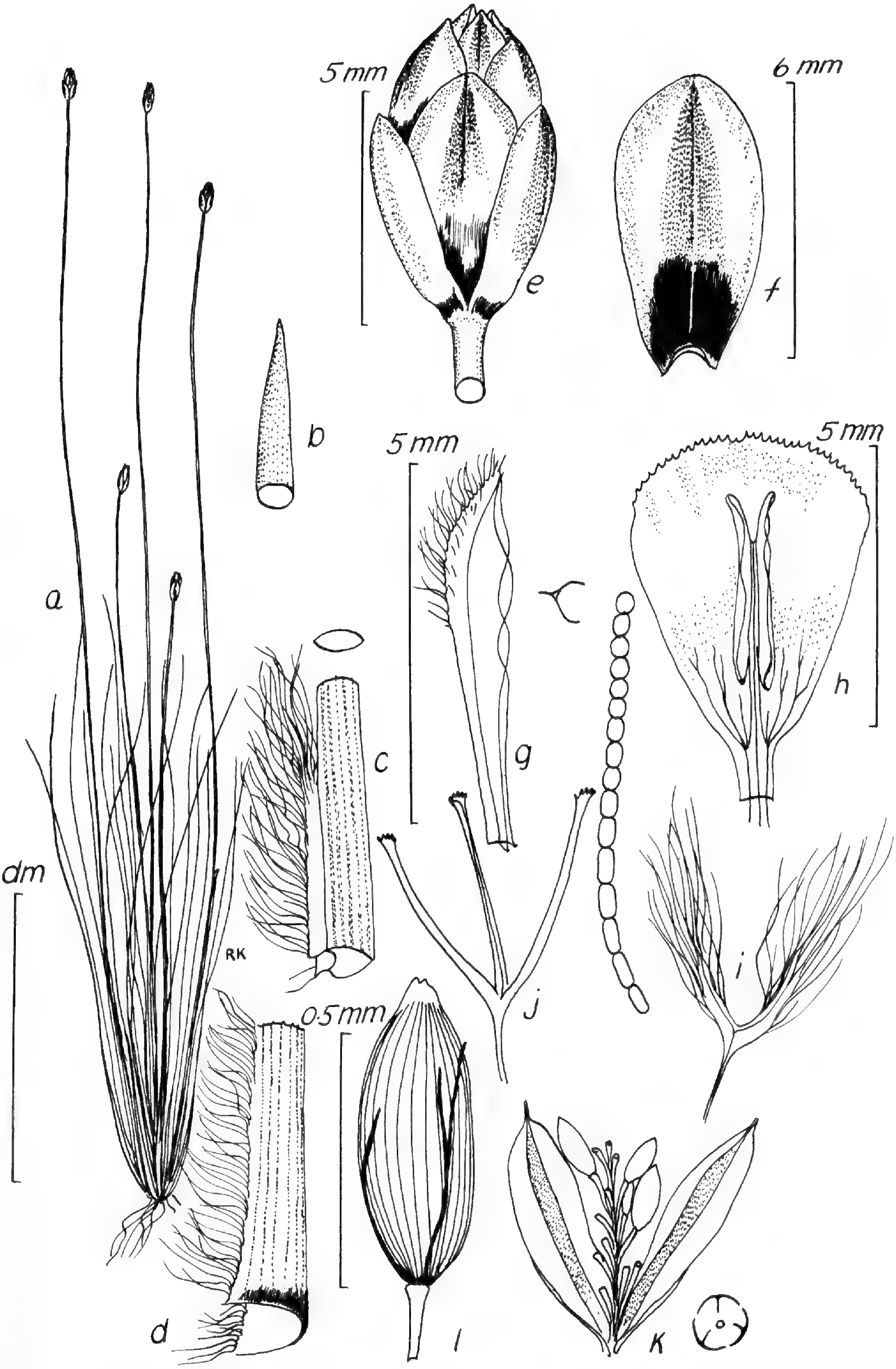


FIGURE 79. Xyris lithophila *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Leaf-sheath junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode, enlarged beard hair apex.—j. Stylar apex.—k. Capsule, opened, one valve removed, showing placentation and septa (stippled) on two valves.—l. Seed.*

base to tip. Anthers narrowly oblong, ca. 2 mm long, deeply bifid and sagittate on filaments ca. 1.5 mm long. Nearly mature fruit cylindric, ca. 3 mm long, the capsule valves deeply septate, the placentae central.

Distribution. Known only from the type locality.

The complex to which this slender plant belongs involves *X. setigera*, *X. delicatula*, and *X. carinata*, all of which are slender-leaved with foliage variously rugulose, the very thin sheath margins delicately pilose or villose. This taxon is distinguished primarily on the basis of smooth scapes (as in *X. setigera*) and conic-subulate tips to its slender leaves. The leaf tips not excentrically pointed, bract edges entire, and bract backs with very distinct dorsal areas are not usual in the complex.

80. Xyris carinata Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 36, fig. 21A–E. 1963. TYPE: Venezuela. T. F. Amazonas: occasional in *Bonnetia*–grass savanna, summit Cerro Guanay, Caño Guaviarito, 1,800 m, Río Manapiare, Río Ventuari, 4 Feb. 1951, *B. Maguire, K. D. Phelps, C. B. Hitchcock & G. Budowski 31773* (holotype, NY; isotypes, US, VEN). Figure 80.

Slender, cespitose perennial 2–3 dm high, the stem short. Leaves erect or ascending, 1–1.5 dm long; sheaths mostly less than ½ as long as blades, pilose-ciliate, at very base brown or stramineous and papillose-rugulose, more scabrid and rugose above, reddish, tapering to blade, eligulate or with a short, broad, rounded-scarious ligule, ecarinate; blades narrowly lineal, twisted and flexuous, flattened (oblong in cross section), 0.8–1 mm wide, narrowed above middle, then abruptly bluntly conic-tipped, smooth, the edges thick and rounded, tuberculate-rugose, the sides strongly verrucose-rugose, green with maroon tints. Scape sheaths shorter than leaves, tubular, twisted and costate, open distally, tipped with cusplike, erect, blunt blades. Scapes flexuous and twisted, distally terete, 0.7–0.8 mm thick, papillose-rugulose. Spikes ellipsoid, aging obovoid, 7–8 mm long, dull brown or tan, of several erect but loosely imbricate, firm, spirally arranged bracts with narrowly elliptic, subapical dorsal areas and papillose, rounded backs; lowest sterile bracts much smaller than the fertile bract, ovate, narrowly rounded, grading into the fertile bracts, the outer fertile bracts narrowly obovate or oblong, ca. 7–8 mm long, narrowly rounded, subentire, with narrow, short, subapical carinae, the inner bracts progressively more folded and carinate. Lateral sepals free, subequilateral, oblanceolate, ca. 6 mm long, acute, tan with the thin, darker keel ascending-ciliate from middle to apex. Petal blades narrowly obovate, ca. 5 mm long, yellow. Staminodia bibrachiate or (anomalously) compound, 2- or 4-branched, the branches long-penicillate. Anthers oblong, deeply bifid, deeply sagittate, ca. 2 mm long on filaments ca. 1 mm long. Capsule narrowly obovoid-cylindric, ca. 4 mm long, the ovary trilocular with septa breaking from axis at maturity, falling with valves. Seeds numerous, ellipsoid, ca. 0.7 mm long, acute, dark amber, longitudinally with ca. 12–14 strong ribs per side.

Distribution. High, sandy rocky savanna at medium to high (over 1,000 meters) elevations, southern Venezuela and contiguous Brazil.

Additional specimens examined. BRAZIL. TERR. RÓRAIMA: vic. Auaris 4°3′N, 64°22′W, upper slopes of Serra Parima, S of Auaris, 1,400–1,520 m, rocky outcrop in seepage, Feb. 1969, *Prance et al. 9808* (F, K, U, US); same locality, 1,200 m, 30 July 1974, *Prance et al. 21564* (U, NY, US, GH). VENEZUELA. T. F. AMAZONAS: cumbre del Cerro Autana, 1,230–1,240 m, 20–22 Sep. 1971, *Steyermark 105142* (US); Sierra Parima, cabeceras del Río Matacuni, a lo largo de la frontera Venezolana–Brasilera, 1,500 m, 19 May 1973, frontera no. 7, 4°5′N, 64°40′24″W, *Steyermark 107505* (F, MO, US, VEN). BOLÍVAR: altiplanicie del Auyan-tepui, sector SSW de la meseta, al W de la cumbre sur, ca. 2,070 m, 27 Aug. 1983, *Huber et al. 8079* (NY, VDB, VEN); Mount Auyan-tepui, 2,200 m, Dec. 1937, Jan. 1938, *Tate 1320* (NY).

Yet another of the growing number of species from the Guayana Highlands that, while placed in *Nematopus*, actually have

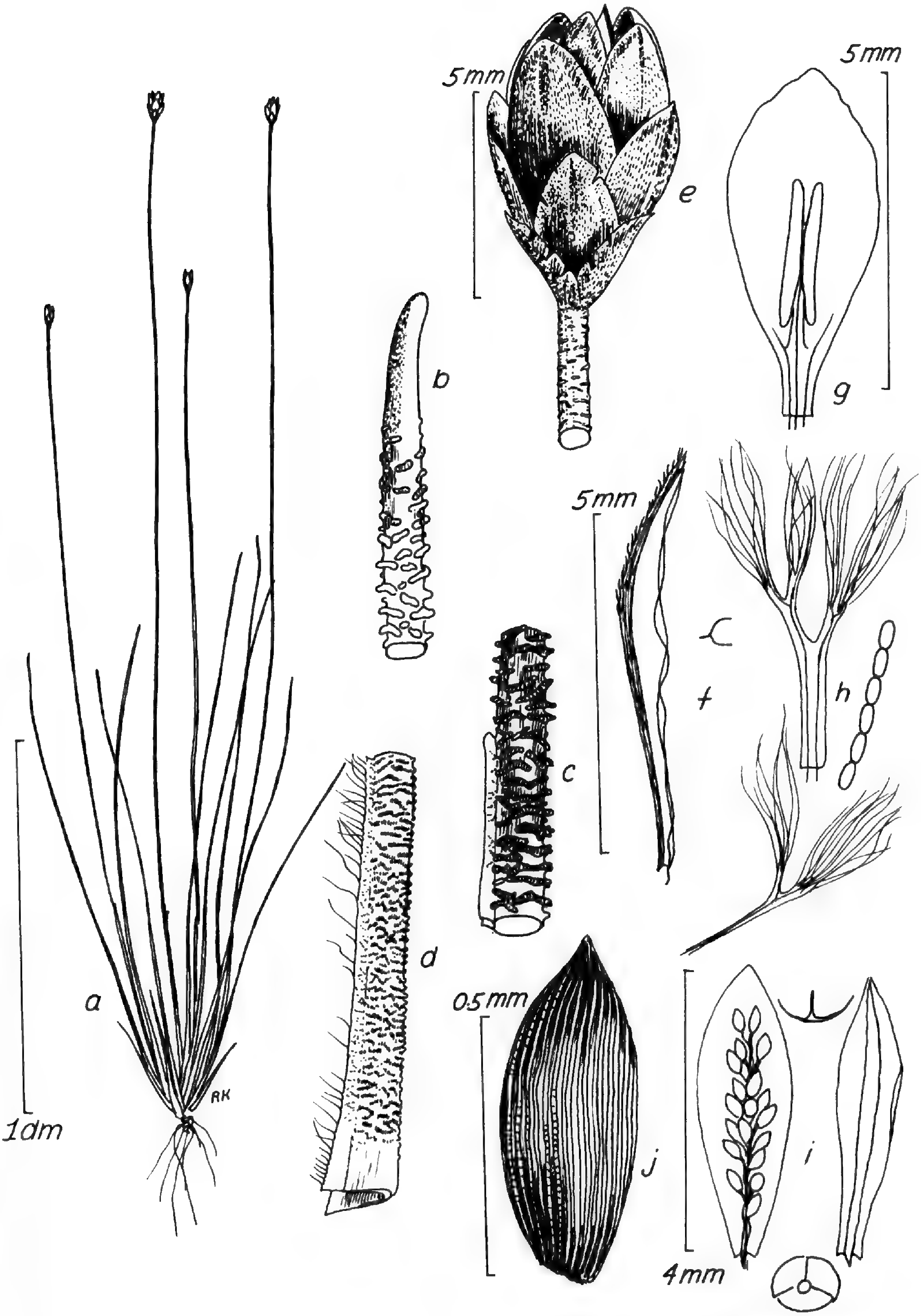


FIGURE 80. Xyris carinata *(from the type).—a. Habit sketch.—b. Leaf tip.—c. Leaf sheath–blade junction.—d. Leaf base (more reduced than other leaf sketches).—e. Spike.—f. Lateral sepal.—g. Petal blade, stamen.—h. Staminodia, one of them compound.—i. Capsule outline, placenta superimposed; inner view of one valve showing septum.—j. Seed.*

axile placentation. Further study of this species complex, which is around *X. setigera*, may require reduction of several of these entities to the level of variety or subspecies.

81. Xyris setigera F. Oliver, Trans. Linn. Soc. London, Bot. 2: 285, pl. 50A, figs. 1–8. 1887. TYPE: Venezuela. Bolívar: Roraima (Venezuela), 4,000 ft., 4 Dec. 1884, *Everard F. im Thurn 62* (lectotype, K; isolectotypes, BM, US). Figure 81.

Xyris setigera var. *elongata* Steyerm., Fieldiana, Bot. 28(1): 112. 1951. TYPE: Venezuela. Bolívar: Ptari-tepui, dry sandy and rocky sandstone exposures on level ground adjacent to swamp on plateau portion of southeast-facing slopes, 1,600 m, 1 Nov. 1944, *J. A. Steyermark 59660* (holotype, F; isotypes, GH, NY).

Densely cespitose, stiffish perennial, mostly 1.5–6 dm high; stems contracted to slightly elongated. Leaves erect to spreading flabellately or ascending, 0.5–2.5 dm long; sheaths dark to pale, red-brown or purple-red, mostly more than ½ as long as blades, the edges long-ciliate, narrowing gradually from the dilated, scabro-rugose (rarely smooth) base into the blades, there eligulate or in high-elevation forms sometimes producing a ligule to 2 mm long, the blades narrowly linear to filiform (in high-elevation forms), usually flattened, 0.5–3 mm wide, at apex excentrically short-spinulose or narrowly conic-subulate, the margins thick, scabro-ciliate or tuberculate-scabrid with strumose, antrorsely or retrorsely bent, simple or branched trichomes or tubercles (rarely smooth in high-elevation forms), the surfaces deep green to maroon or olive, tuberculate-rugose or smooth, punctate. Scape sheaths shorter than leaves, the bases tubular, multicostate and keeled, often reddish or roseate or lucid brown, open distally, keeled, producing a short, strong blade similar to leaves. Scapes straight or flexuous, twisted, terete distally, ca. 0.5–1 mm thick, smooth, often lustrous, punctate, maroon to green. Spikes ovoid to ellipsoid, 0.5–1 cm long, aging obovoid or turbinate, pale to deep brown, of several loosely spirally imbricate, stiff bracts usually without distinct dorsal areas (occasional extremes with narrow, indistinct dorsal areas); sterile bracts few, oblong, spreading, ecarinate, smaller than and grading into fertile bracts, these oblong to narrowly obovate, ecarinate, 6–7 mm long, narrowly rounded apically, entire, aging lacerate, the backs slightly convex. Lateral sepals free, subequilateral, mostly oblanceolate, 5–6 mm long, acute, dark reddish brown, the keel at middle and above lacerate-serrulate to nearly entire. Petal blades broadly obovate, ca. 6 mm long, yellow, the rounded apex subentire. Staminodia bibrachiate, the slender branches densely long-penicillate. Anthers 1.7–2 mm long, narrowly oblong, deeply bifid and sagittate, on filaments 0.8–1 mm long. Capsule cylindric-ellipsoid, ca. 4.5 mm long, the placentation axile, the septa separating from the central (placental) axis as the valves part. Seeds numerous, ellipsoid-ovoid, ca. 0.5–0.6 mm long, 2-apiculate, dark amber, longitudinally finely but strongly ribbed and with several less distinct cross-lines.

Distribution. Medium- to high-elevation, sandy or rocky savanna, centering in the massifs of the Gran Sabana, Estado Bolívar, Venezuela, southward shortly over the border of Brazil, eastward into eastern Guyana and northern Territorio Roraima, Brazil.

Additional specimens examined. BRAZIL. RORAIMA: Mt. Roraima, *E. F. Thurn 62* (the type for the species at K shows that some of the set could have come from the Brazil side of Roraima); ? Philipp Swamp, 5,100–5,200 ft., 11 Nov. 1927, *Tate 336* (K—? locality listed for Brazil, British Guiana, and Venezuela, depending on collector at this site). GUYANA: Kaieteur Plateau, 2 May 1944, *Maguire & Fanshawe 23164* (K); southern Pakaraima Mts., Kopinang Savanna, Kopinang Falls, 2,700 ft., 29 Aug. 1961, *Maguire et al. 45988* (K, VEN). VENEZUELA. (Note—this is perhaps the most common and commonly collected species in Estado Bolívar; therefore few citations are given here. A complete list will be made available later.) BOLÍVAR: Cienagas del Cerro Uaipan, 1,750 m, Río Caroní, 26 Nov. 1946, *Cardona 200g* (US, VEN); 2 km S of La Ciudadella, 1,300 m, 3 Dec. 1973, *Davidse 4699* (MO, VDB); ca. 17 km NE Ikabarú, 1,100 m, 7 Oct. 1982, *Huber et al. 6727* (MYF, VDB, VEN)—this material has dorsal areas; sabanas, sector norte de la Gran Sabana, 1,030 m, 5 Mar. 1982, *Huber et al. 7337* (MYF, VDB, VEN); cumbre del Cerro Chirikayne ca. 15 km NW Sta. Elena de Uairen, 1,580 m, 25 June 1983, *Huber et al. 7601* (MYF, VDB); Cerro Venado ca. 20

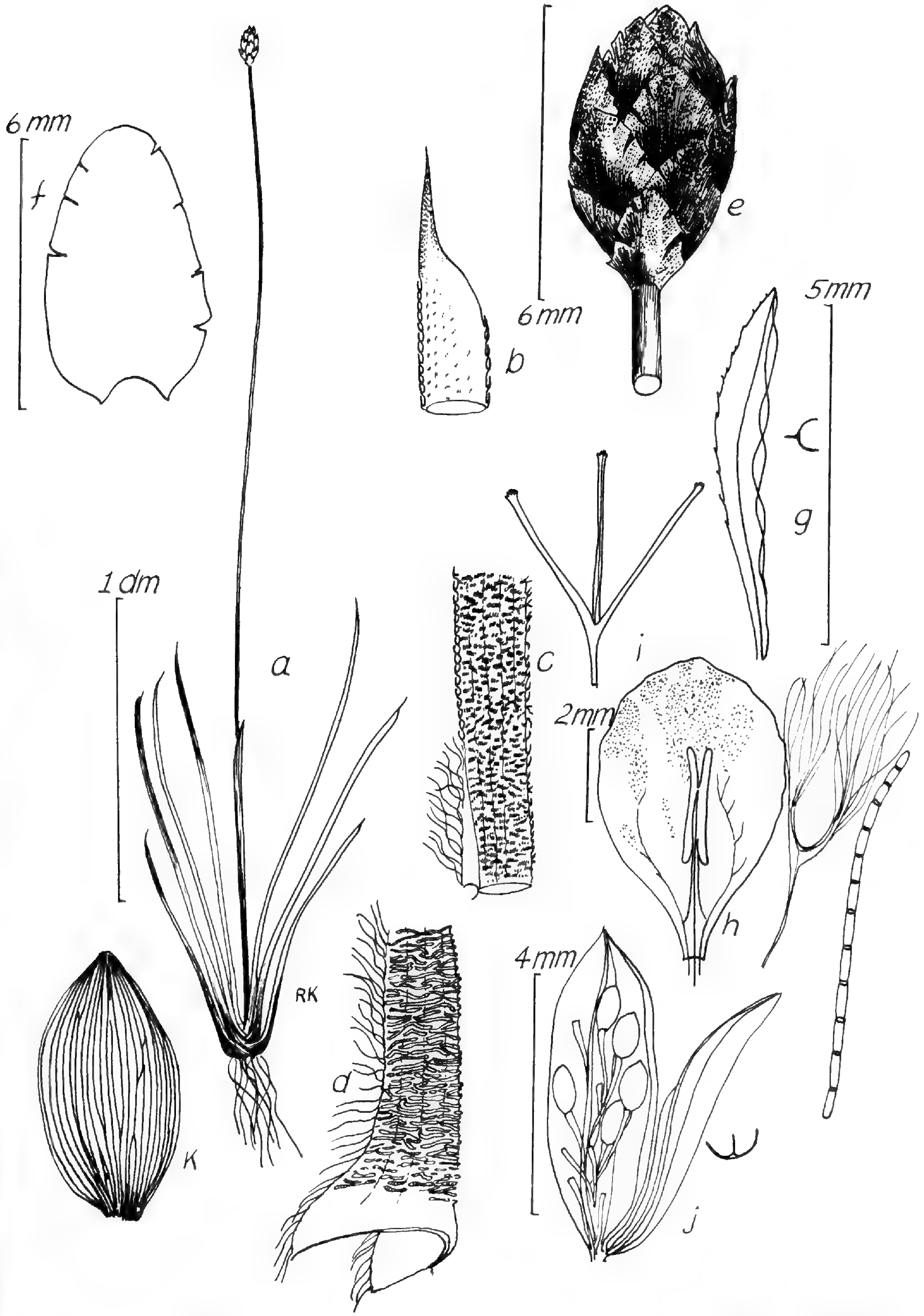


FIGURE 81. Xyris setigera (Kral 70630).—*a. Habit sketch.—b. Leaf apex.—c. Leaf at sheath–blade junction.—d. Leaf base.—e. Spike.—f. Fertile bract outline.—g. Lateral sepal.—h. Petal blade, stamen, staminode, staminodial beard hair.—i. Stylar apex.—j. Capsule, dehisced, showing placentation and side view of one valve.—k. Seed.*

km E de Canaima, 1,300 m, 31 Aug. 1983, *Huber et al. 8251* (NY, VDB, VEN); Macizo del Chimantá, sector SSE suroriental del Acopan-tepui, 1,920 m, 13–16 Feb. 1984, *Huber et al. 9061* (NY, VDB, VEN); Chimantá, Churi-tepui, 2,250 m, 28 Mar. 1984, *Huber 9271* (MYF, VDB); Brazo Occidental del Auyantepui, 1,650 m, 13 Nov. 1984, *Huber 9732* (MYF, VDB); ca. 5 km NNW Parupa, 1,400 m, 20 Nov. 1984, *Huber 9841* (MYF, VDB); Meseta Guaiquinima, sector nororiental, ca. 2,000 m, 21 Nov. 1984, *Huber 9877* (MYF, VDB); ca. 30 km ESE Kamarata, 900 m, 12 Dec. 1984, *Huber et al. 9919* (MYF, VDB); just S of summit La Escalera, 24 July 1983, *Kral & Gonzalez 70364, 70365* (BM, F, K, L, MO, NY, U, US, VDB, VEN, and others); 28 km E of Kavanayen, 25 July 1983, *Kral & Gonzalez 70432* (NY, US, VDB, VEN); 46 km N of Sta. Elena, 27 July 1983, *Kral & Gonzalez 70557* (F, K, MO, NY, SP, US, VDB, VEN); 8 km N of San Rafael, 29 July 1983, *Kral & Gonzalez 70580* (BM, F, K, L, MO, NY, SP, US, VDB, VEN, and others); 15 km S of San Rafael, 29 July 1983, *Kral & Gonzalez 70627* (BM, F, K, L, MO, NY, SP, US, VDB, VEN); 3 km S summit La Escalera, 1,300 m, 30 July 1983, *Kral & Gonzalez 70630* (BM, F, K, L, MO, NY, U, US, VDB, VEN, and others); savanna between San Raphael and Enemasic, 1,200 m, 5 Feb. 1952, *Maguire 33174* (NY, US, VEN); Kavanayen, ca. 1,200 m, 9 Aug. 1970, *Moore et al. 9646* (US, VEN); cumbre de Uaipan, 1,900 m, Jan. 1948, *Phelps 375* (NY, US); Plateau of Auyan-tepui, central northern section of eastern branch, 1,940 m, 27 Aug. 1983, *Prance & Huber 28270* (MYF, NY, VDB); Roraima, Emerald Swamp, 1,520 m, 25 Sep. 1944, *Steyermark 58611* (F, NY, VEN); Ptari-tepui, 1,600 m, 1 Nov. 1944, *Steyermark 59664* (F, NY, US, VEN); mesa between Ptari-tepui and Sororopan-tepui, 1,615 m, 15–17 Nov. 1944, *Steyermark 60239* (F, K); Auyan-tepui, 1,660–1,800 m, 11 May 1964, *Steyermark 93684* (NY, U, US, VDB, VEN); Gran Sabana, km 148, 1,350–1,400 m, 21 Dec. 1970, *Steyermark et al. 104168* (U, US, VBD, VEN); 47 km N de Sta. Elena, S del Río Yuruaní, 1,200 m, 25 Aug. 1976, *Steyermark et al. 112341* (F, K, NY, US); Meseta del Jaua, Cerro Jaua cumbre, 28 Feb.–5 Mar. 1974, *Steyermark et al. 109427* (K, NY, US, VEN); Cerro Marutari, 1,200 m, 2 Jan. 1981, *Steyermark 123857* (NY, VDB); Meseta de Sarisarinama, 1,280 m, 14 Feb. 1981, *Steyermark 124319* (NY, VDB); Luépa (Ciudadela) savanna 200 m W of checkpoint, *Thomas 2702* (NY).

This species is, not surprisingly, the most variable xyrid in the Guayana Highlands, with populations being found throughout the Gran Sabana at elevations extending from 700 to 2,000 meters or more on tepuis. Those of the lower and middle elevations within this area mostly conform to the described morphology pretty well, with the foliage generally coarsely rugose; the leaf blade edges roughened with stiff, often branched hairs; the leaf tips excentrically short-spinulose; and the spike bracts many, dark, and erose with age. At the higher elevations in the tepuis, usually at ca. 2,000 meters upward, however, the plants are more slender in scape and leaf; the leaf tips are subulate-conic (rather than excentrically spinulose) with the surfaces and edges becoming smoother; and the blades are narrower and approaching terete. These are problem plants; many are in loans annotated *X. setigera* var. *elongata* Steyerm. Some need further study, as they border on or are the same as *X. byssacea*. A smut fungus infects flowers to produce a bright orange fruiting mass on the spikes, hence the erroneous records that some *Xyris* corollas are "orange."

82. Xyris riparia Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 20, fig. 5A–E. 1963. TYPE: Venezuela. Bolívar: frequent in clumps at stream edge, scrub forest near Summit Camp, 1,925 m, Chimantá Massif, central section, 2 Feb. 1955, *J. A. Steyermark & J. J. Wurdack 361* (holotype, NY; isotypes, MO, US, VEN). Figure 82.

Cespitose, slender, stiffish perennial ca. 4–5 dm high, the stems short to elongate, forming frondlike plates of leaves. Leaves spreading flabellately to erect, 1–2.5 dm long; sheaths coarsely to finely long-ciliate-margined (sometimes sparsely so), as long as blades, deeply dull reddish brown, dull brown or castaneous, scabro-rugose or smooth, tapering gradually from the dilated base to the blade, the backs narrowly rounded or keeled and scabrid, usually eligulate or with a short, erect ligule under 0.5 mm long; blades linear, flattened, slightly twisted, 2–3 mm wide, tapering gradually from ca. middle to apex, then abruptly narrowed to an excentric, narrowly conic-acute to short-subulate tip; margins thin or pale-incrassate, smooth to papillate, tuberculate or scabro-ciliate or ciliolate with pale hairs, the surfaces yellow-green to reddish, few-nerved, punctate. Scape sheaths shorter than principal leaves, the tubular base lustrous reddish or castaneous, multicostate above, ciliate-keeled, open, with a short, erect

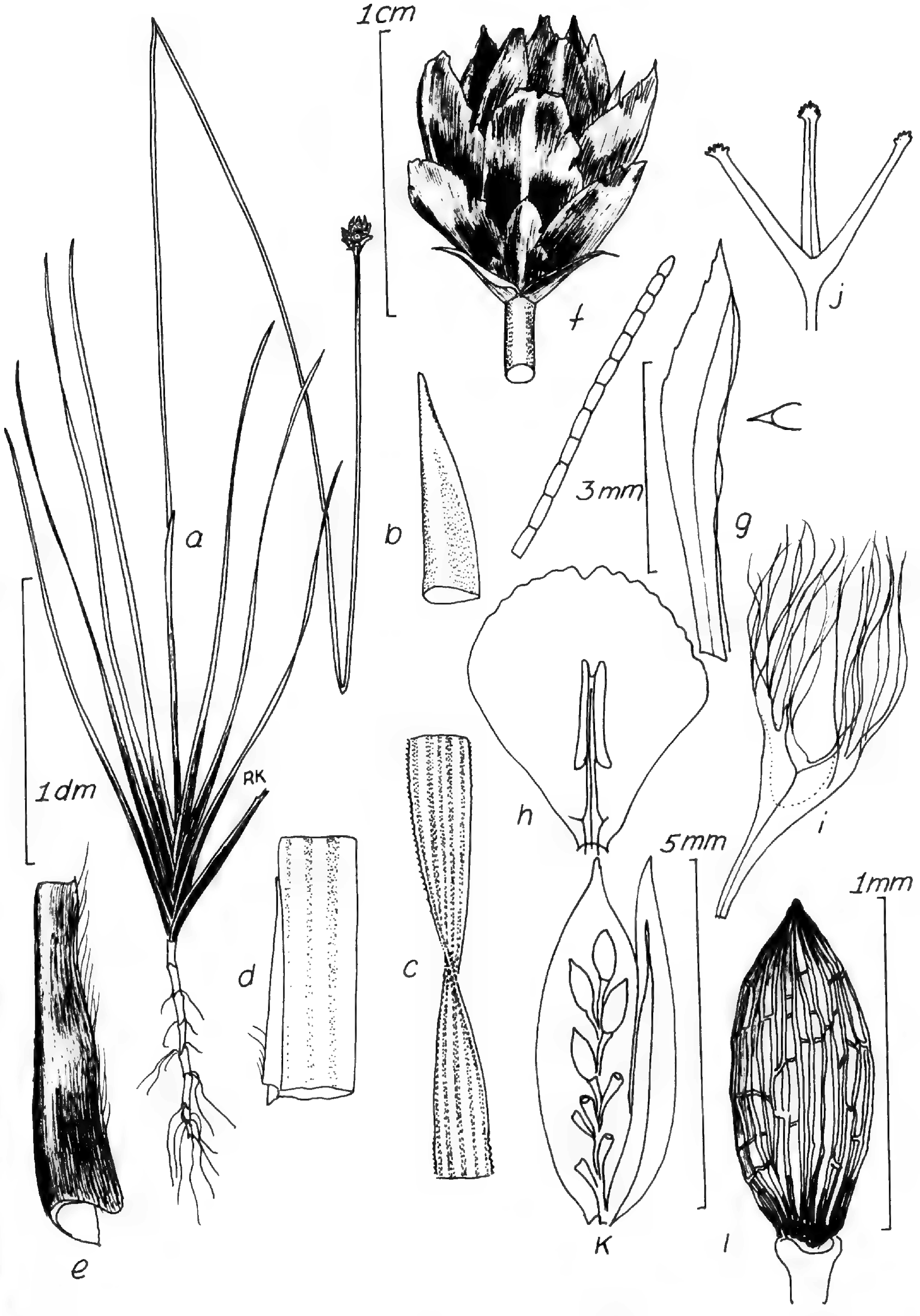


FIGURE 82. Xyris riparia *(from the type).—a. Habit sketch.—b. Leaf apex.—c. Leaf, midblade.—d. Leaf blade–sheath junction.—e. Leaf base.—f. Spike.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode.—j. Stylar apex.—k. Capsule, one valve removed; side view of one valve to show septum and side view of placenta.—l. Seed.*

blade. Scapes straight or slightly flexuous, twisted distally, subterete or broadly oval in cross section, ca. 1 mm wide, ecostate, sometimes with few very low ridges, punctate. Spike broadly obovoid, drying turbinate, ca. 1 cm long, reddish brown, of several, firm, papillose bracts without dorsal areas and loosely imbricate in near vertical rows; sterile bracts with lowermost lance-ovate, much shorter than and narrower than the fertile bracts, carinate, grading into fertile bracts, these numerous, oblong to narrowly ovate, 6–8 mm long, narrowly rounded, entire, aging lacerate, the margins often narrowly squarrose. Lateral sepals linear-oblanceolate, 6.5–7 mm long, acuminate, dark red-brown, the firm, broad keel slightly lacerate distally. Petal blades broadly obovate, ca. 5 mm long, yellow, the broadly rounded apex crenulate. Staminodia clavate, indistinctly bibrachiate, the irregular margins long-penicillate. Anthers lance-oblong, ca. 2 mm long, shallowly bifid and sagittate, on filaments ca. 1 mm long. Capsule narrowly ellipsoid, ca. 5 mm long, the placentation appearing central but dehiscing valves with strong septa toward base. Seeds numerous on short, stout funiculi, narrowly ovoid, ca. 0.9–1 mm long, deep amber, apiculate, longitudinally strongly multiribbed and cross-lined.

Distribution. Local in high-elevation savanna, the Chimantá Massif and Cerro Guaiquinima, Estado Bolívar, Venezuela. The few known records, in addition to the type are as follows.

Additional specimens examined. VENEZUELA. BOLÍVAR: Cerro Guaiquinima, savanna vic. Cumbre Camp, 2,000 m, 25 Dec. 1951, *B. Maguire 32751* (NY); same locality, 1 km S of Cumbre Camp, 1,800 m, 29 Dec. 1951, *B. Maguire 32798* (NY); Macizo del Chimantá, sección centro-suroriental del Churi-tepui, ca. 2,250 m, 10–12 Feb. 1984, *Huber & Colella 8998* (VDB, VEN)—this an extreme bordering on *X. setigera.*

The material from Cerro Guaiquinima should perhaps be considered varietal, being more scabrid in sheath, more ciliate in leaf, and with a shorter range in leaf length, but at this stage of knowledge of the genus it is perhaps best to be conservative. In such a connection, it might be noted that there are many similarities between this taxon and the more common *X. setigera,* certainly as to the punctate leaves and scapes, the complex harsh hairs on edges of the leaf blade, and the excentrically spinulose-subulate leaf tips.

83. Xyris roraimae Malme in Pilger Notizbl. Bot. Gart. Berlin 6: 117. 1914. TYPE: Venezuela. Bolívar: "Auf den unteren Campos," 1,700 m, Jan. 1910, *Ule 8546* (lectotype, B; isolectotype and phototype, US). Figure 83.

Tall, solitary or small-tufted, brittle perennial to 1 m high or slightly higher, the stems contracted, the foliage totally papillose-rugulose, dull yellow-green. Leaves erect or ascending, twisted, 2–4 dm long; sheaths long-ciliate, ½ as long as blades or longer, abruptly dilated at very base, castaneous, thence abruptly narrowing, dull brown, gradually tapering into the blade, there eligulate or with a short, erect, ciliate ligule less than 0.5 mm long; blades strongly flattened, linear, 3–5 mm wide, above middle tapering to an erect, narrowly acute or acuminate, somewhat thickened, erect or incurved apex, the margins pale ciliate and tuberculate, the surfaces dull yellow-green, strongly nerved longitudinally. Scape sheaths shorter than leaves, twisted, carinate and strongly costate, opening toward apex, keeled, producing a very short, incurved blade. Scapes lineal, twisted and flexuous, flattened and ancipital distally, 2–3 mm wide, 2-costate, the costae reaching the edges and densely pale ciliate. Spikes broadly ovoid, ellipsoid, or cylindric, 1–3 cm long, blunt, pale red-brown or tan, of very many spirally imbricate, thin bracts without dorsal areas and, when young, with narrow but distinctive, reddish, scarious, lacerate borders; lowermost sterile bracts smallest, broadly ovate to suborbicular, slightly carinate, grading gradually into the fertile bracts, these broadly obovate to suborbicular, 5–6 mm long, ecarinate, aging lacerate (the red border friable and deciduous early). Lateral sepals free, very inequilateral, often exserted apically, oblanceolate, 4.5–5.5 mm long, acute, thin,

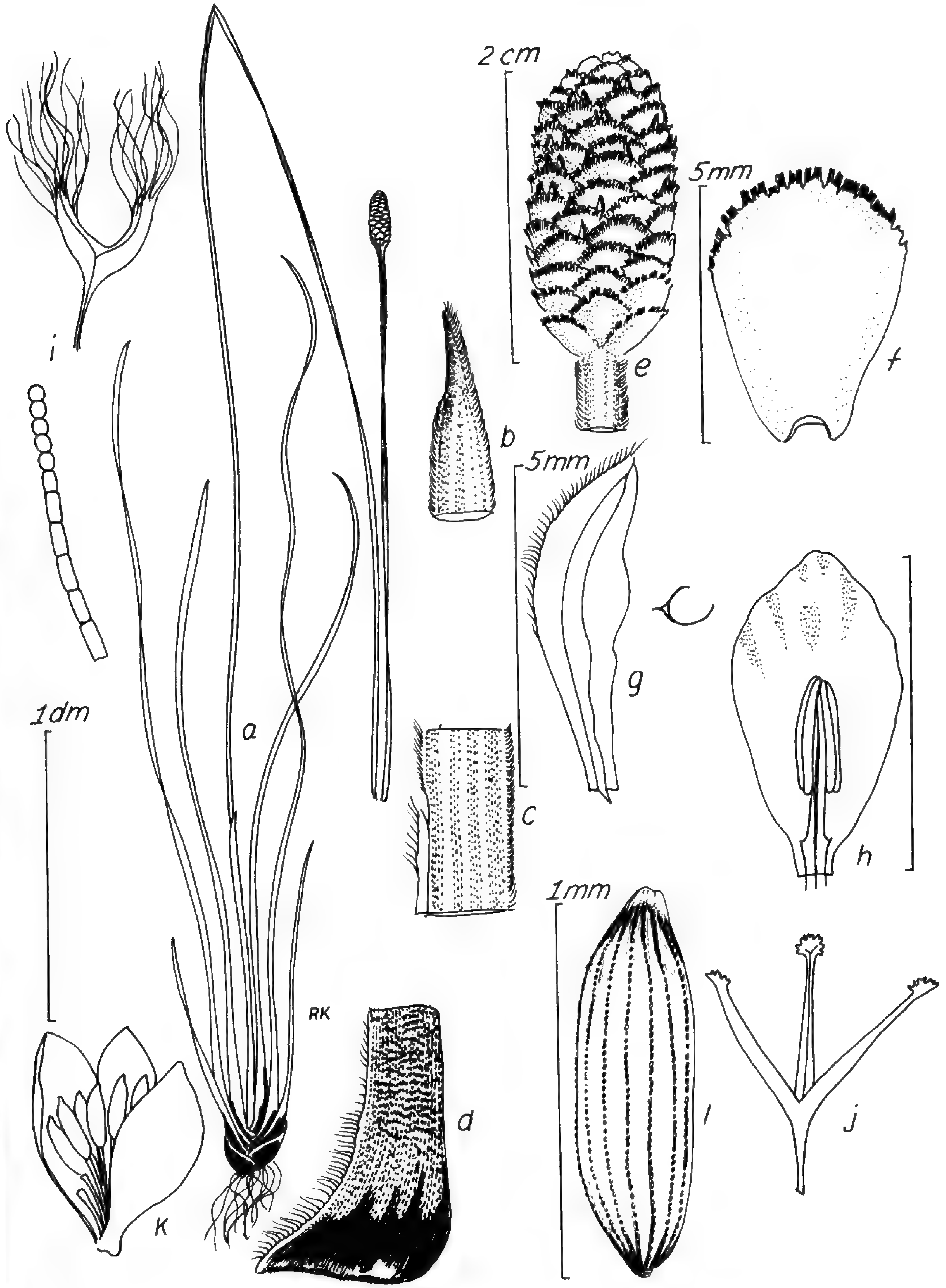


FIGURE 83. Xyris roraimae (Kral 70560).—*a. Habit sketch.—b. Leaf apex.—c. Leaf sheath–blade junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen.—i. Staminode.—j. Stylar apex.—k. Open capsule.—l. Seed.*

with the broad keel lacerofimbriate or ciliate from ca. middle to apex. Petal blades obovate, ca. 5 mm long, yellow, the narrowly rounded apex subentire. Staminodia bibrachiate, the flat, narrow branches long-penicillate distally. Anthers lance-oblong, ca. 2 mm long, shallowly bifid apically, the base deeply sagittate, on filaments ca. 1 mm long. Capsule broadly obovoid, 2.5–3 mm long, the placentation basal, the valves without septa. Seeds ellipsoid-cylindric, ca. 1 mm long, amber, apiculate, finely but distinctly ribbed longitudinally.

Distribution. Savanna bogs, medium elevations (ca. 700–1,500 meters), Gran Sabana, Estado Bolívar, Venezuela; Guyana; occasional in the campos rupestres, the planalto of Brazil in Minas Gerais and Goiás. My Brazilian specimens tend to be proportionately larger in height (to 1.5 meters) and in spike diameter, but otherwise appear the same as the Venezuelan collections.

Additional specimens examined. BRAZIL. MINAS GERAIS: wet slopes over arenaceous rock, above Rio Itacambirucu, ca. 8 km WSW of Grão Mogul, 600–750 m, 10 July 1985, *Kral et al. 72705* (SP, VDB, and to be distributed) grass–sedge campo, Morro do Onca, 950–1,000 m N of Jouachim Felicio, 6 July 1985, *Kral et al. 72628* (SP, VDB, and to be distributed); below sandstone bluffs, Morro do Jucao, NNW Joachim Felicio, 1,100 m, ca. 14 km N of Jouaquim Felicio, 7 July 1985, *Kral et al. 72659* (SP, VDB, and to be distributed). GUYANA: Mt. Roraima, Philipp Swamp, 5,100–5,200 ft. (also at Glycon Swamp), 11 Nov. 1927, *Tate 348* (K). VENEZUELA. BOLÍVAR: bog ravine, 1 km E of Kavanayen, 26 July 1983, *Kral 70448* (VDB, VEN); 7 km E of Kavanayen, 1,100 m, bog, 26 July 1983, *Kral & Gonzalez 70466* (BM, F, K, L, MO, NY, SP, U, US, VDB, VEN, and others); S side of road, 1.5 km E of Kavanayen, Gran Sabana, *Kral & Gonzalez 70539* (F, MO, NY, SP, US, VDB, VEN); 46 km N of Sta. Elena on E side of Ven. 10, ca. 800 m, 28 July 1983, *Kral & Gonzalez 70560* (BM, F, L, MO, NY, SP, U, US, VDB, VEN, and others); colinas above Ven. 10, 8 km N of El Salto Yuruani, ca. 750 m, 29 July 1983, *Kral & Gonzalez 70582* (US, VDB, VEN); ca. 2 km S due E of Kavanayen, ca. 1,060 m, 15 Dec. 1984, *Kral 72089* (MYF, VDB, VEN, and to be distributed); Ilu-tepui, Gran Sabana, Río Aponangao at 1,200 m, 27–28 Mar. 1952, *Maguire 33646* (NY); Gran Sabana, cabeceras Río Aponguao, a lo largo Arauta-paru, km 148, 20 Dec. 1970, *Steyermark et al. 104116* (US, VEN); savanna with *Stegolepis* 16 km from Kavanayen, 1,340 m, 19 Dec. 1979, *Steyermark* with *Pruski 121052* (US, VEN).

This species, locally abundant in the rapateaceous bogs of the Gran Sabana, is at once one of the tallest of Venezuelan xyrids and the most roughened in foliage, the epidermal roughening giving the plants a glazed, dull, yellow-green color which is very distinctive in the field. Its spikes are a lovely tint of golden brown and on close inspection show a fine red color of bract border. Even larger versions of this attractive (for a *Xyris*) plant are to be found in the planalto of Brazil, where they belong to the most difficult complex around *X. ciliata* Thunb.

84. Xyris schneeana Lyman B. Smith & Steyerm., Acta. Bot. Venez. 1(7): 149–150. 1965. TYPE: Venezuela. Bolívar: Auyan-tepui, altiplanicie, 19 Apr. 1956, *Ludwig Schnee 1577* (holotype, MY; phototype, US). Figure 84.

Cespitose low perennial 1–3 dm high, the stems contracted. Leaves stiff, spreading flabellately, 5–10 cm long; sheaths as long as blades or longer, long-ciliate, papillose-rugulose, tan, much dilated at very base, thence narrowing gradually to blade, strongly keeled, eligulate, the blades flat, straight, 2–3 mm wide, lineal, abruptly narrowed at apex to an obtuse or broadly incurved-acute tip, this frequently apiculate, the margins white-ciliolate, the surfaces dull green, low-multiribbed, scaberulous-rugulose. Scape sheaths overtopping most leaves, the bases tubular, multicostate, carinate, above open, ciliate, the blade a mere apiculus. Scapes dull green, straight or flexuous, terete or oval distally, ca. 0.5 mm thick, with several low costae, the surface entirely rugulose-papillate or scaberulous. Spikes ovoid-ellipsoid, ca. 5 mm long, drying obovate, dark olive-castaneous, of several loosely subdecussate, thin bracts without evident dorsal areas, the sterile ones ca. 4, ecarinate, rounded, shorter than the few fertile bracts, these oblong, ca. 5 mm long, navicular but ecarinate, broadly rounded, entire or erose. Lateral sepals free, very inequilateral, oblong-elliptic to spathulate, ca. 5–5.5 mm long, acute or obtuse, dark and thin, the narrow, darker keel serrulate-ciliolate above middle, the apex often exserted. Petal blades elliptic, 5 mm long, yellow, the apex broadly acute,

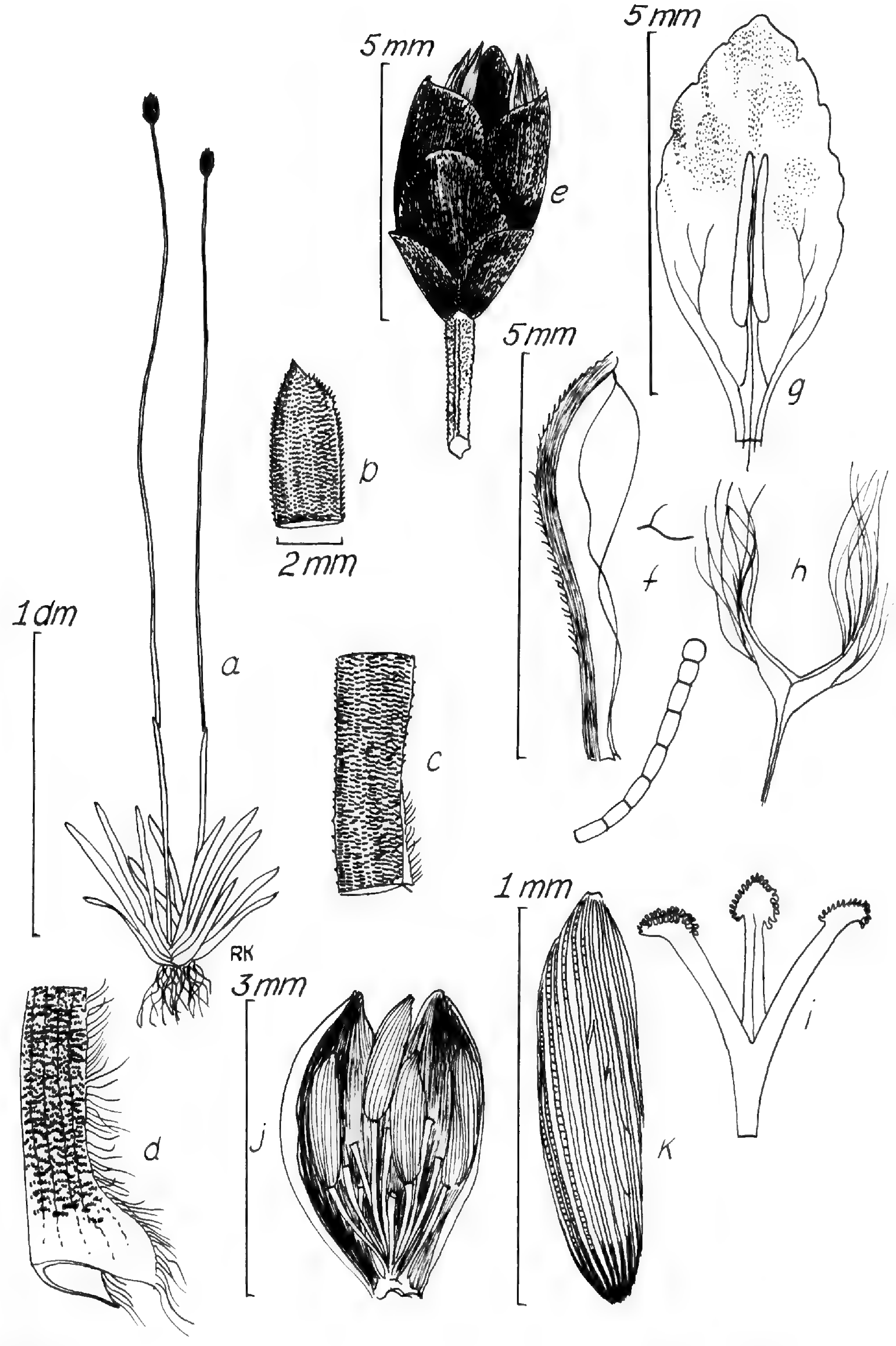


FIGURE 84. Xyris schneeana (Steyermark et al. 128918).—*a. Habit sketch.—b. Leaf apex.—c. Leaf at blade-sheath junction.—d. Leaf base.—e. Spike.—f. Lateral sepal.—g. Petal blade, stamen.—h. Staminode.—i. Stylar apex.—j. Capsule, dehiscing, showing two valves, placentation.—k. Seed.*

the margin sinuate. Staminodia bibrachiate, the branches long-penicillate. Anthers lance-oblong, ca. 1.7–2 mm long, deeply bifid and sagittate, on filaments 0.8–0.9 mm long. Capsule broadly ellipsoid or nearly obovoid, ca. 3 mm long, placentation basal-central. Seeds narrowly ellipsoid or cylindric, ca. 1 mm long, amber, longitudinally finely but distinctly multiribbed.

Distribution. High, sandy, rocky savanna-plain, Chimantá Massif and related tepuis, Estado Bolívar, Venezuela.

Additional specimens examined. VENEZUELA. BOLÍVAR: altiplanicie meridional Acapá-tepui, ubicada en el sector SW del Macizo, 2,200 m, 31 Jan.–Feb. 1984, *Huber & Dezzeo 8636* (NY); cumbre Aprada-tepui, sector sur, ca. 30 km al E de Urimán, ca. 2,500 m, 30 June 1984, *Huber 9580* (MYF, VDB); NW part of summit of Abacapa-tepui, 2,125–2,300 m, 13 Apr. 1953, *Steyermark 74920* (F, NY); sector centro-noreste del Chimantá-tepui, cabeceras orientales del Caño Chimantá, 2,000 m, 26–29 Jan. 1983, *Steyermark et al. 128162* (VDB, VEN); Apacara-tepui, sector Norte del Macizo, 2,200 m, *Steyermark et al. 128372* (VDB, VEN); sección oriental del Chimantá-tepui, cabeceras del afluente derecho superior del Río Tirica (Caño del "Grillo"), 2,450 m, *Steyermark et al. 128918* (VDB, VEN).

The stubby, low habit of the leaves, dull green and papillose-rugulose foliage, small and dark-bracted spikes, and strongly septate capsule valves combine to distinguish this high-tepui endemic.

85. **Xyris consolida** Kral & Lyman B. Smith, Phytologia 53(6): 434–435, figs. 3, 4. 1983. TYPE: Venezuela. Bolívar: Uaipan-tepui, the summit of west Peak, 1,980 m, small, wet grassy swamp on sandstone, 4 Mar. 1967, *G. Agostini & T. Koyama 7462* (holotype, VEN; isotypes, NY, US). Figure 85A, B.

Plants perennial, solitary or in small tufts; leaf and scape surfaces scabrid; habit lax; roots slender; stems contracted. Leaves all basal, ensiform-linear, 1.5–2 dm long, longer than scape sheaths, spreading flabellately; blades flat, strongly compressed, 3–5 mm wide, olivaceous, multinerved longitudinally, transversely rugose; apices abruptly narrowed, incurved-acute at tip, slightly thickened; margins slightly thickened, minutely tuberculate-ciliate to strigo-ciliate or entire; sheaths gradually narrowed from base to apex, carinate, the carinae ciliate with spreading to retrorse hairs, the sides transversely rugulose, dull olive, multinerved longitudinally, lustrous at base, deeply red-brown, the edges narrow, pale, hirsute-ciliate with sordid trichomes. Scape sheaths twisted, carinate, prominently multicostate with carinae and submarginal costae strongly tuberculate and ciliate, the sheath apex with a short, erect, flat blade. Scapes linear, twisted, 4–6 dm high, subterete or slightly compressed, 1–1.5 mm thick, olive, multicostate, with costae scabrous. Spikes ovoid to broadly obovoid or subglobose, 8–10 mm long, 6–7 mm wide, several-flowered, the bracts loosely spirally imbricate, ecarinate, convex-backed, the margins narrowly scarious; sterile bracts several, gradually passing larger into the fertile bracts, 3.5–4.5 mm long, broadly obovate to obovate, rounded, the margins narrowly scarious; fertile bracts broadly obovate, ca. 5 mm long, rounded-convex; dorsal area absent. Lateral sepals ca. ⅓ connate, inequilateral, ca. 5.5 mm long, the lobes oblong, broadly acute or obtuse; keel wide, thin, entire from base to middle, ciliolate-lacerate from middle to apex. Petal blades obovate, 4–4.5 mm long, yellow, the narrowed apex erose. Staminodia bibrachiate, the branches apically long-penicillate. Ripe capsule ellipsoid, 3.5 mm long, the valves without septa, the placentation basal-central. Seeds oblong-ellipsoid, ca. 1 mm long, amber, strongly multiribbed longitudinally.

Distribution. Known only from the type collection (Uaipan-tepui) and from Ptari-tepui, in Estado Bolívar, Venezuela.

Additional specimens examined. VENEZUELA. BOLÍVAR: Ptari-tepui, cumbre; al norte de la Misión de Santa Teresita de Kavanayen, 2,360–2,420 m, 23 Feb. 1978, *Steyermark et al. 115729* (F, MO, US, VEN).

The scabrous foliage, small, dark-bracted spikes, and connate lateral sepals distinguish this rather low plant. At the beginning of the study it was thought that the two collections represented tepui-summit endemics; a closer

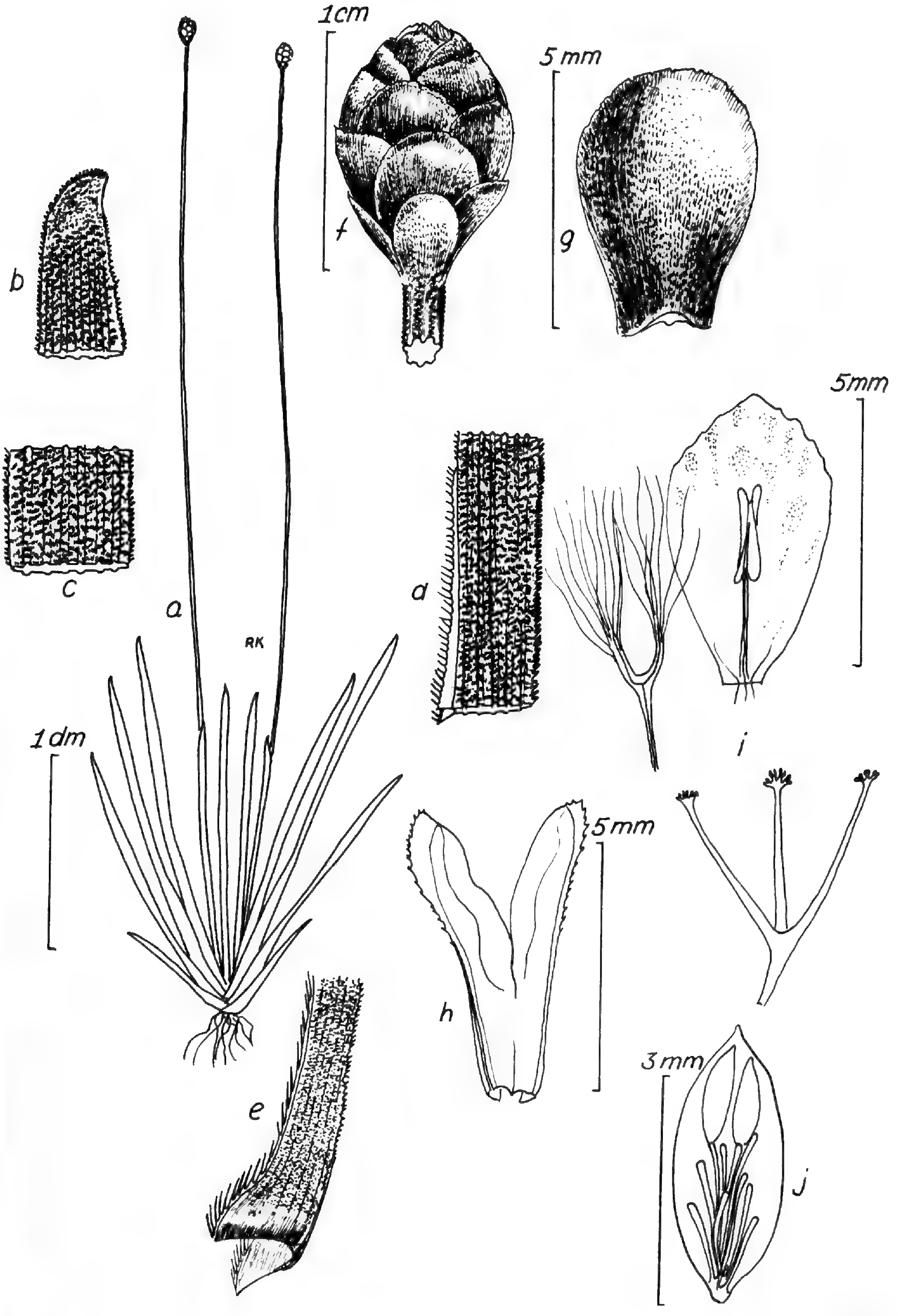


FIGURE 85A. Xyris consolida *(from the type)*.—*a. Habit sketch.—b. Leaf apex.—c. Sector of midblade.—d. Leaf sheath–blade junction.—e. Leaf base.—f. Spike.—g. Fertile bract.—h. Lateral sepals.—i. Petal, stamen, taminode, stylar apex.—j. Median longisection of fruit.*

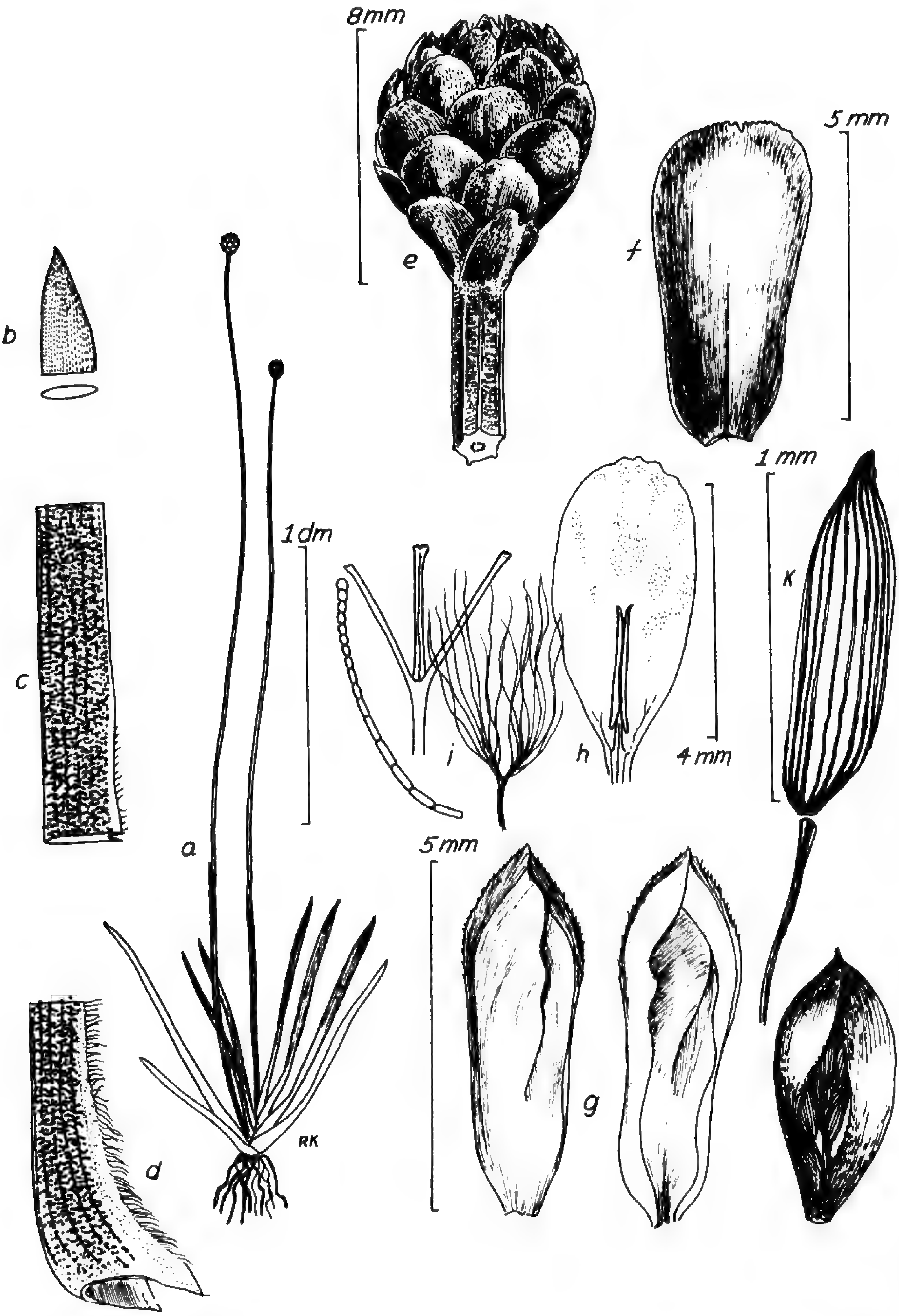


FIGURE 85B. Xyris consolida (Steyermark et al. 115729).—*a. Habit sketch.—b. Leaf tip.—c. Leaf sheath-blade junction.—d. Leaf base.—e. Spike and upper scape.—f. Fertile bract.—g. Two views of lateral sepals.—h. Petal blade, stamen.—i. Staminode, stylar apex.—j. External view of dehiscing capsule.—k. Seed.*

examination revealed that, other than the smooth-margined leaves of the Ptari-tepui material, there are no other significant differences between them.

86. Xyris kukenaniana Kral, sp. nov. TYPE: Venezuela. Bolívar: Dist. Roscio Kukenán-tepui, cumbre del sector más septentrional algo separado del macizo principal. Vegetación herbáceo-arbustiva sobre rocas de arenisca y alrededor de lagunas, 5°16′N, 60°48′W, 2,500 m, 28 Apr. 1984, *O. Huber 9460* (holotype, VEN; isotypes, MYF, NY, VDB). Figure 86.

Planta perennis, caespitosa, humilis. Folia linearia, solum basalia, 6–10 cm longa, erecta vel leviter expansa, vaginis scaporum longiora. Laminae folia principalia vaginis 3–5-plo longiores, planae, leviter compressae, 1–1.5 mm latae, pallidae virides, ad apicem abrupte incurvato-acutae, aliquantum incrassatae, a basin gradatim contractae; margines prominente albociliati aut scabrociliati; paginae longitudine grosse nervatae, glabrae vel papillosae; vaginae ciliato-carinatae, pluricostatae, rugulosae, pallide ferrugineae, marginibus a basin ad apicem longiciliatis, in laminas gradatim convergentibus aut ad apicem curtam pilosam ligulam fascientibus. Vaginae scaporum prominente ciliato-carinatae, grosse nervatae, laminis similis laminis foliorum sed brevibus. Scapi recti vel leviter tortae, 1–2 dm longi, distaliter in sectio transversali elliptici, ca. 1 mm lati, anguste ancipiti, 2–3(–4) costati, costis dense pallide scabrociliatis. Spicae ovoideae, atroferrugineae vel fuliginosae, 7–8 mm longae, pluriflorae, obtusae, bracteis subdecussatis, laxe imbricatis, sine area dorsali, minute papillosis; bracteae steriles plures, triangulatae vel oblongae, 2–3.5 mm longae, ad apicem albociliatae, obtusae, fertilibus breviores et in eas gradatim transientes; bracteae fertiles late obovatae, ca. 5 mm longae, vadose convexae, ecarinatae, apice rotundatae, integrae tum laceratae. Sepala lateralia libera, leviter curvata, subaequilatera, late lanceolata, 4.5–5 mm longa, acuta; ala carinali angusta, parce longiciliata. Laminae petalorum late obovatae, ca. 4 mm longae, luteolae, ad apicem erosae. Antherae oblongae, 1.5 mm longae, profunde bifidae et sagittatae; filamenta ca. 1 mm longa. Staminodia bibrachiata, dense longipenicillatis. Capsula immatura septa efferentes. Semina non visa.

The plant perennial, cespitose, low. Leaves linear, strictly basal, 6–10 cm long, erect to slightly spreading, longer than the scape sheaths. Blades of principal leaves 3–5 times longer than the sheaths, plane, slightly compressed, 1–1.5 mm wide, pale green, at apex abruptly incurved-acute, somewhat thickened, gradually narrowed toward base; margins prominently white ciliate or scabro-ciliate; surfaces coarsely nerved longitudinally, smooth or papillose; sheaths ciliate-carinate, several-ribbed, rugulose, pale red-brown, the margins long-ciliate from base to tip, gradually narrowing into the blades or producing a short, pilose ligule at apex. Scape sheaths prominently ciliate-carinate, coarsely nerved, with blades similar to leaf blades but shorter. Scapes straight or slightly twisted, 1–2 dm long, distally elliptic in cross section, ca. 1 mm wide, narrowly ancipital, 2–3(–4) costate, the costae densely pale scabrociliate. Spikes ovoid, dark red-brown or sooty brown, 7–8 mm long, several-flowered, obtuse, the bracts subdecussate, loosely imbricate, without dorsal area, minutely papillose; sterile bracts several, triangular to oblong, 2–3.5 mm long, white ciliate at apex, obtuse, smaller than the fertile bracts and grading into them; fertile bracts broadly obovate, ca. 5 mm long, shallowly convex, ecarinate, rounded apically, entire, aging lacerate. Lateral sepals free, slightly curvate, subequilateral, broadly lanceolate, 4.5–5 mm long, acute; carinal keel narrow, sparsely long-ciliate. Petal blades broadly obovate, ca. 4 mm long, yellow, erose at apex. Anthers oblong, 1.5 mm long, deeply bifid and sagittate; filaments ca. 1 mm long. Staminodia bibrachiate, densely long-penicillate. Immature capsule producing septa. Seeds not seen.

Distribution. Known only from the type locality.

Superficially *Xyris kukenaniana* resembles *X. setigera* in general spike bract character and color, and in the coarsely ciliate leaf blades, but the former lacks the excentrically spinulose leaf blade apex of *X. setigera*, and its scapes are definitely sharp-edged and ciliate, very unlike the lustrous and ecostate scapes of *X. setigera*.

87. Xyris delicatula Maguire & Lyman B. Smith, Mem. New York Bot. Gard. 10: 23, fig. 7A–F. 1963. TYPE: Venezuela. T. F. Amazonas: frequent in wet hummocks, Camp Savanna, Campo Grande, 1,500 m, Cerro Sipapo (Pa-

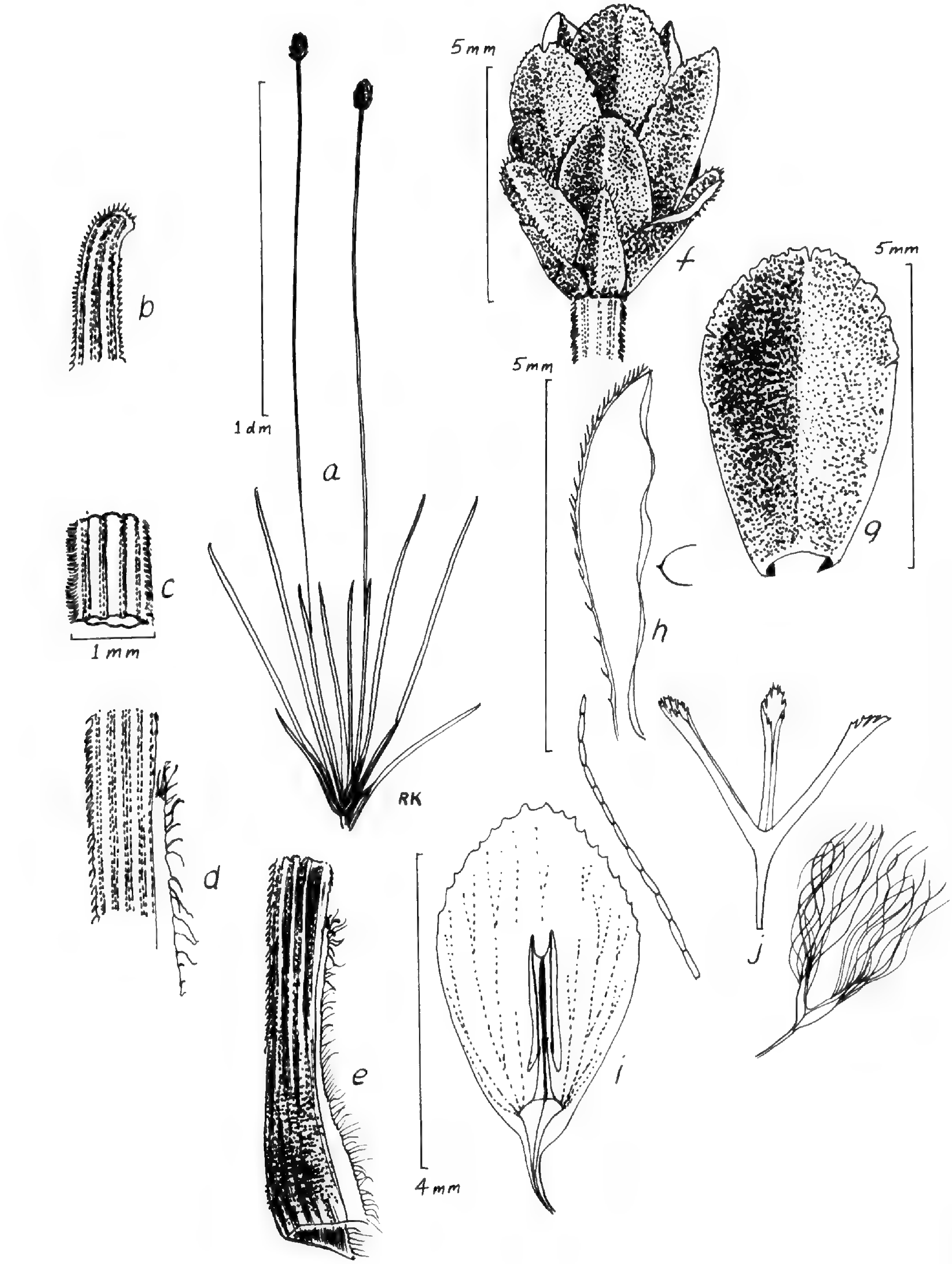


FIGURE 86. Xyris kukenaniana (O. Huber 9460).—*a. Habit sketch.—b. Leaf tip.—c. Sector of leaf at midblade.—d. Leaf blade–sheath junction.—e. Leaf base.—f. Spike.—g. Fertile bract.—h. Lateral sepal.—i. Petal blade, stamen.—j. Stylar apex, staminode, staminodial beard hair, enlarged.*

raque), 10 Dec. 1948, *B. Maguire & L. Politi 27580.* Figure 87.

Slender, densely cespitose perennial 3–5 dm high, the stems contracted. Leaves erect or ascending, 1.5–3 dm long; sheaths less than ½ length of blade, long-ciliate, slightly dilated at very base, ecarinate, pale brown, papillate-rugulose, gradually narrowing, carinate, roseate, at apex producing a narrow

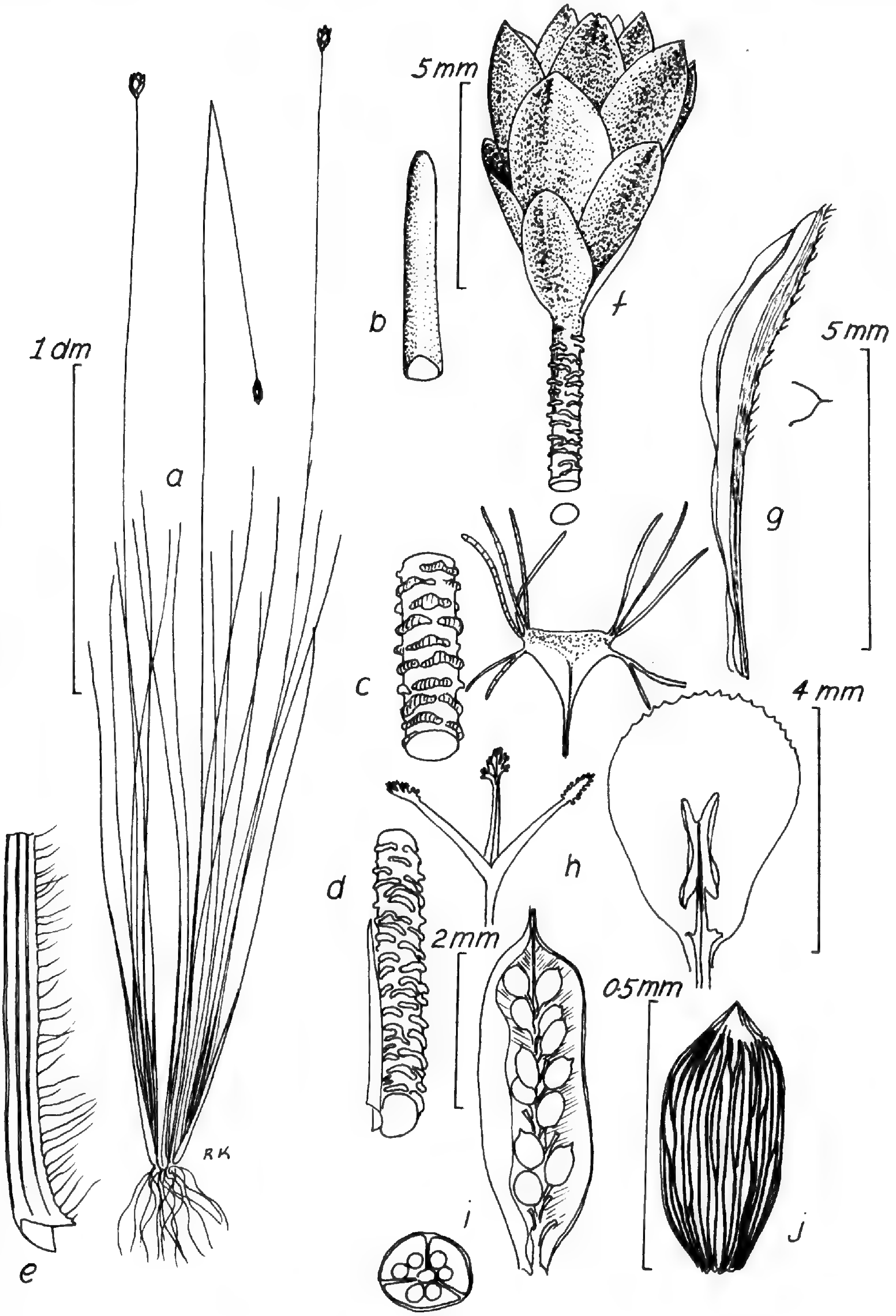


FIGURE 87. Xyris delicatula *(from the type).—a. Habit sketch.—b. Leaf tip.—c. Sector of leaf, midblade.—d. Leaf sheath-blade junction.—e. Leaf base.—f. Spike.—g. Lateral sepal.—h. Stylar apex, petal and stamen, staminode.—i. Capsule, one valve removed.—j. Seed.*

narrowly acute or blunt, scarious, erect ligule to 2 mm long; blades filiform, mostly terete, sometimes slightly flattened, ca. 0.5 mm wide, tapering to a bluntly short-conic, smooth tip above middle, otherwise completely rugose or verrucose, the nerves not evident. Scape sheaths shorter than leaves, strongly rugose, ecarinate, with a very short, blunt cusp above. Scapes straight to flexuous, twisted, distally terete, ca. 0.4–0.5 mm thick, papillose-rugulose. Spikes ellipsoid, drying obovoid, ca. 7–8 mm long, of several firm, erect but loosely spirally imbricate, brown bracts lacking distinct dorsal areas and grading from the smaller, narrowly ovate, slightly carinate sterile bracts to the slightly larger, oblong to narrowly obovate fertile ones, these ca. 6.5–7 mm long, narrowly rounded or broadly acute at apex and with very short apical carinae, the backs convex-rounded, papillate. Lateral sepals free, subequilateral, linear-oblanceolate, ca. 5.5 mm long, acute, erect or excurved, the dark firm keel lacerociliate from middle to apex. Petal blades broadly obovate, ca. 4 mm long, yellow, the broadly rounded apex irregularly denticulate. Anthers oblong, ca. 1.5 mm long, deeply bifid, sagittate, on filaments 0.5 mm long. Staminodes somewhat reduced, broadly bibrachiate, the branches apically sparsely penicillate. Capsule cylindric, ca. 4 mm long, trilocular, the deep septa pulling away from the axis at maturity, thus placentation appearing free-central but really axile. Seeds broadly ellipsoid or ovoid, ca. 0.5 mm long, apiculate, amber, longitudinally finely but distinctly ribbed, some ribs anastomosing.

Distribution. High-elevation tepuis, Territorio Federal Amazonas and Estado Bolívar, southern Venezuela, infrequent.

Additional specimens examined. VENEZUELA. BOLÍVAR: Auyan-tepui, sect. SSE, ca. 12 km al SE del Churun-meru (Salto Churun) 5°47′N, 62°28′W, 2,250 m, *Huber & Medina 8521* (MYF, VEN); Serranía Guanay, sector nororiental, cabeceras mas orientales del Río Paraguaza, 5°55′N, 66°23′W, ca. 1,700 m, 20–28 Oct. 1985, *Huber 11055* (MYF, VDB); altiplanicie del Auyantepui, sector centro-oeste del Brazo Occidental ca. 15 km al WSW Salto Angel, 1,860 m, 19 Jan. 1986, *Huber 11248* (MYF, NY, VDB); Auyan-tepui, sector suroriental, 2,140 m, 26 Feb. 1978, *Steyermark et al. 116055* (a mix with *X. setigera*—US).

This species is peripheral to *X. setigera* and, along with *X. carinata* and *X. byssacea*, develops populations at high elevations that are homogeneous but at the same time distinctive on the basis of fine characters. *Xyris delicatula* is indeed close to *X. setigera* but, while its leaves are harsh as in that species, their tips lack the setiform apex so common in the latter, and its scapes are rugose rather than smooth. Interestingly, this is another taxon in which placentation is evidently axile.

NOTES

A NEW SPECIES OF *OCOTEA* (LAURACEAE) FROM NICARAGUA AND A NOTE ON *OCOTEA JORGE-ESCOBARII*

The *Ocotea* species in Central America form a difficult and incompletely known group. Reasons for this are that the genus is not clearly separated from *Nectandra* and *Phoebe*, that there is a scarcity of flowering collections, and that decisions by earlier botanists are sometimes difficult to understand and the species they described are hard to interpret.

During the preparation of the Lauraceae treatment for the *Flora de Nicaragua*, one undescribed *Ocotea* species was found and is here published. The affinities of the new species, *O. strigosa*, are not clear. It is so inconspicuous that one wonders how it was ever found. Several Nicaraguan collections are referred to *O. jorge-escobarii*, a species recently described from Honduras. An English description and an illustration of this poorly known species are provided.

Ocotea strigosa van der Werff, sp. nov. TYPE: Nicaragua. Matagalpa: W slope and summit of Cerro El Picacho, cloud and elfin forest, 1,350–1,590 m, *Stevens 22181* (holotype, MO; isotype, HNMN). Figure 1.

Frutex vel arbor parva. Ramuli teretes, glabri, sed apicibus strigis brunneis munitis. Gemma terminalis dense cinereo-sericea. Folia alterna, chartacea, 6–9 × 2–3.5 cm, ovata vel anguste ovata, basi obtusa vel acuta, apice acuminata; juvenalia strigosa, vetustiora glabrescentia; super opaca, venatione non manifesta; subtus venatione leviter elevata; domatiis carentia sed infrequenter in axillis venarum pilis erectis praedita. Nervi laterales utroque costae latere 3–6. Inflorescentiae axillares, foliis breviores, strigosae, ad 6 cm longae. Flores albi. Petala 6, aequalia, ca. 1.5 mm longa, extus basi strigosa, apice glabrescentia, intus glabra praeter apicem tepalorum interiorum papillosam. Stamina 9, 4-locellata, glabra, 6 exterioribus filamentis ca. 0.5 mm longis, antheris ca. 0.5 mm longis, apicibus truncatis locellis introrsis, 3 interioribus filamentis ca. 0.7 mm longis, antheris ca. 0.8 mm longis, locellis extrorsis; glandulae staminum interiorum magnae, breviter stipitatae, ca. 0.6 cm diametro; staminodia 3, ca. 0.7 mm longa, apice triangulari. Ovarium glabrum, ellipsoideum, ca. 0.8 mm longum. Fructus ellipsoideus, cupula brevi, ad 1 cm lata, sensim in pedicellum angustata.

Shrubs or small trees. Twigs terete, glabrous at maturity, but the tips with varying amounts of brown, appressed hairs, these sometimes giving a brown cast to the twigs. Terminal bud densely gray-sericeous. Leaves alternate, chartaceous, 6–9 × 2–3.5 cm, ovate or narrowly ovate, the base obtuse or acute, the apex acuminate; strigose above and below when young, becoming glabrescent; upper leaf surface smooth, the venation scarcely or not at all visible; lower leaf surface with venation slightly elevated; lateral veins 3–6 pairs; domatia generally lacking, although occasionally a few erect hairs present in the vein axils. Inflorescences axillary, shorter than the leaves, to 6 cm long, grayish strigose, paniculate. Flowers white; petals 6, equal, ellipsoid, ca. 1.5 mm long, the outside strigose near the base, less so towards the apex, the inside glabrous, but the inner 3 tepals with a papillose tip; stamens 9, 4-celled, the outer 6 with introrse cells, the filament ca. 0.5 mm long, the anther ca. 0.5 mm long, the cells arranged in 2 horizontal rows, apex of anther truncate; inner 3 stamens with extrorse cells, the filaments ca. 0.7 mm, the anther ca. 0.8 mm; staminal glands globose, short-stalked, ca. 0.6 mm diam.; staminodia 3, ca. 0.7 mm long, the head small, triangular. Ovary glabrous, ellipsoid, ca. 0.8 mm long; style robust,

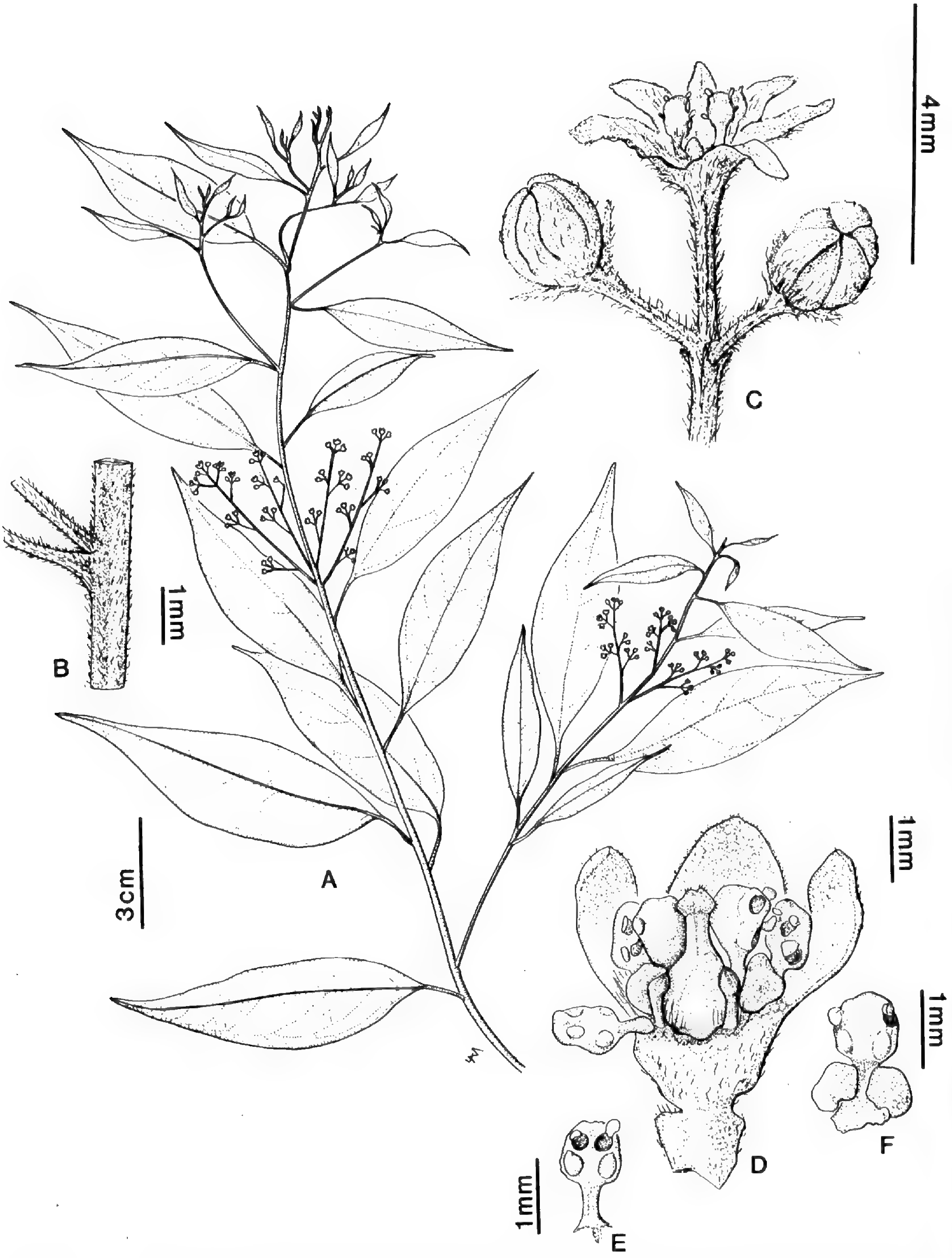


FIGURE 1. Ocotea strigosa.—*A. Habit.—B. Detail of twig, showing pubescence.—C. Detail of inflorescence.—D. Flower, tepals removed, showing stamens, staminal glands, staminodia, and ovary.—E. Outer stamen.—F. Inner stamen with basal glands.*

ca. 0.7 mm long, the stigma triangular. Fruit an ellipsoid berry, ca. 1 cm long, seated on a shallow cupule, ca. 1 cm wide, with a gradually thickened pedicel.

Paratypes. NICARAGUA. BOACO: entre Cerro Alegre y El Roblar, *Moreno 20201* (MO), *20212 B* (MO). JINOTEGA: Montaña Cuspire, *Moreno 8045* (MO); Fila Piedra Pelona, *Moreno 7794* (MO); Volcán Yali, *Moreno 7944, 7965* (both MO). MATAGALPA: El Picacho, *A. Molina R. 30512* (F, MO); Hacienda Santa Maria de Ostuma, *Tomlin 141, 142, 154, 156* (all MO).

Ocotea strigosa is known only from cloud forests between 1,000 and 1,600 m elevation in Nicaragua. One of the most inconspicuous *Ocotea* species in Central America, it can be recognized best by its strigose pubescence and acuminate leaves. Domatia are generally lacking, but occasionally some erect hairs can be found in the axils of the lateral veins. Some leaves of *Stevens 22181* have minute, insect-built cocoons in the vein axils, which are partly covered by stiff hairs. This collection also has a stronger raised reticulation on the lower leaf surface than the other collections.

Ocotea is a difficult genus, not always clearly separated from *Nectandra* and *Phoebe*, and it includes several poorly known species based on incomplete specimens. In Allen's (1945) *Ocotea* treatment of the Central American Lauraceae, *O. strigosa* keys to *O. effusa* (Meissner) Hemsley or *O. klotzschiana* (Nees) Hemsley, both known from Mexico and adjacent areas. *Ocotea strigosa* can be separated from those species by its strigose pubescence, ovate leaves (widest below the middle), and absence of domatia. In Allen's (1945) *Phoebe* treatment, it keys to the vicinity of *P. mollicella* Blake or *P. acuminatissima* Lundell. The first can be immediately recognized by its yellowish tomentum and is probably not closely related. *Phoebe acuminatissima* differs from *O. strigosa* by its narrower leaves, domatia in the lower vein axils, raised reticulation on the upper leaf surface, papillose anther tips, and denser pubescence consisting of shorter hairs. The papillose anthers and tepals and the glaucous cast of the flowers suggest that *P. acuminatissima* does not belong in *Phoebe* but might better be placed in *Ocotea* near the group of *O. helicterifolia* (Meissner) Hemsley.

Ocotea jorge-escobarii Nelson, Ceiba 25: 173. 1984. Figure 2.

Ocotea jorge-escobarii Nelson was recently described and was only known from Honduras. Because the description and discussion of this species were brief, its identity remained problematical. During preparation of the treatment of the Lauraceae for the *Flora de Nicaragua*, several *Ocotea* collections from cloud forests in Nicaragua were found to represent an unknown species. A search in the MO herbarium produced several collections from Honduras, distributed as *Phoebe* species, which belonged in this unknown species. Because one of these collections (*Escobar 247*) was cited as a paratype of *O. jorge-escobarii*, and the specimens agree with the brief description, I place the Nicaraguan collections in *O. jorge-escobarii.* I present here an English description and an illustration of this species.

Trees, to 20 m tall. Twigs ridged or terete, glabrous except for a few appressed hairs near the tip, the terminal bud white-sericeous pubescent. Leaves alternate, glabrous, evenly distributed along the twigs, firmly chartaceous or coriaceous, 10–20 × 4–8 cm, slightly obovate or narrowly obovate, widest above the middle, mature leaves drying pale green, the base cuneate-attenuate, the apex obtuse or slightly acute, the venation scarcely visible on upper surface but visible and slightly raised on lower surface; lateral veins 6–9 pairs; pit domatia present along the midvein and along lateral veins, these without hairs; margin thickened, greenish and often slightly inrolled. Inflorescences axillary, glabrous or with few hairs near base, shorter than the leaves, ca. 6 cm long; flowers glabrous, greenish white; tepals 6, equal, ca. 2 mm long, broadly elliptic; stamens 4-celled, the outer 6 ca. 2 mm long, glabrous, except for some hairs at base of filaments, with introrse cells; inner 3 stamens ca. 2 mm long, the cells extrorse, the filaments glabrous but base of anther densely

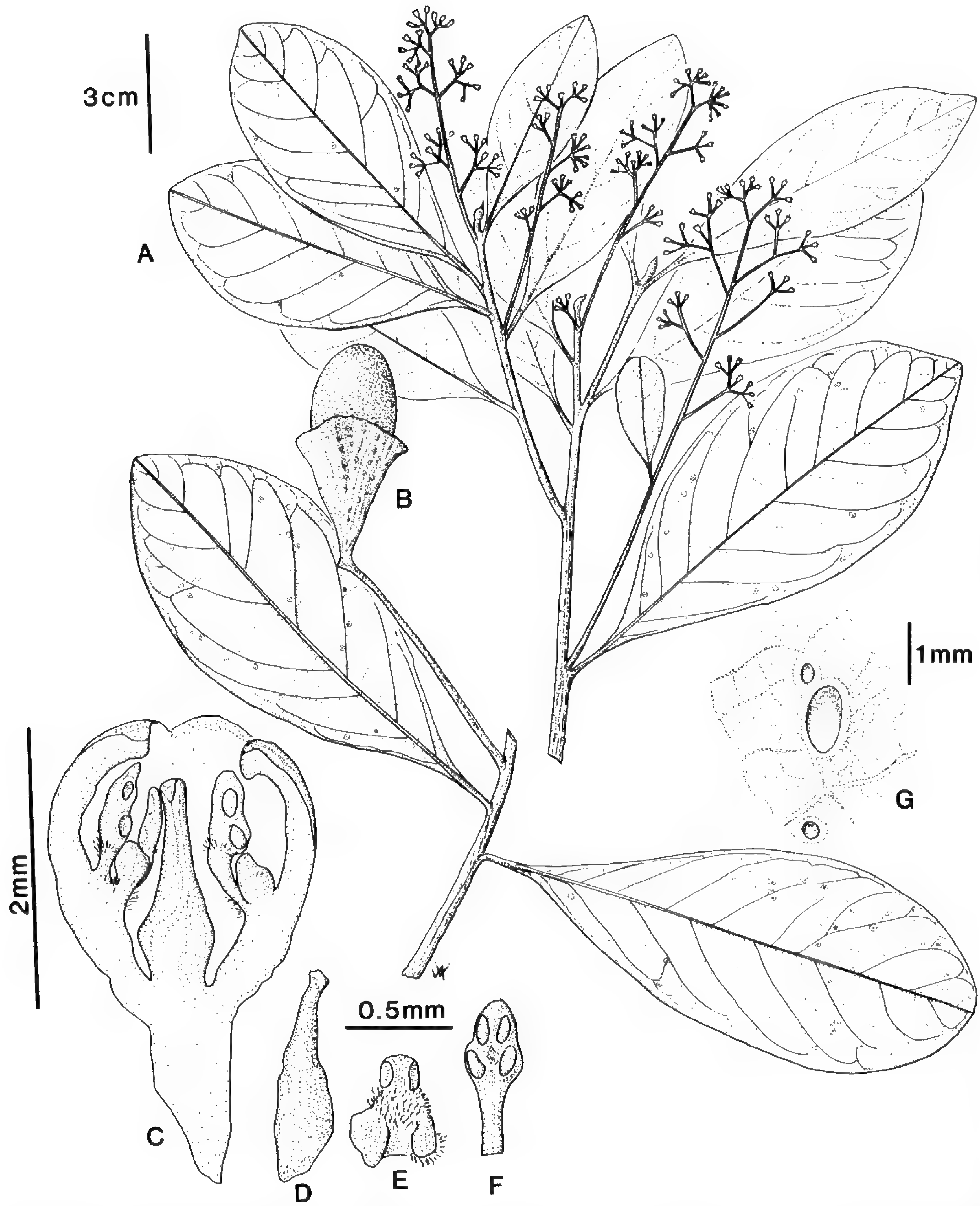


FIGURE 2. Ocotea jorge-escobarii.—*A. Habit.—B. Twig with cupule and fruit.—C. Cross section of flower.—D. Ovary.—E. Inner stamen with basal glands.—F. Outer stamen.—G. Detail of leaf, showing pitlike domatia.*

pubescent on the side facing the ovary, staminodia lacking; staminal glands large, ca. 0.8 mm diam.; floral tube ca. 1 mm deep, glabrous except for a ring of hairs at the upper margin; ovary glabrous, ellipsoid, gradually narrowed into style, the ovary and style ca. 2 mm long. Fruit an ellipsoid berry, ca. 3 cm long, 2 cm wide, cupule a large, thick cup, ca. 2.5 cm wide at rim and 1 cm deep, with many small warts and a few longitudinal ribs, which may be a drying artifact.

Specimens seen. HONDURAS. OLANCHO: Montaña Los Zapotes, *Mejia 138* (MO); same locality, *Sosa 191* (MO); same locality, *Alverado 130* (MO); same locality, *Escobar*

247 (MO); same locality, *Mejia Orduñez 146* (MO). NICARAGUA. MATAGALPA: El Arenal, between Aranjuez and Santa Martha, *A. Molina 20345* (F, MO). JINOTEGA: Ocotillo near Sta. Lasthenia, *L. Williams et al. 27783, 20794* (F); Sta. Maria de Ostuma, *L. Williams et al. 23435* (F). ZELAYA: Cerro El Hormiguero, *Pipoly 5166* (MO); Cerro La Pimienta, *Grijalva 363* (MO).

Ocotea jorge-escobarii, known only from cloud forests in Nicaragua and Honduras between 1,000 and 1,600 m elevation, is closely related to such species as *O. meziana* Allen from Panama and Costa Rica, *O. barbatula* Lundell from Guatemala, *O. viridiflora* Lundell from Chiriquí, Panama, and possibly to other species, such as *O. laetevirens* Standley & Steyerm., *O. verapazensis* Standley & Steyerm., and *O. eucymosa* Lundell. Characters shared by most species in this group are pale green drying leaves and the presence of pit domatia away from the midrib. The new species can be recognized easily by its leaf shape (widest above the middle), unusually large cupules, and thickened, slightly inrolled leaf margin. Specimens have been annotated earlier as *O. meziana* vel aff., *O.* aff. *laetevirens*, and *O. veraguensis* and may be found in additional herbaria under these names. The material from Honduras was all annotated as *Phoebe* species. Nelson compares this species with *Ocotea bernoulliana* Mez; this species differs in its dark green drying leaves and in its inflorescences, which are longer than the leaves. *Ocotea bernoulliana* is a rarely collected species, to me known only with certainty from the type.

I thank Dr. J. Dwyer for correcting the Latin description and Dr. J. Rohwer for bringing the publication of *O. jorge-escobarii* to my attention. John Myers skillfully made the illustrations.

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A NEW AND ENDANGERED SPECIES OF *DAPHNOPSIS* (THYMELAEACEAE) FROM ECUADOR

Six species of *Daphnopsis* C. Mart. & Zucc. are known to occur in Ecuador (Nevling, 1959, 1978). The species are distinctive, but sterile collections may be confused with sterile collections of *Schoenobiblus* C. Mart. & Zucc. There is no reliable way to distinguish sterile *Daphnopsis* from *Schoenobiblus* other than by direct comparison of specimens. Fertile specimens of *Daphnopsis* are easily distinguished from *Schoenobiblus* C. Mart. by the presence of a calyx tube.

The following species was discovered in 1980. Since then, the forests at the only known locality have been cleared for farmland (Dodson, pers. comm.). Only scattered groups of trees persist along the creekbeds. The individuals from which the type was collected have been destroyed. With continued development of the lowland forest of Ecuador, it is likely that the species will soon be eliminated, if it is still extant.

Daphnopsis grandis Nevling & Barringer, sp. nov. TYPE: Ecuador. Los Rios: El Centinela, Montas de 11a road from Patricio Pilar to 24 de Mayo, km 12, 600 m, 6 Apr. 1980, *Dodson & Gentry 10295* (holotype, SEL; isotype, MO).

Species insignis foliis 45–65 cm longis 15–18 cm latis, inflorescentiis saepe caulifloris, hypanthio anguste obconico 10–12 mm longo, staminibus alternisepalo sessilibus.

Small tree to 5 m tall; young stems glabrous; older stems covered by a smooth gray-brown cortex. Leaves alternate; petioles 1.5–2 cm long, terete, wrinkled; blade narrowly obovate, 45–65 cm long, 15–18 cm wide, subcoriaceous, glabrous above and below, the base cuneate, the margin revolute when dry, the apex acuminate, the venation pinnate, prominent, the secondary veins straight, subparallel. Staminate inflorescence on leafless stems or rarely terminal, umbelliform, sericeous; primary peduncle 3–4 cm long; rachis 1–3 mm long; secondary peduncle 3–4 mm long. Staminate flowers 20–30 per inflorescence, white, sericeous; pedicel 3–4 mm long; hypanthium narrowly obconic, 10–12 mm long, glabrous within; calyx lobes triangular, reflexed, 3–4 mm long, 2–3 mm wide; petals absent; stamens 8, obdiplostemonous, the antisepalous whorl inserted on the calyx lobes, the filaments 1 mm long, the anthers 1 mm long, the alternisepalous whorl inserted 1–1.5 mm below the mouth of the hypanthium, sessile, anthers less than 1 mm long; disk cupuliform to tubular, 1–2 mm long, free, undulate; pistillode 2 mm long, glabrous, on a gynophore less than 1 mm long. Pistillate inflorescence on leafless stems or rarely terminal, umbelliform, sericeous; primary peduncle 1.2–1.7 cm long; rachis 2 mm long; secondary peduncle 1–1.5 mm long. Pistillate flowers not seen. Immature drupe ovoid, 6–7 mm long, the style and base of the hypanthium persistent, the pedicel to 5 mm long.

Additional specimen examined. ECUADOR. LOS RIOS: El Centinela, Montas de 11a road from Patricio Pilar to 24 de Mayo, 2 Oct. 1979, *Dodson, Gentry & Schupp 8694* (F, MO, SEL).

Daphnopsis grandis is known only from the type locality in northern Los Rios Province, Ecuador. It is easily distinguished from all other species of *Daphnopsis* by its obovate leaves 45–65 cm long, cauliflorous inflorescences, and long, tubular-funnelform hypanthia. It is also unusual to find the upper whorl of stamens with filaments while the lower whorl is sessile. The species is so distinctive that it is difficult to establish its affinities. The cauliflorous inflorescences, free disk, and appar-

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ent lack of true dichotomous branching place the species in subgenus *Neivira* (Griseb.) Nevling (1959). It appears to be most closely related to *D. gemmiflora* (Miers) Domke from Brazil but differs by its large leaves, pistillode 2 mm long, and sessile whorl of anthers. *Daphnopsis grandis* can be distinguished from all other known Ecuadorean species by the following key.

KEY TO THE SPECIES OF *DAPHNOPSIS* IN ECUADOR

1a. Young growth tomentose to sericeous; disk annular; shrubby tree growing above 2,400 m .... *D. macrophylla* (Kunth) Gilg
1b. Young growth glabrous or glabrescent; disk cupuliform or coroniform.
  2a. Calyx tube more than 7 mm long; trees growing below 1,500 m.
    3a. Leaves over 40 cm long, over 10 cm wide; inflorescences umbelliform; branching monopodial .... *D. grandis* Nevling & Barringer
    3b. Leaves under 30 cm long, under 10 cm wide; inflorescences racemose, sessile, 3–8-flowered; branching dichotomous .... *D. occulata* Nevling
  2b. Calyx tube under 5 mm long.
    4a. Petioles 4–6 cm long; inflorescence umbelliform; rudimentary petals present; branching dichotomous; small tree growing below 1,500 m .... *D. americana*, subsp. *ecuadorensis* (Domke) Nevling
    4b. Petioles 1–4 cm long; inflorescence racemiform; rudimentary petals absent; branching monopodial.
      5a. Petioles 1–2 mm long; leaves 18–27 cm long; inflorescences 8 cm long; small tree growing below 1,500 m .... *D. zamorensis* Domke
      5b. Petioles 2–4 mm long; leaves 3–8 cm long; inflorescences 1–2 cm long; shrubby tree growing above 2,400 m .... *D. espinosae* Monachino

We thank Dr. Calaway H. Dodson and the curators of F, MO, and SEL for providing material and information. Research was funded in part by the Tieken Fund of the Field Museum.

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A NEW SPECIES OF *DIOCLEA* KUNTH (DIOCLEINAE, FABACEAE) FROM THE VENEZUELAN GUAYANA

Study of collections with fruit from the Venezuelan Guayana, particularly those of Steyermark, has resulted in the identification of a new species of *Dioclea*. Prior to the availability of these collections many specimens of this new species were determined incorrectly as *D. macrocarpa* Huber (1909).

Dioclea ruddiae R. H. Maxwell, sp. nov. TYPE: Venezuela. Amazonas: Cerro Huachamacari, Río Cunucunuma. Occasional in slope forest near Camp 2, 1,100 m, 16 Dec. 1950, *Maguire, Cowan & Wurdack 29930* (holotype, US; isotypes, F, K, GH, IAN, MO, NY, P, RB, S, U, US). Isotypes may have been annotated *Dioclea macrocarpa* Huber by me from 1969 to 1980. Figure 1.

Foliola subcoriacea, subconduplicata, elliptica, ad ca. 12.5 × 8 cm, basi rotundata; stipulis non productis, acutis. Flores ca. 1.5 cm longi, calycis lobis 4, supero lobo calycis integro; vexillum valde reflexum, orbiculari; carinis obtusis rostratis; staminibus 10, antheris perfectis; ovario 4-ovulato. Legumina turgida, ad ca. 13 × 4 × 3 cm, indehiscentia, seminibus 1–4; seminibus ellipsoideis; hilo oblongo, ca. 5.5 mm longo.

Lianas, to 30 m tall; stems terete, the younger stems with mostly appressed, ferruginous pubescence, the older bark glabrous, splitting horizontally, the lenticels light brown and conspicuous. *Leaves* trifoliolate, the leaflets subcoriaceous, subconduplicate, the lamina mostly elliptic, the terminal leaflet lamina to ca. 12.5 × 8 cm, the laterals to ca. 11 × 6 cm, the upper surface reticulate, somewhat sulcate, glabrous or glabrescent on the primary veins, the lower surface with light brown pubescence, the apices acute or with drip tips to 2 cm long, the bases rounded, the primary lateral veins in 6–9 pairs; petioles 4–9 cm long, the rachis 5–25 mm long, this and petiole with sparse, mostly ascending pubescence, the pulvinules ca. 7 mm long, densely pubescent; stipules not produced below insertion, acute, 1–3 mm long; stipels caducous or possibly absent. *Inflorescence* axillary, single, 11–35 cm long, ferruginous pubescent, flowering to ca. ⅘ its length; tubercles short-clavate; bracts acute, ca. 2.5 mm long, semipersistent, inserted at the base of the tubercle stalk; bracteoles ovate, ca. 2 × 1.5 mm, persistent; pedicels ca. 5 mm long. *Flowers* with buds straight, the lower calyx lobe upcurved, flowers ca. 1.5 cm long, the calyx tube ca. 7 mm long, ferruginous pubescent, black velutinous inside extending up the lobes, the upper lobe obtuse, entire, ca. 7 × 5 mm, the lateral lobes slightly falcate, ca. 8 × 3 mm, the lower lobe lanceolate, ca. 10 × 4 mm; standard strongly reflexed, orbicular, ca. 9 × 10 mm with a claw ca. 4 mm; wings obliquely oblong, ca. 6 × 7 mm with a claw ca. 5 mm long; keels obliquely oblong, 4–6 mm long with a claw ca. 5 mm long, the upper margin basally auriculate, unlobed, the beak obtuse; stamens 10, pseudomonadelphous, the base of the vexillary filament free ca. 2 mm, sparsely pubescent, the anthers perfect, ca. 1 mm long; pistil straight ca. 10 mm then geniculate, rising distally ca. 6 mm, the ovary ca. 5 mm long, sessile, ca. 4-ovulate, hirsute with mixed canescent, fuscous and ferruginous pubescence, the hairs to 1 mm long, the style hirsute, swollen distally then narrowing to the incurved, somewhat subterminal stigma. *Fruit* turgid, fleshy, oblong, to ca. 13 × 4 × 3 cm, indehiscent, the exocarp with brown pubescence, becom-

ANN. MISSOURI BOT. GARD. 75: 730–732. 1988.

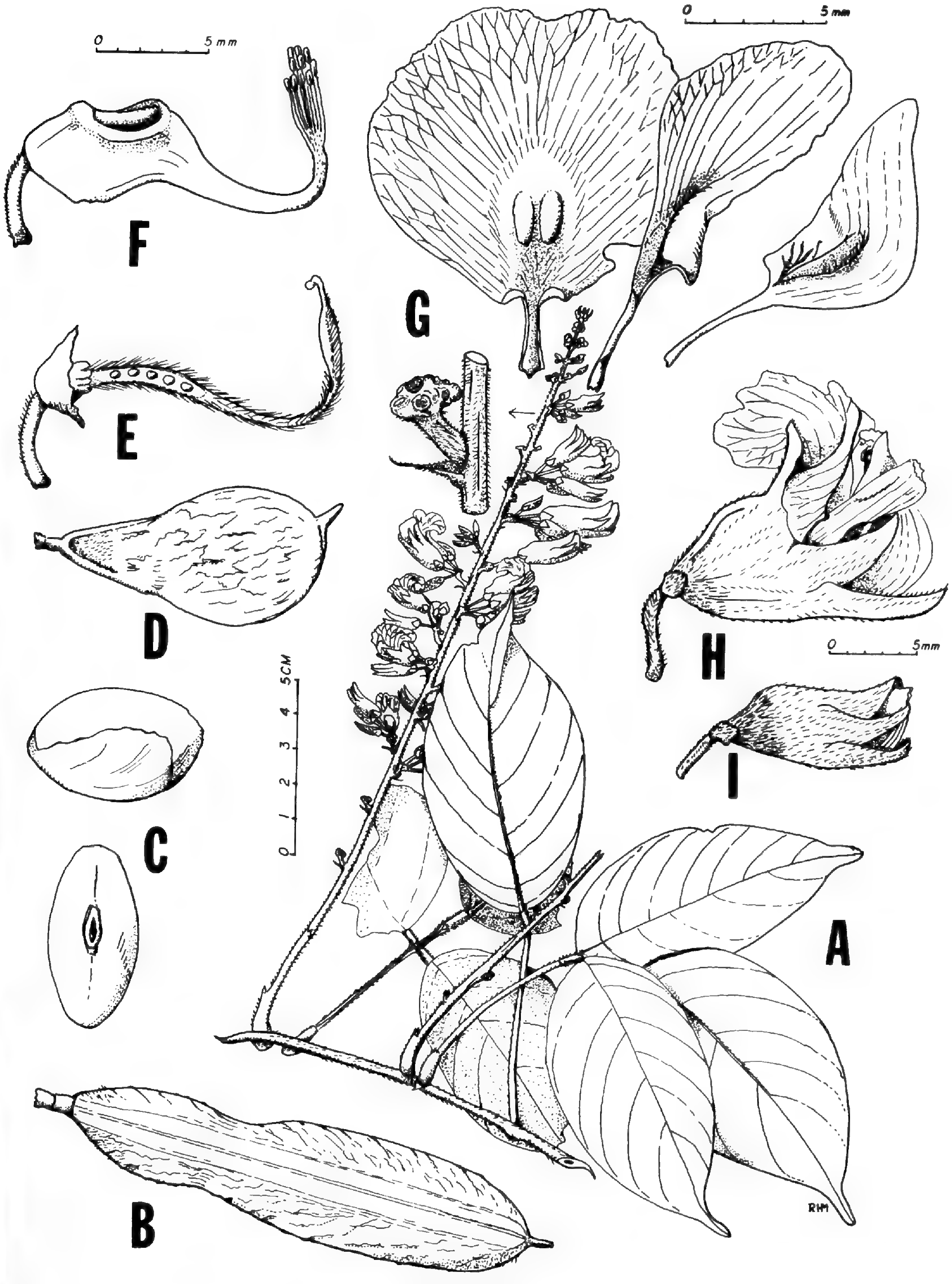

Figure 1. Dioclea ruddiae.—*A. Flowering branch,* Steyermark et al. 92713 *(US).—B. Fruit, 3-seeded, dorsal view,* Steyermark 107174 *(US).—C. Seeds, dorsal and lateral views (with packing attached),* Steyermark 107174 *(NY).—D. Fruit, 1-seeded,* Steyermark 107174 *(NY).—E. Pistil showing ovule position,* Maguire et al. 29930 *(S).—F. Staminal sheath with pseudomonadelphous stamens,* Maguire et al. 29930 *(S).—G. Petals, standard, wing and keel,* Steyermark et al. 92713 *(K).—H. Flower,* Maguire et al. 29930 *(US).—I. Flower bud,* Maguire et al. 29930 *(US).*

ing glabrescent, the upper suture raised, culminating in a persistent, upturned beak, the lower suture indistinct, 1–4-seeded; seeds soft, ellipsoid, to ca. 4.5 × 3.2 × 2.2 cm, the hilum oblong, ca. 5.5 mm long.

Selected specimens examined. VENEZUELA. AMAZONAS: Sierra Parima, a unos 6–7 km al Oeste de la frontera Venezolana-Brasilera, *Steyermark 107174* (NY, US). BOLÍVAR: south of El Dorado, *Gentry et al. 10464* (JEF, MO); Distr. Roscio, sabanas y arbustales en la cumbre del Cerro Chirikayen, *O. Huber & Alarcón 7628* (JEF, MYF); Cerro Venamo (parte Sur-Oeste), Cerca de los Limites con la Guayana Inglesa, *Steyermark et al. 92713* (K, US).

Flowering collections date from January, March, and June in Bolívar, Venezuela. December flowering is reported in Amazonas, with fruit appearing 18 April through 23 May. Collectors report the calyx magenta, the petals lavender or magenta to purple, with the target spot on the standard yellow.

Collectors further report the species occasional to locally frequent from roadsides, savannas, and wooded hills and slopes to upland, humid forest. The altitude range is 795–1,580 m. Habitat may separate *Dioclea ruddiae* from the closely related *D. macrocarpa* Huber, where the habitat is noted as from floodplains and riverbanks in Brazil, Colombia, Ecuador, Guyana, Peru, and Surinam in addition to Venezuela.

The distinguishing characters within *Dioclea* of this new species are the stipules not produced below insertion, 10 perfect anthers, and the oblong seed hilum. These characters place the species in section *Macrocarpon* Amshoff (1939). The turgid, fleshy fruit, however, is distinct within section *Macrocarpon* and the closely related section *Platylobium* Benth. (1859) but similar to several species in section *Pachylobium* Benth. (1839), such as *D. malacocarpa* Ducke and *D. pulchra* Moldenke.

Dioclea macrocarpa differs from *D. ruddiae* by possessing papyraceous leaflets, mostly glabrous or glabrecent beneath; inflorescences frequently in cauliflorous clusters; calyx tube glabrous or canescent puberulent; 4–8 ovules; and fruit flat, ca. 1 cm thick, frequently over 20 cm long, 3–8-seeded, with both sutures raised and with closely parallel ribs, the upper suture culminating in a short downturned beak. Fruit and seed have been illustrated by Ducke (1925).

In contrast, *Dioclea ruddiae* has subcoriaceous, subconduplicate leaflets, pubescent beneath; inflorescences seen are axillary and single; calyx tube with ferruginous pubescence; ca. 4 ovules; and fruit turgid, ca. 3 cm thick, to ca. 13 cm long, 1–4-seeded, with the sutural ribs indistinct, the upper suture culminating in a slender, upturned beak.

It is probable that reexamination of collections determined *Dioclea macrocarpa* from the Venezuelan Guayana will yield additional *D. ruddiae.*

The new species is named in honor of Dr. Velva E. Rudd, a renowned legume specialist and source of encouragement and support for other legume workers. I wish to thank Dr. Julian Steyermark for the opportunity to work on the *Flora of the Venezuelan Guayana* and for commenting on this mansucript. For the opportunity to study *Dioclea* material, I also thank the herbaria directors and curators of MO, NY, and US, in particular, as well as A, F, GH, IAN, MYF, S, and VEN.

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A NEW SPECIES OF *ILEX* (AQUIFOLIACEAE) FROM CENTRAL AMERICA

While preparing a treatment of the Aquifoliaceae for *Flora de Nicaragua*, several specimens not referable to any described species of *Ilex* were encountered. The specimens were obviously related to the widespread *Ilex guianensis* (Aublet) O. Kuntze but differed in several key characters of leaf venation and fruit morphology. Further study of the material available in European and American herbaria proved these to represent a new species, described below.

Ilex tectonica Hahn, sp. nov. TYPE: Belize. Toledo, Columbia Forest Reserve, vicinity of forest camp, ca. 6 miles due south of Cabro, in upper Río Grande drainage area, ca. 1,000 ft., high forest, tree, 45 m tall, dbh 70 cm, 5–9 May 1976, *G. R. Proctor 36093* (holotype, MO; isotype, BM). Figure 1.

Ex affinitate *I. guianensis* et *I. belizensis* ab utroque praecipue natura foliorum, laminis chartaceis, marginibus planis, apicibus caudatis, venationibus subtus distincte reticulatis luteisque, etiam fructibus ovoideis, stigmatum vestigiis prominentibus, conice angularibus, elevati supra pericarpia distincta.

Tree to 45 m tall, to over 1 m dbh, laxly branched; trunk reportedly buttressed; bark pale brownish gray on mature stems, with oval lenticels 1 mm long, the new stems drying black or dark brown with white spots; stipules triangular, 2 mm long, 1 mm wide, subtending inflorescences or not. Leaves elliptic, chartaceous, the apex shortly caudate, the base acute, slenderly attenuate, 7–10 cm long, 3.5–4.5 cm wide, the margin usually entire, sometimes minutely spinulose toward the apex, epunctate, venation elevated abaxially, brochidodromous, semicraspedodromous, reticulate, the veins yellow and obvious; petiole thickened, adaxially channeled, 4–8 mm long. Inflorescence of axillary dichasia branched to 2–3 orders, clustered on reduced stems while in flower, later expanding when in fruit, the main rachis and rachillae winged or flattened, the primary rachis 8–13 mm long, the secondary rachillae 3–5 mm long, the tertiary rachillae 1–3 mm long; bracts triangular, paired, 1–1.5 mm long, sometimes deciduous; bracteoles similar but smaller. Flowers (4–) 5-merous, regular, actinomorphic, unisexual; staminate flowers with sepals acute, 1 mm long, sometimes irregular at the apex; petals broadly elliptic, obtuse-rounded at the apex, thinner along the margin, basally united with the filaments, 2–2.5 mm long, 1.5 mm wide; stamens antisepalous; filaments 2–3 mm long; anthers 1 mm long; pistillodium conical, 1 mm long; carpellate flowers not seen. Fruit ovoid, 5–6 mm long, 4 mm diam.; pericarp thin, red at maturity; stigma persistent and conspicuous in profile, conical; mesocarp fleshy but scant; pyrenes crescent-shaped, triangular in cross section; endocarp ligneous, striated abaxially.

Additional specimens examined. HONDURAS. ATLANTIDA: Reserva Forestal de Lancetilla, *Hazlett 2928* (MO, F); Lancetilla Valley near Tela, *Standley 53191, 54736* (A), *55449* (A, F). YORO: SW of La Florida, 8 km by Agua Zarca, *Hazlett 3105* (F, MO). NICARAGUA. CHONTALES: 4 km al NW de Santo Domingo, *Aranda et al. 83* (MO). MATAGALPA: near Peñas Blancas, *Molina s.n.* (F). ZELAYA: Kurinwasito, 50 km SE de Rio Blanco, *Sandino 4845* (MO); ca. 5 km al S de Waslala, *Grijalva & Moreno 1205* (MO).

Common names. San Juan macho, sibuc che, powder stick (Belize), camibar, areno (Nicaragua), San Juan campano, San Juan arenillo (Honduras).

Typically found in tall moist forests, *I. tectonica* is sometimes found with pines in drier mixed forests. Throughout its known range, the species flowers in the dry season of April and May and fruits through July. According

ANN. MISSOURI BOT. GARD. 75: 733–735. 1988.

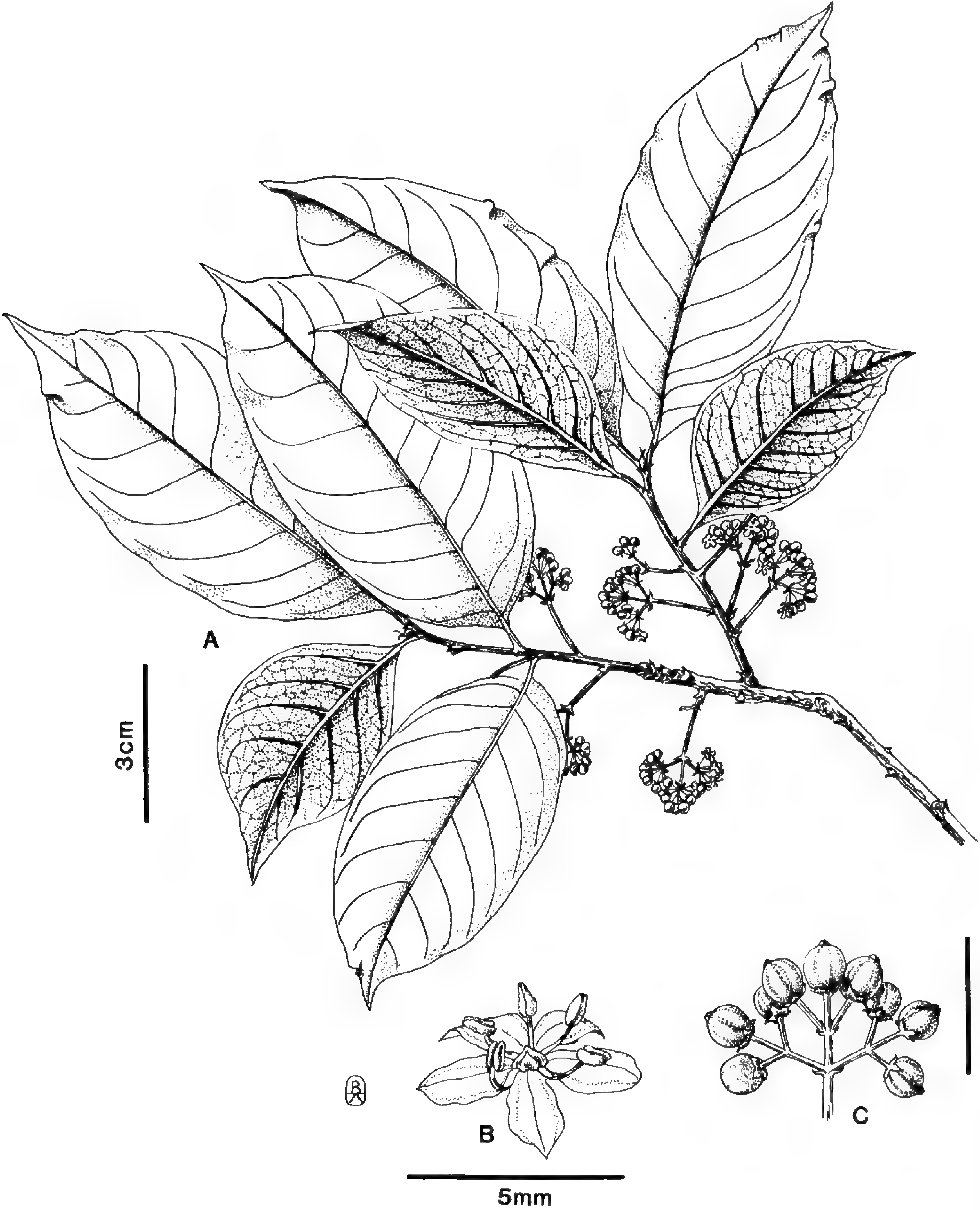

FIGURE 1. Ilex tectonica.—*A. Flowering branch (*Proctor 36093*).—B. Staminate flower (*Proctor 36093*).—C. Infructescence (*Grijalva & Moreno 1205*).*

to label information (*Molina s.n.* and *Hazlett 3105*), it is utilized for timber. In recognition of this, the specific epithet, derived from the Greek *tektonikos* (used for construction), is applied.

Components of the *Ilex guianensis* species complex are found throughout the Caribbean and present some of the most difficult taxonomic problems among neotropical members of the genus. The widespread distribution and relatively homogeneous morphology typical of many coastal strand and scrub species hold true for individuals of this complex growing in such associations. A considerable amount of the confusion, therefore, is due solely to the insular distribution of this group and the synonymy common to pan-Caribbean taxa. However, the ability of the group to invade recently disturbed areas in the highlands of Central America and the Caribbean Islands and apparent hybridization with native upland congeners present additional taxonomic challenges. A key to the Central American members of the *Ilex guianensis* complex is presented below.

1a. Leaves coriaceous, margins usually revolute, apex usually obtuse or retuse, sometimes slightly acute; new stems drying gray or green; coastal scrub, inland savannas, occasionally moist forests and disturbed upland clearings; Atlantic coast of Central America and northern South America, Gulf of Panama, and the Greater Antilles .... *Ilex guianensis*

1b. Leaves chartaceous, margins flat, apex acute; new stems drying black or brown.
    2a. Young stems drying black; secondary leaf venation obscure; fruits spherical; stigmatic residue spreading, not prominent in profile above the pericarp; advanced forest on limestone; Belize .... *Ilex belizensis*
    2b. Young stems drying brown with white lenticels; secondary leaf venation distinct, reticulate, the veins yellow; fruits ovoid; stigmatic residue angular-conical, raised above the pericarp; moist forest or mixed with pines; Belize, Honduras, and Nicaragua .... *Ilex tectonica*

I thank Bente King for providing the illustration, Harold Robinson for suggesting the specific epithet, and John Dwyer for supplying the Latin diagnosis.

—*William James Hahn, Department of Botany, NHB-166, Smithsonian Institution, Washington, D.C. 20560, U.S.A.*

NOTES ON *OLDENLANDIA FILICAULIS* AND *OLDENLANDIA TENUIS* (RUBIACEAE)

During an expedition to the northwestern portion of the state of Bolívar, Venezuela, in 1985, collections were made of a slender-stemmed, rubiaceous annual belonging to the genus *Oldenlandia.* An attempt to identify the material led to a study of *O. filicaulis* Schum. and *O. tenuis* Schum. Both species were described originally from the state of Piauhy, northeastern Brazil, at a considerable distance from the Venezuelan locality.

As first described by Schumann (1889), *O. filicaulis* has heterostylous flowers with infundibuliform corollas 4 mm long, whereas *O. tenuis* has homostylous flowers with broader-tubed corollas 2 mm long equaling or slightly exceeding the calyx lobes. Further examination of these taxa showed that the isosyntypes of *O. filicaulis* (*Blanchet 2703, 2742,* and *Martius 2476*) have the stems much more branched with opposite branching and relatively smaller capsules, as contrasted with the rather few, flexuous, alternately branched stems and broader fruiting capsules of *O. tenuis.* Moreover, the isosyntypes of *O. filicaulis* have filiform stems, filiform-acicular leaves 0.1–0.3 mm wide, and minute capsules 1.2–1.5 mm wide, whereas *O. tenuis* has slightly broader stems, leaves up to 1 mm wide, sometimes varying to subspatulate and broadened above the middle, and broader capsules mainly 2 mm wide. The long-exserted anthers of the isosyntypes of *O. filicaulis,* furthermore, are in contrast to the sessile and included ones of *O. tenuis.*

The Venezuelan specimens from northwestern Bolívar state differ from both Brazilian taxa in having a mainly solitary, simple, or slightly branched stem above with more numerous and shorter internodes averaging (6–)8–12 on a stem and 13–17 mm long, instead of, as in the Brazilian taxa, 3–8 to a stem and (12–)15–30 mm long. The leaves and calyx lobes of the Venezuelan plants have the margins more abundantly setulose-aculeate, but this character appears variable in the Brazilian taxa, from entire to varying numbers of aculeae.

Contrary to Schumann's description of the corolla length of 4 mm for *O. filicaulis,* examination of isosyntype and other material of this species showed corolla length variation usually to be 2–2.5 mm. A specimen of *Ule 7419* (F) from Bahia showed the longest length of 2.5–3 mm. In general, the corolla of *O. filicaulis* has a narrower, more elongated infundibuliform corolla tube than *O. tenuis.*

When compared with the corollas of the Brazilian taxa, the Venezuelan plant agrees with the type of corolla exhibited by *O. tenuis,* showing a broad tubular, short corolla 1.8–2 mm long, which is only slightly longer than the calyx, with sessile anthers included at the summit of the corolla tube. Additionally, the Venezuelan specimens also have the alternate branching of the stem characteristic of *O. tenuis.* A specimen collected by *Otto Huber et al. 1399* (VEN) from Territorio Federal Amazonas, Venezuela, has the short broad corolla and sessile, included anthers of *O. tenuis,* but the slender stem with opposite branches, few internodes, and minute capsules, sharing the characters common to *O. filicaulis.*

If one relies on the characters of few-branched stems with alternate branching, sessile included anthers, and capsules ca. 2 mm wide, then most of the specimens of this *Oldenlandia* complex would fall into *O. tenuis.* Such specimens are known from the Brazilian states of Ceará, Piauhy, Parahyba, Rio Bran-

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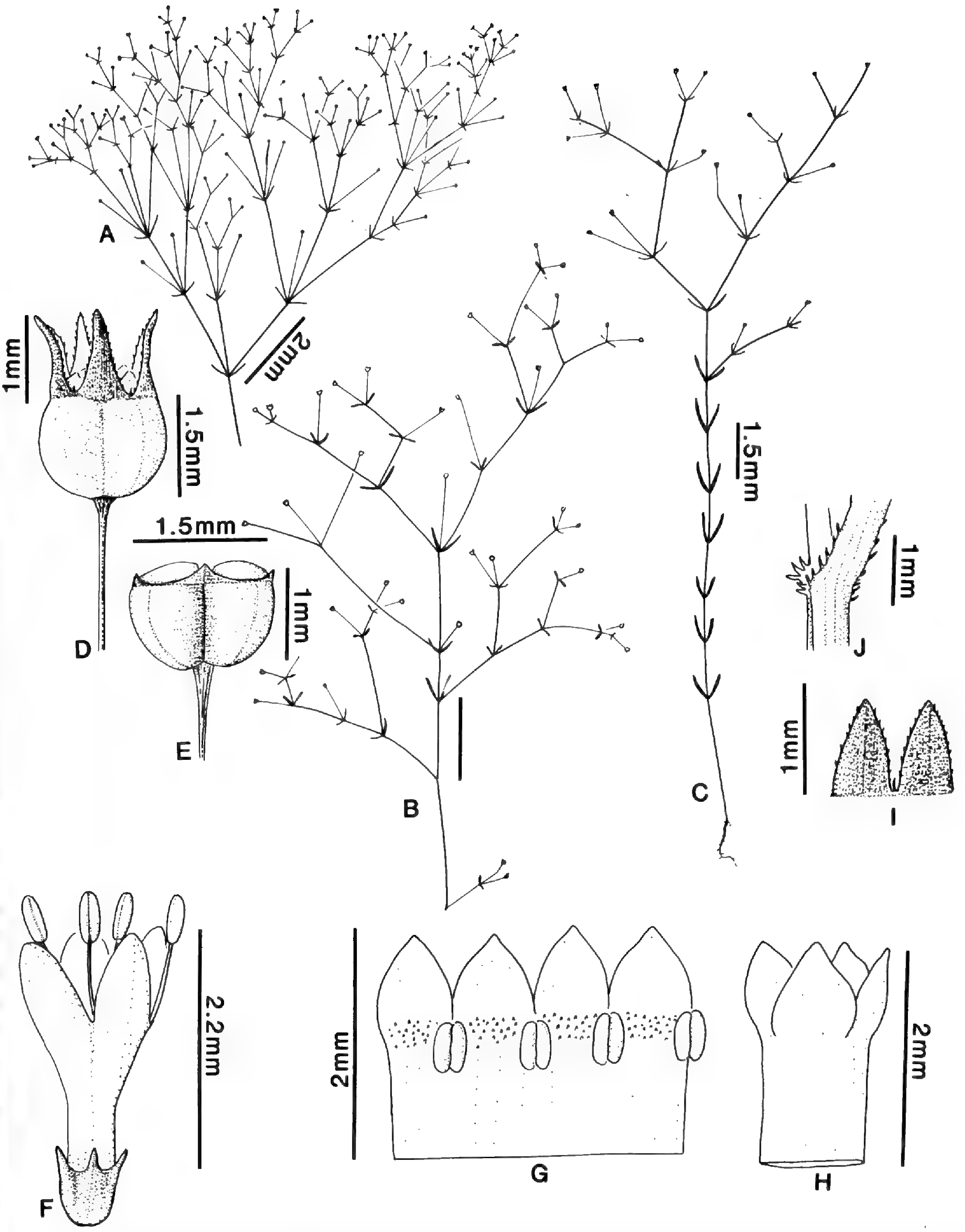

FIGURE 1.—*A. Habit of* Oldenlandia filicaulis, *showing much-branched, opposite lateral axes (isotype,* Blanchet 2742*)*.—*B. Habit of* Oldenlandia tenuis, *showing alternately branched, main lateral axes (*Drouet 2244*)*.—*C.* Oldenlandia tenuis, *showing more numerous and shorter internodes (*Steyermark, Holst & Manara 131298*)*.—*D. Fruiting specimen of* O. tenuis.—*E. Fruit of* O. filicaulis.—*F.* Oldenlandia filicaulis, *flower, with calyx and corolla*.—*G.* Oldenlandia tenuis, *corolla, interior view*.—*H.* Oldenlandia tenuis, *corolla, exterior view*.—*I.* Oldenlandia tenuis, *showing 2 calyx lobes with squamelline gland (*Steyermark et al. 131298*)*.—*J.* Oldenlandia tenuis, *base of leaf, showing aculeate margins.*

co, and Terr. do Roraima, from Guyana, and from northwestern Venezuela, if we include the collections obtained in the latter area. *Oldenlandia filicaulis*, on the other hand, appears to be rarer and occurs in the Brazilian states of Piauhy, Bahia, and Pará and in Venezuela from Territorio Federal Amazonas. Both taxa were collected from the Brazilian state of Piauhy.

Although it is possible that only one variable species is represented among the specimens studied, the two taxa may be considered as separate and distinct until more intensive investigation has been completed.

KEY TO THE SPECIES

1a. Corolla slightly longer than the calyx, 1.8–2 mm long, broadly cylindric; anthers included, sessile; branching of stem alternate, irregular, with relatively few axes; capsule 1.5–2 mm wide; leaves 0.5–0.7(–1) mm wide, linear-subulate to subspatulate, sometimes broader near the middle; stem 0.5–0.7 mm thick .... *O. tenuis*

1b. Corolla ca. 2½ times longer than the calyx, 2–3 mm long, infundibuliform; anthers long exserted; branching of stem opposite, with numerous axes; capsule 1.2–1.5 mm wide; leaves 0.1–0.3 mm wide, linear-acicular, uniform in width; stem 0.3–0.5 mm thick .... *O. filicaulis*

Oldenlandia filicaulis K. Schumann, Mart. Fl. Bras. 6(5): 271. 1889.

Specimens examined. BRAZIL. PIAUHY: prope Utinga in Sertão fluvii Rio de San Francisco, *Blanchet 2742* (isosyntypes, F, NY); ad Villa de Barra, *Blanchet 2703* (photo of isosyntype at B; F, NY); in arenosis humidis ad praedium Serra Branca, *Martius 2476* (M). PARAIBA: proximo ao mangue, Bahia de Traicão, *Coehode Toraes 2270* (NY). BAHIA: Remanso, *Ule 7419* (F, K). PARÁ: Pará, Gurupá, campina da Serraría Xingú, *Silva & Rosario 4989* (F, NY, VEN); Munic. de Almeirim, *Santos 660* (NY); Visên, *Tavares 7* (NY). VENEZUELA. AMAZONAS: between airport of Puerto Ayacucho and Samariapo, 5°37′N, 67°36′W, 75 m, *Huber, Cárdenas & Pijykko 1399* (VEN, intermediate between *O. filicaulis* and *O. tenuis*).

Oldenlandia tenuis K. Schumann, Mart. Fl. Bras. 6(5): 273. 1889.

Specimens examined. BRAZIL. CEARÁ: Lagoa do Tarrape, Bairro de Bemfria, Fortaleza, *Drouet 2244* (F, MO, NY); Ceará, *Freire Allamão 23849* (F); Tapera, *Pickel 402 B* (NY); Tapera, *Reiss 4023* (F); Fortaleza, *J. Huber 48* (F). TERR. RORAIMA: Dormida, foothills of Serra da Lua, *Prance et al. 9178 A* (F, NY). PARAHYBA: terrenos litoraneos arenosos, *Coelhode Toraes 2228* (NY, US). PIAUHY: prope Buritisaes towards Mocambo, *Martius 2504* (photo of type from M at F, NY). RIO BRANCO: Serra do Mel, *Ule 8327* (F). GUYANA: Rupununi: Manari, 3°28′N, 59°41′W, *Maas & Westra 3676* (NY, U). VENEZUELA. BOLÍVAR: Dtto. Cedeño, 74 km SW of Caicara del Orinoco, 7°10–15′N, 66°25–30°W, *Steyermark, Holst & Manara 131298* (MO, VEN); 22.5 km SW of Caicara del Orinoco, SW of Sacuima, 7°36′N, 66°15′W, *Steyermark, Holst & Manara 131226* (MO, VEN).

I wish to thank the curators of F, NY, and US for the loan of specimens. The work was completed during a grant from NSF (BSR-8515205).

LITERATURE CITED

SCHUMANN, K. 1889. Martius, Fl. Bras. 6(5): 271–273.

—Julian A. Steyermark, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.

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Cover illustration. *Prunus fortunensis* McPherson, by John Myers.

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REPRODUCTIVE BIOLOGY OF FRESHWATER AQUATIC ANGIOSPERMS: AN INTRODUCTION

Aquatic flowering plants have long held a special appeal for plant biologists. Many features of aquatics, such as convergent reduction of vascular systems and reproductive structures, vegetative polymorphism, widespread asexual propagation, and unusual pollination systems, contribute to some of the most perplexing phylogenetic, evolutionary, and taxonomic problems in angiosperm systematics. The study of the mode of operation and diversity of reproductive systems is fundamental to understanding the evolution of taxa, but unfortunately these systems continue to be less well known in aquatics than in terrestrial groups. In the now classic book, *The Biology of Aquatic Vascular Plants* (1967; Edward Arnold Publishers, Ltd., London), Sculthorpe reviewed the literature on reproductive systems of aquatic angiosperms. There have been significant contributions to our understanding during the 20 years since Sculthorpe's book; the purpose of this series of papers is to present some of these contributions.

Invasion of the aquatic habitat has occurred numerous times throughout angiosperm evolution. A diverse array of monocot and dicot taxa are "aquatic," although the precise definition of the term can be debated. Differences of opinion notwithstanding, approximately 18 monocot and 10 dicot families comprise principally aquatic members. In addition, there are numerous examples of aquatic genera in largely terrestrial families (e.g., *Pistia, Orontium, Peltandra,* Araceae; *Armoracia, Cardamine,* Cruciferae; *Megalodonta,* Asteraceae) and aquatic species in otherwise terrestrial genera (e.g., various species of *Polygonum,* Polygonaceae). The greatest diversity of aquatic angiosperms is found in freshwater environments: 104 genera (ca. 90%) in the principally aquatic families occur in freshwater, whereas only 12 genera are marine. The high frequency of freshwater aquatics could well reflect the comparative ease of adapting to freshwater versus marine conditions.

"It is in their reproductive phase that vascular hydrophytes betray their terrestrial ancestry most clearly." This statement by Sculthorpe (1967) illustrates an obvious aspect of aquatic angiosperms: the vast majority produce aerial flowers and share general features of pollination with their terrestrial counterparts. The evolutionary or perhaps phylogenetic constraint to retain aerial flowers is especially well illustrated in *Utricularia* (Lentibulariaceae), where aerial flowers are produced even though the rest of the plant is submerged and highly modified for life under water.

There can be little question that the aquatic environment imposes a strong and unique set of physical and biotic constraints on its inhabitants. For instance, the high specific heat of water, manifested in slow vernal warming and autumnal cooling, undoubtedly influences flowering patterns as well as the spectrum and availability of pollen vec-

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tors. Thus, it is not unreasonable to expect reproductive patterns or "strategies" in aquatics that are different from those of terrestrial plants. These expectations are best realized in taxa that exhibit hydrophilous pollination systems. In hydrophily, a suite of characters has evolved that allow for the aquatic medium itself to play an intimate role in pollen transfer; these reflect strong evolutionary concessions to life in the aquatic milieu. This plethora of specialized features makes phylogenetic and evolutionary interpretations of hydrophilous taxa difficult because affinities with any presumably ancestral, aerial pollination systems are obscured. Few such reproductive patterns have been deciphered in aerial-flowered aquatics, where much of our understanding derives from the general similarity with terrestrial relatives. The role that flower production in close proximity to the water has played in molding reproductive systems is seldom addressed; we possess limited insight into reproductive features of aerial flowers that are consequential to an aquatic existence.

This series of papers covers a range of topics concerning reproductive systems in aquatic angiosperms. Barrett and Ornduff consider evolutionary aspects of heterostyly in *Eichornia* (Pontederiaceae) and *Villarsia* (Menyanthaceae), respectively. The importance of anemophily is addressed in two contributions: Cook presents an overview of anemophilous aquatic taxa, and Osborn & Schneider discuss the evolution of anemophily from entomophilous systems in *Brasenia* (Nymphaeaceae). Wiersema surveys the diversity of reproductive strategies in *Nymphaea* (Nymphaeaceae), and Haynes addresses the importance of reproductive systems and how they pertain to the problem of aquatic weeds. Papers by Cox & Knox, Les, and Philbrick present various aspects of the evolution and diversity of hydrophilous breeding systems. Cox & Knox present evidence for the importance of two-dimensional pollination in *Amphibolis antarctica* (Potamogetonaceae) and *Ruppia polycarpa* (Ruppiaceae). Possible relationships between hydrophily, genetic variability, and evolution are addressed by Les, and in the last contribution, Philbrick proposes a hypothesis for the evolution of underwater outcrossing from aerial pollination systems.

These papers were presented at the annual meeting of The Botanical Society of America and The American Society of Plant Taxonomists, The Ohio State University, Columbus, Ohio, August 1987. The contents of the published papers may be modified from the oral presentations. Financial support for the symposium was provided in part by The Botanical Society of America.

—*C. Thomas Philbrick, Department of Ecology and Evolutionary Biology, U-43, The University of Connecticut, Storrs, Connecticut 06268, U.S.A.*

EVOLUTION OF BREEDING SYSTEMS IN *EICHHORNIA* (PONTEDERIACEAE): A REVIEW[1]

Spencer C. H. Barrett[2]

ABSTRACT

Eichhornia *is of New World origin and comprises eight species of freshwater aquatics in the monocotyledonous family Pontederiaceae.* Eichhornia *flowers display a broad range of morphological specializations associated with their pollination mechanisms and breeding systems. These range from large-flowered, outcrossing, tristylous populations to small-flowered, predominantly self-fertilizing, semi-homostylous populations. Two sources of evidence indicate that the major pathway of breeding system evolution in the genus involves the repeated breakdown of tristyly to give rise to selfing semi-homostylous populations: the occurrence of semi-homostylous forms in each of the primarily tristylous species (*E. azurea, E. crassipes, E. paniculata*) and the presence of residual heteromorphisms, associated with the tristylous syndrome, in the largely autogamous semihomostylous species (*E. diversifolia, E. heterosperma, E. paradoxa*). It is suggested that genetic bottlenecks associated with long-distance dispersal and colonization of aquatic habitats with uncertain moisture regimes play major roles in disrupting the maintenance of tristyly. This leads to the breakdown of the polymorphism and the evolution of semi-homostyly.*

Eichhornia (Pontederiaceae) is a small genus comprised of eight species of freshwater aquatics and palustrial herbs. All species, with the exception of the exclusively African *E. natans*, are native to the New World tropics. *Eichhornia azurea* and *E. paniculata* are used as pond ornamentals, and *E. crassipes* (water hyacinth) has spread, with man's aid, from lowland tropical South America to become one of the world's most noxious aquatic weeds.

The flowers of *Eichhornia* are usually mauve-blue and showy, and are pollinated primarily by bees and butterflies. They display a broad range of morphological specializations associated with their pollination mechanisms and breeding systems. The variation ranges from large multicolored tristylous flowers adapted to outcrossing to small uniformly colored self-fertilizing homostylous flowers. This diversity provides suitable experimental material for studies of breeding system evolution. The present review summarizes work on this topic with special attention to the evolutionary breakdown of tristyly and the responsible ecological and genetic factors.

Heterostyly is a genetically controlled floral polymorphism in which plant populations contain two (distyly) or three (tristyly) morphs that differ primarily in style and stamen length, pollen size, and incompatibility behavior. The polymorphism promotes disassortative mating between the floral morphs and is reliably reported from 24 angiosperm families of which just three (Lythraceae, Oxalidaceae, Pontederiaceae) contain tristylous members (Ganders, 1979). A common feature of heterostylous breeding systems is their propensity to become evolutionarily modified in the direction of increased self-fertilization. The main pathway is by the formation of self-compatible homostyles. Plants in these groups possess anthers and stigmas at the same level within a flower and, as a result, are largely autogamous. In tristylous species homostyles often have only one of their two anther sets adjacent to the stigma and as a result are referred to as semi-homostylous (Stout, 1925; Ornduff, 1972). The breakdown of heterostyly to homostyly represents a paradigm for studies of the evolution of self-fertilization in plants, because the direction of change is readily interpretable, genetic modifications are often simply inherited, and alterations in the floral polymorphisms that influence mating behavior can usually be detected without difficulty under field conditions (Barrett, 1988a).

We have investigated the pathways and mechanisms of breeding system evolution in *Eichhornia*

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[1] *I thank Jim Eckenwalder, Jennifer Richards, Tim Dickinson, Steve Price, Jan Anderson, Lorne Wolfe, Deborah Glover, Joel Shore, Robin Scribailo, Brian Husband, Martin Morgan, Peter Toppings, Petra Donnelly, and Chris Eckert for advice and assistance; Elizabeth Campolin for drawing the figures; and the Natural Sciences and Engineering Research Council of Canada for financial support.*

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by adopting the comparative approach employed by many plant systematists and evolutionists (e.g., Stebbins, 1957; Baker, 1966; Grant & Grant, 1965; Lloyd, 1965; Moore & Lewis, 1965; Raven, 1979). Here the working hypothesis is that among closely related taxa of outcrossers and selfers the former condition is usually ancestral and the latter derived. Stebbins (1974) has argued that this pathway has been followed by more lines of evolution in the flowering plants than has any other.

To test this hypothesis in *Eichhornia* two types of evidence were sought. Population studies of outcrossing taxa were conducted to establish whether, under present conditions, the shift from outcrossing to selfing is occurring. Of primary importance in these studies is to determine whether genetically based differences in mating patterns occur both within and between populations of the tristylous taxa. A second line of enquiry has involved interspecific studies of the floral biology of selfing taxa to discover whether residual tristylic traits are evident (see Crowe, 1964). Their occurrence can be taken as evidence of descent from tristylous ancestors, unless we are prepared to accept that tristyly is in *statu nascendi* within different selfing lineages of the genus. Given the rarity of the polymorphism in the angiosperms as a whole, this evolutionary scenario seems unlikely (see Eckenwalder & Barrett, 1986).

This review summarizes evidence in favor of the derived nature of selfing taxa and evaluates several hypotheses concerned with the selective mechanisms responsible for the breakdown of tristyly. Before this is done, however, a brief summary of the systematic and ecological characteristics of the genus is required.

SYSTEMATICS AND ECOLOGY

Taxonomy. Most floristic works and regional floras follow Solms-Laubach (1883) and Schwartz (1927, 1930) in their treatments of *Eichhornia* (e.g., Alexander, 1937; Schulz, 1942; Castellanos, 1958; Agostini, 1974; Rosatti, 1987). Schwartz recognized two sections in the genus, the primitive *Protoeichhornia* composed of *E. paniculata* and *E. paradoxa*, and the more advanced *Eichhornia* ("*Eueichhornia*") containing *E. azurea*, *E. crassipes*, *E. natans*, and *E. diversifolia*. More recently, two frequently overlooked species, *E. heterosperma* and *E. meyeri*, have come to be recognized. *Eichhornia heterosperma*, first described in 1939 from Venezuela by Alexander (Smith, 1939) and very similar in vegetative traits to *E. azurea*, is widely distributed in Central and South America and is misidentified in most collections (Horn, 1987). Similarly, *E. meyeri* has most often been treated as a synonym of *E. paniculata*, which it resembles closely. It is known from a few localities in Paraguay and from the type locality in the Chaco of Argentina (Schulz, 1942).

Phylogeny. A recent cladistic analysis of the Pontederiaceae by Eckenwalder & Barrett (1986) is of interest because most cladograms produced were in conflict with Schwartz's sectional treatment of *Eichhornia* and the genus was paraphyletic under most methods of cladogram construction. Of particular relevance to breeding system evolution was the placement of tristylous and homostylous taxa. Two contrasting patterns emerged from the analyses, neither of which is supported by microevolutionary studies presented below. Most cladograms separated homostylous species of *Eichhornia* as a clade not closely associated with tristylous *Eichhornia* and *Pontederia* but allied instead to *Heteranthera*. This seems unacceptable because of the clear relationships among species such as *E. azurea* (tristylous) and *E. heterosperma* (homostylous), and *E. paniculata* (tristylous) and *E. meyeri* (homostylous). A second pattern derived homostylous taxa from tristylous ancestors, but in this case all homostylous taxa were united as a monophyletic group implying a single origin for homostyly. However, evidence presented below indicates that tristyly has broken down repeatedly within *Eichhornia*, implying multiple origins for homostyly in the genus. These disparities probably result from the choice of characters used in cladogram construction. The parallel evolution of the selfing syndrome in different homostylous taxa may provide enough characters to unite species during tree construction. This difficulty has been recently discussed at length by Wyatt (1988) in his review of phylogenetic aspects of the evolution of self-pollination.

Genetic systems. Breeding systems and chromosome numbers of *Eichhornia* species are given in Table 1. Three of the eight species are primarily tristylous, and the remaining five are semi-homostylous. However, because of considerable intraspecific variation in floral traits, it is important to note that these terms refer to the most common condition within each species. In *Eichhornia* polyploidy and aneuploidy are derived from an original base number of $x = 8$. Unlike other heterostylous groups (e.g., *Turnera ulmifolia* L., Barrett & Shore, 1987), there is no evidence of an association between breeding system and ploidal level. Tristyly and semi-homostyly occur at the diploid and tetraploid level.

TABLE 1. *Genetic systems, life forms, and distributions of* Eichhornia *species. Breeding systems indicated are the most common condition within each species.*

Taxon	Major Breeding System	Chromosome Number (n)	Life Form	Clonal Propagation	Native Distribution
E. azurea (Swartz) Kunth	tristylous	16	floating-leaved aquatic, long-lived perennial	++	widespread, Neotropics
E. crassipes (Mart.) Solms-Laub.	tristylous	16	free-floating aquatic, long-lived perennial	+++	widespread, lowland South America
E. paniculata (Spreng.) Solms-Laub.	tristylous	8	emergent aquatic, short-lived perennial or annual	−	locally abundant, northeast Brazil, Cuba, Jamaica, Nicaragua, Ecuador
E. heterosperma Alex.	semi-homostylous	15	floating-leaved aquatic, perennial	++	widespread, Neotropics
E. diversifolia (Vahl) Urb.	semi-homostylous	15	floating-leaved aquatic, perennial or annual	+	widespread, Neotropics
E. natans (Beauv.) Solms-Laub.	semi-homostylous?	—	floating-leaved aquatic, perennial or annual	+	widespread, Africa
E. paradoxa (Mart.) Solms-Laub.	semi-homostylous	8	emergent aquatic, annual	−	rare, Guatemala, Venezuela, Brazil
E. meyeri Schulz	semi-homostylous?	8	emergent aquatic, annual	−	rare, Paraguay, Argentina

Distribution. The three diploids of *Eichhornia* have narrower distributions than the tetraploids (Table 1) have. In particular, *E. paradoxa* and *E. meyeri* are rare with relatively few known localities. The distribution patterns of the three diploids support Schwartz's (1927) view that the species are phylogenetically old and that their current distributions may represent relict areas of previously wider ranges. The remaining New World *Eichhornia* species all have widespread distributions throughout lowland South America, Central America, and parts of the Caribbean. Unlike the diploids, which are annual or short-lived perennial emergent aquatics with no clonal propagation, all tetraploids exhibit extensive lateral growth either through a branching internode system or by stolons. Fragmentation facilitates clonal regeneration, and all tetraploid species, particularly *E. crassipes*, are capable of prolific vegetative spread. The ability to disperse by seeds and floating vegetative fragments may contribute to the wider distributions of tetraploid than diploid taxa.

The Pontederiaceae are of New World origin with all but one species of *Eichhornia* native to the Neotropics. The African *Eichhornia natans* is likely descended from New World ancestors following long-distance dispersal. Its homostylous breeding system would favor establishment and subsequent spread in Africa following long-distance dispersal from the New World. The most likely progenitor of *E. natans* is *E. diversifolia*, which is very similar in appearance and has been considered conspecific by some taxonomists. The small seeds of *Eichhornia* species and their occurrence in habitats frequented by migratory water birds provide opportunities for long-distance dispersal. This may account for the disjunct and scattered distributions of many of the species.

Ecology and life history. There have been no detailed ecological studies of the life history, demography, or habitat preferences of *Eichhornia* species in their native ranges. The following field observations, while rudimentary, may stimulate more in-depth work as well as providing the necessary ecological background from which to discuss the reproductive biology and evolution of breeding systems in the genus.

Eichhornia species are exclusively freshwater aquatics. They occupy a diversity of wetland habitats ranging from large water bodies, such as major river systems, lakes, and reservoirs, to extensive marshlands, seasonal pools, and low-lying pastures. Several species are also capable of colonizing sites disturbed by man, such as rice fields, irrigation canals, and drainage ditches. It is not uncommon to find two or three species of *Eichhornia* at the same site. Significant features of aquatic habitats that determine the presence of individual taxa appear to be permanency of the habitat, water level fluctuations, and overall water depth. These factors not only influence the type of regeneration strategy employed by *Eichhornia* species, but also the composition of the aquatic community and hence the degree of interspecific competition.

Eichhornia azurea is a large, long-lived, mat-forming perennial which most commonly occurs in permanent water bodies such as rivers, lakes, and extensive marshlands. The long duration of its pre-reproductive phase restricts the species from colonizing habitats subject to seasonal desiccation. The mat-forming *Eichhornia crassipes* possesses a similar ecology, although it is capable of reaching reproductive maturity more rapidly (Barrett, 1980a) and is often found in more seasonal environments. Unlike *E. azurea*, which is a rooted, floating-leaved aquatic, the free-floating *E. crassipes* is able to colonize environments that experience large fluctuations in water level (Barrett, 1977a, 1979). *Eichhornia heterosperma* commonly occurs in shallow lakes and ponds. Its abundance in the highly seasonal environments of the Llanos of Venezuela and in the caatinga of northeast Brazil indicates that it is capable of withstanding habitat desiccation, presumably as rhizomes or seed. *Eichhornia paniculata* occurs in seasonal pools, rice fields, and low-lying pastures. In comparison with the preceding species, it is capable of colonizing more terrestrial environments that experience only limited periods of inundation. The life history of *E. paniculata* depends largely on available moisture. When available for extended periods, plants perennate; however, at many locations in northeast Brazil and in Jamaica, populations are annual and regenerate from seed (Barrett, 1985a). An annual life history is also implicated for *E. meyeri* in the seasonal environment of the Chaco of Argentina (Schulz, 1942).

Owing to the rarity of *E. paradoxa*, little is known of its ecology. I have observed two populations in northeast Brazil. At one site in Paraiba state the species was growing in a roadside depression with *E. paniculata*; at the other location it occupied a low-lying floodplain of the São Francisco River. These observations suggest that the species prefers seasonally inundated sites.

Eichhornia diversifolia is most commonly found in seasonal ponds that experience large water-level fluctuations. During the vegetative growth period it is often in water 1–2 m deep, and as the water level drops, plants flower and mature seed. The species usually behaves as an annual and may require water-level fluctuations for successful seed germination and establishment. *Eichhornia diversifolia* colonizes rice fields and can be considered a fugitive species adapted to temporary aquatic environments. Habitat descriptions on herbarium specimens and flora accounts of *E. natans* in Africa suggest a similar ecology. The species is reported as a rice field weed in Nigeria (Vaillant, 1967).

Reproductive biology. The contrasting breeding systems and life histories of *Eichhornia* species are associated with diverse reproductive attributes (Table 2). In general, the outcrossing species possess large showy flowers, inflorescences with many flowers, high pollen–ovule ratios, and heavier seeds in comparison with selfing species. It is important to emphasize that each *Eichhornia* species shows considerable variation in reproductive traits. The values presented in Table 2 are from a single population of each species and were chosen to illustrate overall trends in reproductive traits among species. With the exception of data presented for *E. meyeri*, all values are based on field-grown plants. Exceptions to the trends discussed above are apparent, however, such as in *E. paniculata*, where individual flowers are similar in size to several of the selfing taxa. Inflorescences of this species contain many more flowers (up to 300) than other *Eichhornia* species so that the overall floral display of plants is by no means diminished because of their smaller flowers. Figure 1 illustrates the dramatic difference in floral display of tristylous *E. crassipes* and semi-homostylous *E. paradoxa*.

TRISTYLY IN THE PONTEDERIACEAE

The tristylous syndrome. To understand the evolutionary modifications of tristyly in the Pontederiaceae it is necessary to describe the morphological, physiological, and functional aspects of trimorphic incompatibility. Populations of tristylous plants are composed of three floral morphs known as the long-, mid-, and short-styled morphs (hereafter referred to as L, M, S). Each plant possesses flowers with two anther levels that correspond to the stigma levels in the remaining two morphs. Thus, as illustrated in Figure 2, there is a reciprocal positioning of anthers and stigmas in the three floral morphs. Pollinations between anthers and stigmas of equivalent height result in seed set and are termed "legitimate" following Darwin (1877). The remaining pollinations are referred to as "illegitimate" and result in little or no seed set.

A unique feature of tristylous plants is the pro-

TABLE 2. *Reproductive attributes of New World species of* Eichhornia. *Values are the mean for a representative population sample of each species sampled from the native range.* Eichhornia meyeri *glasshouse-grown plants.*

Taxon	Flower Breadth (in mm)	Number of Flowers per Inflorescence	Ovule Number per Flower	Pollen–Ovule Ratio	Seed Weight (mg)
E. azurea	44.0	46.2	169.7	204.0	1.062
E. crassipes	58.2	17.2	150.0	255.2	0.297
E. paniculata	24.0	82.0	109.7	192.2	0.147
E. heterosperma	16.1	6.8	134.0	60.7	1.104
E. diversifolia	20.6	3.8	225.5	43.2	0.074
E. paradoxa	17.6	2.0	172.8	37.9	0.083
E. meyeri	16.9	26.0	273.1	18.8	0.281

duction, by the two anther levels within a flower, of distinct pollen phenotypes that differ in their size and incompatibility behavior. Associated with pollen heteromorphism are differences in the amount of pollen produced by the three stamen levels. Long-level anthers produce small numbers of large-sized pollen grains; mid-level anthers produce intermediate amounts of mid-sized pollen grains; and short-sized anthers produce large numbers of small-sized pollen grains. Several other floral polymorphisms often accompany the stamen–style trimorphism (e.g., stigmatic papillae length, style coloration, pollen exine sculpturing). These traits often vary among taxa in their occurrence and expression.

Genetic studies of the inheritance of tristyly in the three tristylous families indicate that the most common mode of control is by two diallelic loci (*S*, *M*) with *S* epistatic to *M* (Fig. 2). With this genetic control and legitimate mating among the morphs, an isoplethic equilibrium (1 : 1 : 1) is the only possible condition in large populations, provided that the morphs are of equal fitness (Fisher, 1941, 1944; Heuch, 1979). This expectation provides a "standard" for a fully functional tristylous system, and surveys of style morph frequencies in natural populations can be viewed as the logical starting point for studies directed toward understanding the causes of modification in tristylous systems.

In no species of *Eichhornia* or *Pontederia*, the two tristylous genera of Pontederiaceae, does the expression of tristyly conform to all of the features described above. The tristylous syndrome of *Pontederia* most closely resembles this hypothetical state with the major departure involving the self-incompatibility system. In the four taxa of *Pontederia* that have been examined experimentally the M morph is moderately self-compatible when pollinated with pollen from long-level anthers, whereas incompatibility expression in the L and S morphs is considerably stronger (Ornduff, 1966; Barrett, 1977b; Glover & Barrett, 1983; Barrett & Anderson, 1985). The significance of this variation to the functioning of tristyly is unclear, since it is not associated with modifications in the stamen–style polymorphism or features of pollen trimorphism.

While trimorphic incompatibility is a stable feature of populations of *Pontederia* species (see Price & Barrett, 1982; Barrett et al., 1983), this is not the case in *Eichhornia*. Only in *E. azurea* do populations occur that possess self-incompatibility, strong pollen trimorphism, and the three style morphs (Barrett, 1978). Even in this species, however, monomorphic populations are common, and genetic modifications favoring self-fertilization occur in Central America. In the remaining tristylous taxa, self-compatibility occurs and is associated with weak heteromorphisms of pollen size. Differences in the degree of pollen heteromorphism among *Eichhornia* species are illustrated in Figure 3. The greatest difference in the mean size of pollen originating from the two anther levels within a flower occurs in the self-incompatible *E. azurea*. Differences are less evident in the two self-compatible tristylous species, *E. crassipes* and *E. paniculata*. In the remaining homostylous species there is evidence of slight differences in pollen size distributions in *E. heterosperma* and *E. diversifolia*, whereas in *E. paradoxa* pollen originating from the two anther levels is uniform in size.

Self-compatible tristyly. In the vast majority of heterostylous plants the floral polymorphisms are associated with a sporophytically controlled self-incompatibility system (Ganders, 1979). Absence of such a system in most *Eichhornia* species raises the issue as to whether illegitimate matings are frequent under field conditions and whether the stamen–style polymorphism functioning alone is effective at promoting disassortative mating among the floral morphs. Two studies involving

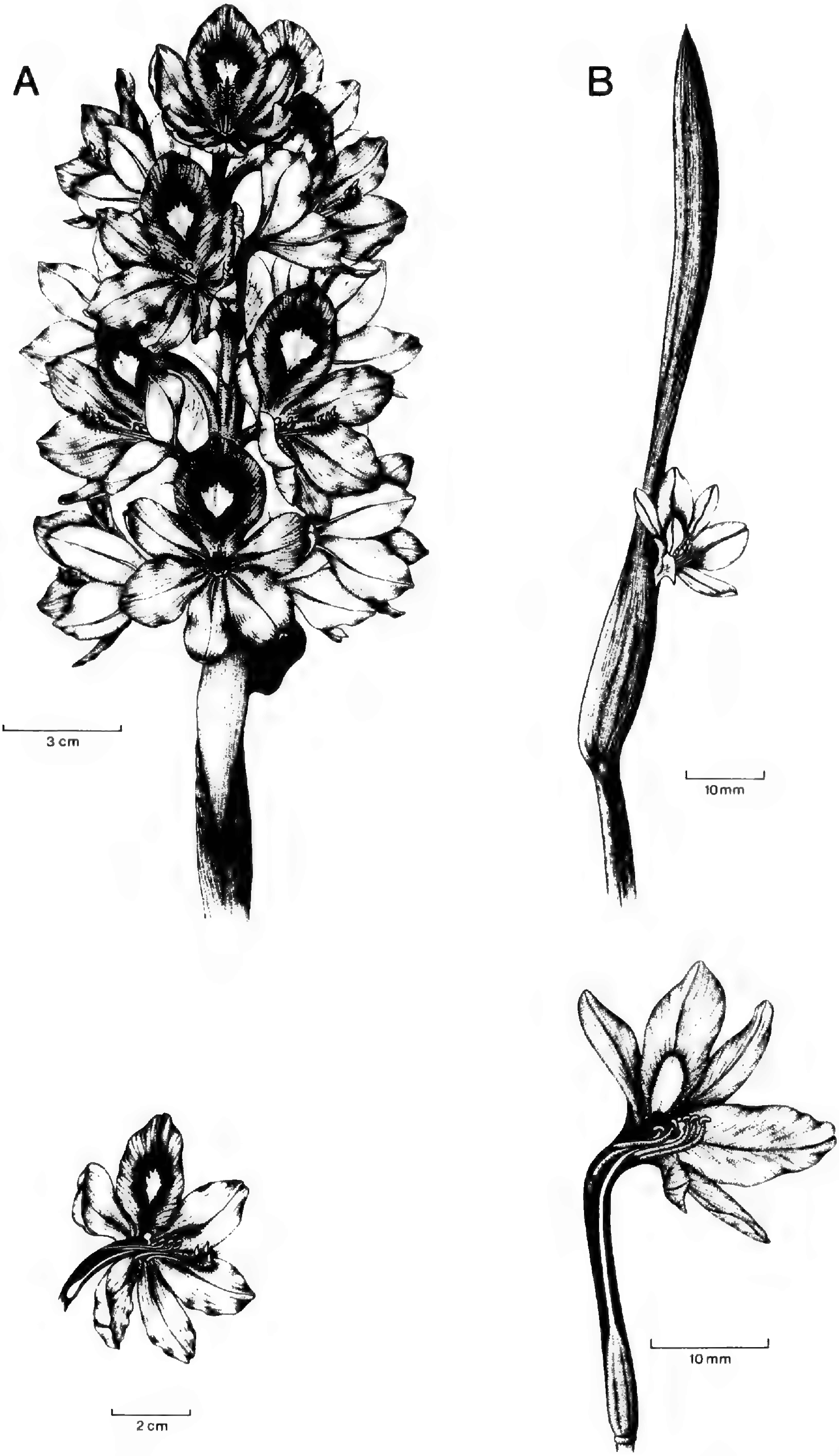

FIGURE 1. *Floral displays in a tristylous and a semi-homostylous species of* Eichhornia.—*A.* Eichhornia crassipes, *S morph from Boca de Jari, Lower Amazon, Brazil.*—*B.* E. paradoxa, *semi-homostylous M morph from Propriá, Sergipe, northeast Brazil.*

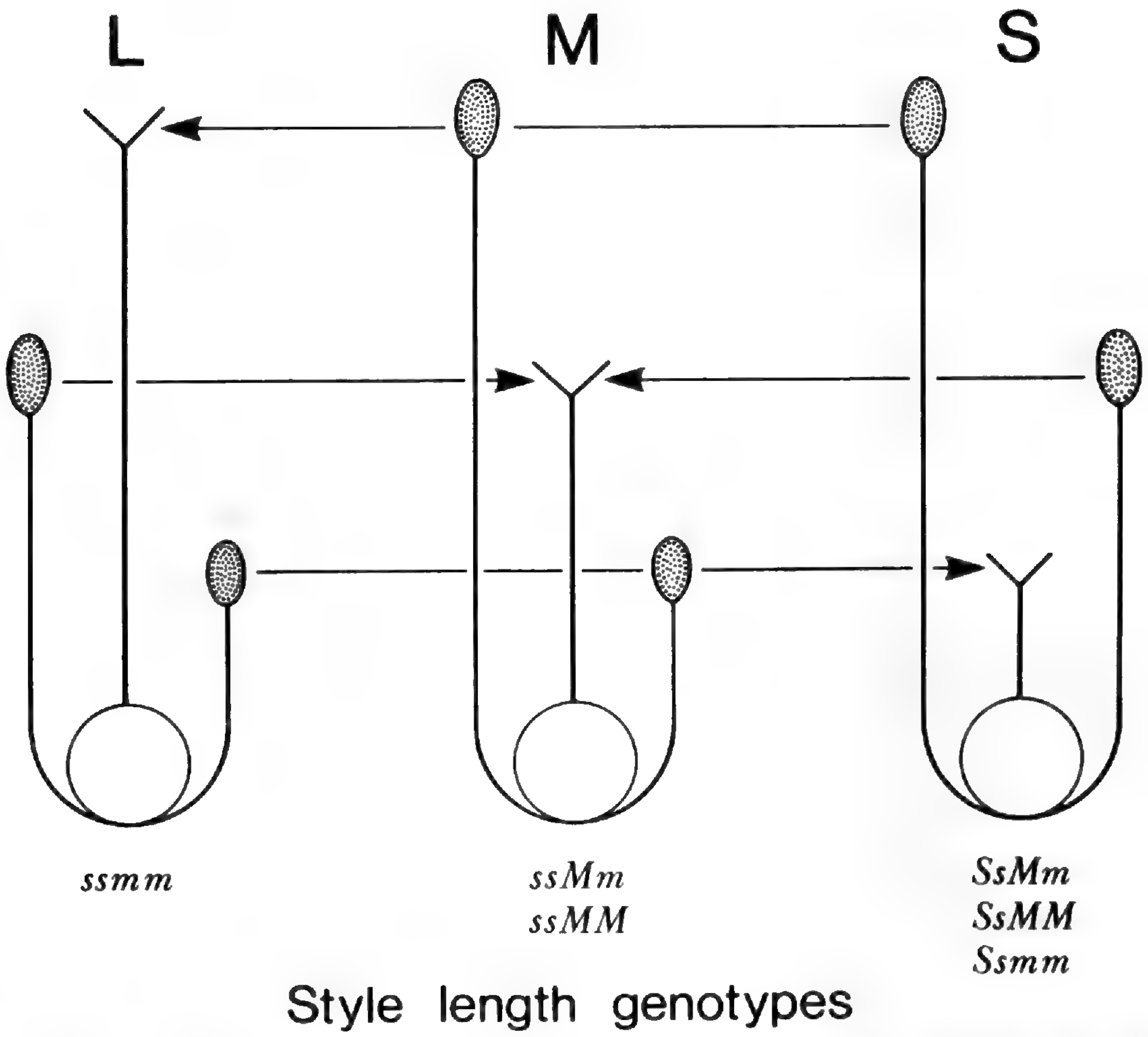

FIGURE 2. *Schematic diagram of the relative positions of styles and stamens in the floral morphs of a tristylous species. Legitimate pollinations are indicated by arrows. Genotypes of the floral morphs under the two-locus model (*S, M*) for the inheritance of tristyly in* Eichhornia *are shown.*

marker genes indicate that the mating system of floral morphs in self-compatible tristylous populations can involve a high level of outcrossing (Glover & Barrett, 1986a; Barrett et al., 1987). Progeny test data from *E. paniculata* (Table 3) reveal that the floral morphs are largely outcrossing and that most matings are disassortative in nature. This indicates that self and intramorph matings occur infrequently in this population. Such an effect could result from the operation of a cryptic heteromorphic incompatibility system of the type demonstrated in *Amsinckia* (Weller & Ornduff, 1977; Casper et al., 1988). However, this does not appear to be the case. In a controlled pollination experiment on *E. paniculata* that compared the competitive ability of self, illegitimately outcrossed, and legitimately outcrossed pollen, using the *GOT-3* marker locus, Glover & Barrett (1986a) found no evidence of a residual or cryptic trimorphic incompatibility system. Outcrossed progeny were always favored over selfed progeny irrespective of whether they were legitimate or illegitimate.

The results from *E. paniculata* are relevant to the question of whether self-compatibility in tristylous *Eichhornia* species is a derived condition involving relaxation of self-incompatibility. Following this view we might have anticipated some residual influence of the ancestral incompatibility system favoring legitimate over illegitimate matings. However, this was not detected, perhaps because the action of numerous modifier genes has removed all traces of the functional aspects of trimorphic incompatibility. The prepotency of cross-pollen over self-pollen might then be explained as a manifestation of inbreeding depression operating via extensive pollen–pistil interactions and genetically unrelated to the original incompatibility system (Barrett, 1988b).

Comparative evidence from other heterostylous families indicates that self-compatibility is commonly derived from self-incompatibility (Ganders, 1979). Most workers (e.g., Charlesworth & Charlesworth, 1979) have favored the idea that the evolution of self-incompatibility precedes the development of the stamen–style polymorphism in heterostylous groups (although see Richards, 1986).

Function of tristyly. Although the progeny test data from Recife demonstrate high levels of disassortative mating in *E. paniculata*, this does

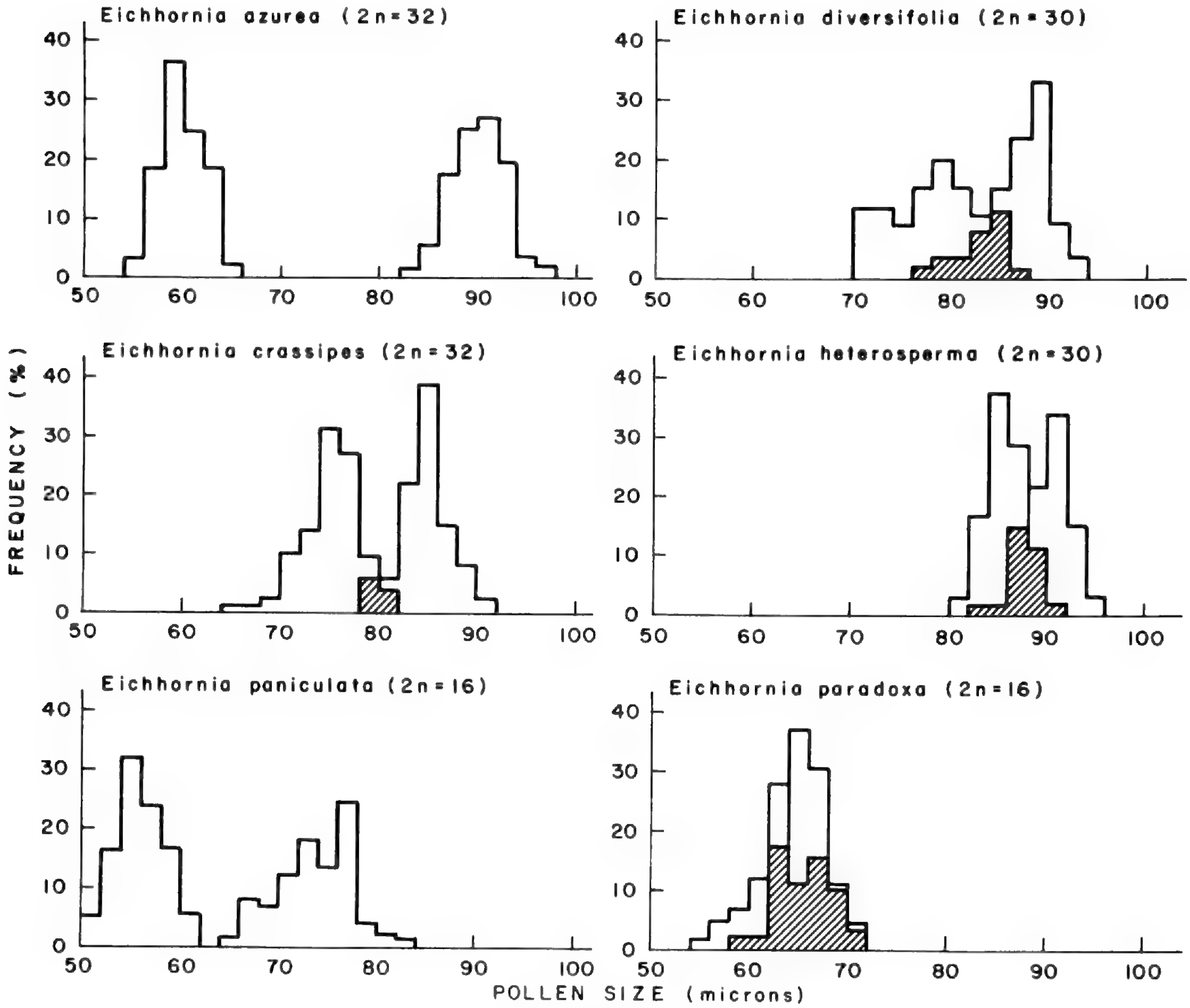

FIGURE 3. *Patterns of pollen-size heteromorphism in six species of* Eichhornia *with contrasting breeding systems. The distributions for each species were obtained by measuring the equatorial axis of 200 dry pollen grains originating from the two stamen levels of a flower. To facilitate comparisons among species, all measurements were conducted on the M morph (*E. azurea, E. crassipes, E. paniculata*) or semi-homostylous derivatives of the M morph (*E. diversifolia, E. heterosperma, E. paradoxa*). Note the overall differences in pollen size between diploid and tetraploid species.*

not prove that tristyly promotes legitimate pollination, as Darwin (1877) originally proposed. This is because in a self-compatible species intermorph illegitimate matings contribute towards estimates of disassortative mating. Using the progeny test method, it is not possible to distinguish between cross-pollinations involving legitimate and illegitimate pollen that originate from the same plant (Barrett et al., 1987). However, in some heterostylous species, these pollen types differ in size, and it is therefore possible to measure the magnitude of legitimate and illegitimate pollination in natural populations by inspecting the pollen loads of open-pollinated stigmas (Ganders, 1979). The extensive overlap in the size of pollen that originates from different anther levels of self-compatible *Eichhornia* species (Fig. 3) precludes this method. However, stigmatic pollen loads have been examined in *Pontederia* species, where size trimorphism is well developed, and significant levels of legitimate pollination were recorded in several natural populations (Glover & Barrett, 1983, 1986b; Price & Barrett, 1984; Barrett & Glover, 1985). These studies therefore provide support for the Darwinian hypothesis of the adaptive significance of tristyly.

BREAKDOWN OF TRISTYLY

Disruption of population structure. For tristyly to function effectively, populations should contain the three floral morphs and provide sufficient pollen and nectar rewards to attract specialized long-tongued pollinators, usually bees. Several influences can disrupt population structure to yield populations composed of one or two morphs. In *E. crassipes* and *E. azurea*, founder effects and rampant clonal propagation are major disruptive influences on tristyly. This is well illustrated by the geographical distribution of floral morphs in *E. crassipes* (Fig. 4). The S morph is absent from many parts of the New World range as well as from the Old World. In the latter case genotypes of the S morph were not among clones transported to the Old World by man. The M morph predominates in most regions, while the L morph appears sporadically (Barrett, 1977a). In a survey of 196 sites throughout the New World range of *E. crassipes*, Barrett & Forno (1982) found that 77% of the colonies located were monomorphic for style length, 18.4% were dimorphic, and only 4.6% were trimorphic. The rarity of *E. crassipes* populations containing the three floral morphs results from the high dispersal of the free-floating life form coupled with rapid clonal propagation. These factors result in inequalities of representation of founding genotypes. In addition, the short-lived nature of many populations and ecological restrictions on seedling establishment (Barrett, 1980a, b) retard further progress toward isoplethic population structure.

Founder events have also played a disruptive effect on the maintenance of tristyly in *E. paniculata*. Although clonal propagation is absent from this species, repeated colonizing episodes and stochastic influences on population size play a major role in determining morph frequencies in populations. Surveys of population structure in northeast Brazil and Jamaica (Barrett, 1985b and unpubl. data) have revealed a pattern reminiscent of that found in *E. crassipes* (Table 4). The S morph is absent from Jamaica and underrepresented in many populations from Brazil. The M morph predominates in dimorphic populations and, with one exception (see below), is the only morph that has been observed in monomorphic populations.

Absence of the S morph from parts of the range of *E. crassipes* and *E. paniculata* and its underrepresentation in Brazilian populations of *E. paniculata* may be explained by founder events and fluctuations in population size. Since both species are highly self-compatible, polymorphic populations can arise from selfing and segregation of genotypes heterozygous at the *S* and *M* loci. However, since the dominant *S* allele governing the expression of short styles is only carried by the S morph, separate introduction(s) of this morph are necessary for it to become established in a region. In contrast, the *m* allele can be carried by all three morphs and the *M* allele by the M and S morphs. Computer simulation studies by Heuch (1980) on the effects of random fluctuations of population size in tristylous systems confirm that the S morph is most often lost from populations. The same processes, on a neighborhood scale, may also account for the low average frequency of the S morph in trimorphic populations of *E. paniculata* (Table 4). Thus a genetic constraint imposed by the inheritance of tristyly interacting with random ecological processes plays a major role in disrupting the maintenance of population trimorphism.

TABLE 3. *Estimates of the mating system of floral morphs in a tristylous population (B5) of* Eichhornia paniculata *at Recife, northeast Brazil. Outcrossing rates and levels of disassortative mating were estimated from open-pollinated progeny arrays using six isozyme loci or the two loci governing style length, respectively. After Glover & Barrett (1986a) and Barrett et al. (1987).*

Measurement	Floral Morphs L	M	S
Outcrossing rate	0.98	0.97	0.93
N	480	520	480
Standard error	0.021	0.018	0.022
Disassortative mating	0.90	0.93	0.83
N	652	721	665
Standard error	0.034	0.052	0.052

Disruptions of trimorphic population structure in *Eichhornia* may not necessarily lead to genetic modifications of the breeding system. In *E. azurea* and *E. crassipes*, clonal regeneration and the low frequency of sexual reproduction in many monomorphic and dimorphic populations limit opportunities for evolutionary change. However, under conditions where sexual reproduction is favored, e.g., in strongly seasonal aquatic environments, there may be strong selection pressures to increase fecundity, particularly if pollinating agents are scarce (Barrett, 1979).

Semi-homostyle formation. In each of the three tristylous species of *Eichhornia* there is evidence of the breakdown of tristyly and the evolution of semi-homostyly (Barrett, 1978, 1979, 1985a). Semi-homostyles in *Eichhornia* occur primarily at the geographical margins of the neotropical ranges of species either as local populations (*E. azurea*, *E. paniculata*) or as variants in otherwise unmodified population systems (*E. crassipes*). In each species, semi-homostyles are highly autogamous be-

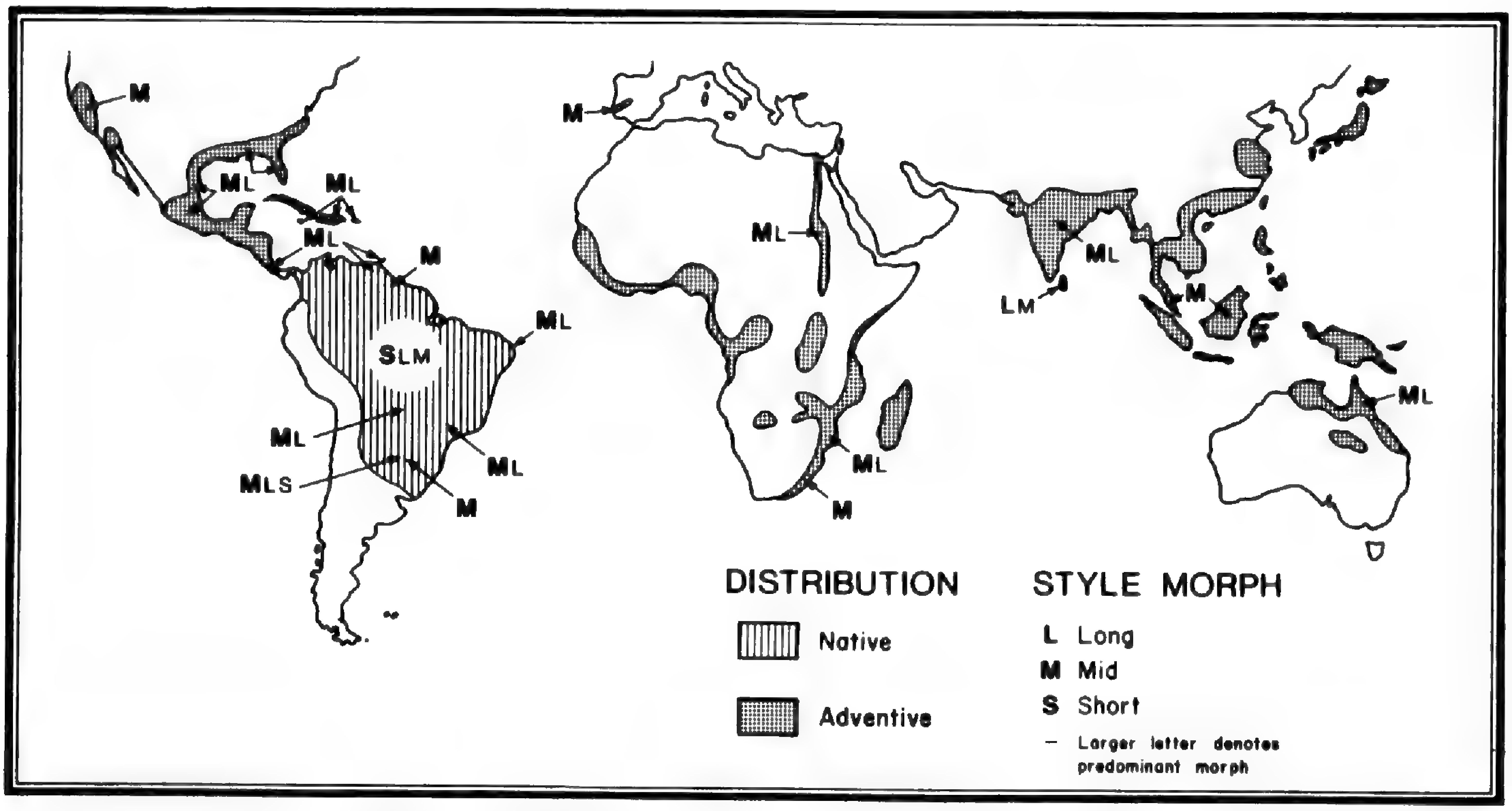

FIGURE 4. *The geographical distribution of style morphs in* Eichhornia crassipes. *Modified from Barrett (1977a) and Barrett & Forno (1982).*

cause of the close juxtaposition of stigmas and anthers.

In *E. azurea* and *E. paniculata*, semi-homostylous populations differ from their outcrossing progenitors in several floral traits. They often possess smaller, less showy flowers, reduced numbers of flowers per inflorescence, weak pollen heteromorphism, and lower pollen–ovule ratios. As described above, these differences parallel those that distinguish outcrossing and selfing species of *Eichhornia* (Table 2). This point is well illustrated by comparing the degree of pollen heteromorphism displayed by populations of *E. paniculata* with contrasting mating systems (Fig. 5). The difference in size of pollen produced by contrasting stamen levels is large in tristylous populations, whereas dimorphic and monomorphic populations show increasing pollen-size overlap. The weakening of pollen heteromorphism accompanying the evolution of semi-homostyly probably reflects relaxed selection pressures and the random accumulation of small mutations affecting pollen size. These patterns suggest that pollen size is a canalized trait in outcrossing populations and that heteromorphism is maintained by strong stabilizing selection. The functional significance of pollen-size heteromorphism to pollen–pistil interaction in heterostylous species is still a matter of some conjecture (see Ganders, 1979).

Semi-homostylous variants are most common in *E. paniculata*. They predominate in Jamaica and are frequently encountered in dimorphic and monomorphic populations in northeast Brazil. In tristylous populations, however, they occur rarely, suggesting some selective disadvantage. The development of semi-homostyly in *E. paniculata* occurs most commonly in the M morph (Fig. 6), with populations displaying various floral modifications in different parts of the range of the species (Barrett, 1985a). This suggests that the breakdown of tristyly is occurring repeatedly in the species. Semi-homostylous variants in *E. paniculata* are not exclusively derived from the M morph. Occasionally, modified L plants are encountered in populations from northeast Brazil, and material from

TABLE 4. *Average frequencies of the floral morphs in populations of* Eichhornia paniculata *from northeast Brazil and Jamaica. The majority of M plants in nontrimorphic populations exhibit modifications of the short-level stamens (see text).*

Region	Number of Populations Sampled	Frequencies L	M	S
Northeast Brazil				
Trimorphic	58	0.374	0.370	0.256
Dimorphic	21	0.336	0.664	—
Monomorphic	5	—	1.00	—
Jamaica				
Dimorphic	7	0.211	0.789	—
Monomorphic	19	—	1.00	—

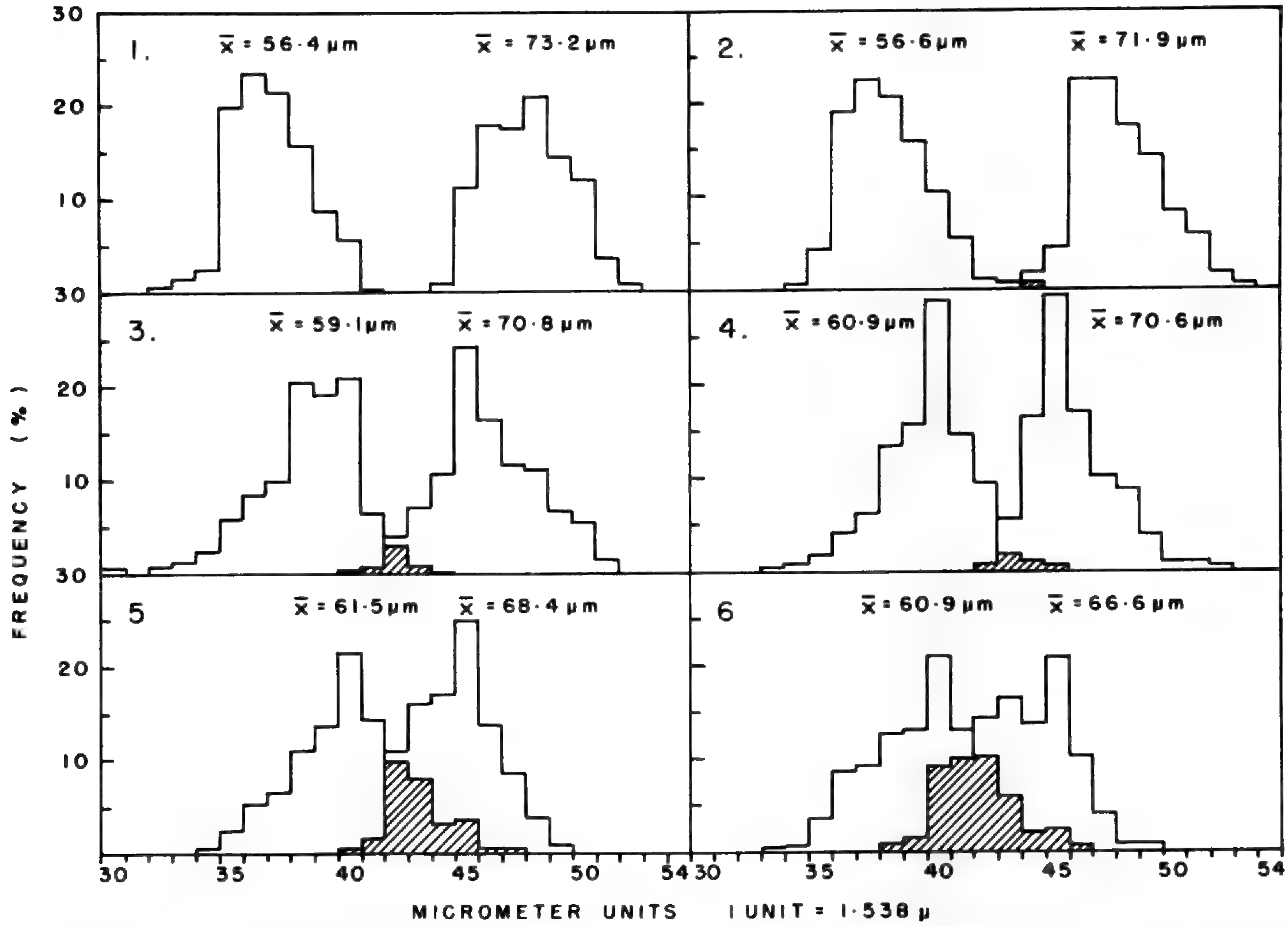

FIGURE 5. *Patterns of pollen-size heteromorphism in six populations of* Eichhornia paniculata *with contrasting breeding systems. The distributions for each population were obtained by measuring the equatorial axis of 200 dry pollen grains originating from the two stamen levels of a flower. To facilitate comparisons among populations, all measurements were conducted on six flowers from six plants of the M morph in each population. Plants of the M morph in nontristylous populations possessed varying degrees of genetic modification of the short stamen level (see text for details). Populations 1–4 are from northeast Brazil, populations 5 and 6 are from Jamaica. Populations 1 and 2 are trimorphic, 3 is dimorphic (L, M), and 4–6 are monomorphic (M).*

the only reported occurrence of the species in Central America (*Haynes 8442, 8603,* (ALU) Rio Las Lajas, Department of Rivas, Nicaragua) is composed exclusively of semi-homostylous long-styled plants. Ongoing genetic and developmental studies (Richards & Barrett, 1984 and unpubl. data) of the range of semi-homostylous variants in *E. paniculata* are aimed at determining the inheritance patterns and developmental pathways responsible for the breakdown of tristyly in the species.

In *E. crassipes* semi-homostyle formation is apparently rare. I have observed semi-homostyles in only two populations. Both were dimorphic (L, M), and in each case the modified phenotypes only differed from unmodified forms in the relative lengths of their reproductive parts (Barrett, 1979 and unpubl. data). If these phenotypes became reproductively isolated from their unmodified progenitors, it is likely that genetic modifications in other aspects of their reproductive biology would occur.

The reported semi-homostyles in a population of *E. crassipes* from Costa Rica are also modified forms of the M morph (Barrett, 1979). However, in contrast to *E. paniculata,* where alterations involve elongation of short-level stamens, the breakdown of herkogamy in this population of *E. crassipes* is primarily the result of shortening of long-level stamens. This indicates that a different developmental pathway is involved. In addition, the recent discovery in *E. crassipes* of a semi-homostylous L morph in northeast Brazil (S. C. H. Barrett, unpubl. data) indicates that, in common with *E. paniculata,* semi-homostyle formation can occur in both M and L morphs.

The arrangement of reproductive organs in semi-homostylous populations of *E. azurea* suggests that they are M variants with elongated short-level stamens (Barrett, 1978 and unpubl. data). Why the M morph of *Eichhornia* species appears to be more prone than other morphs to genetic modifications favoring increased levels of self-fertilization

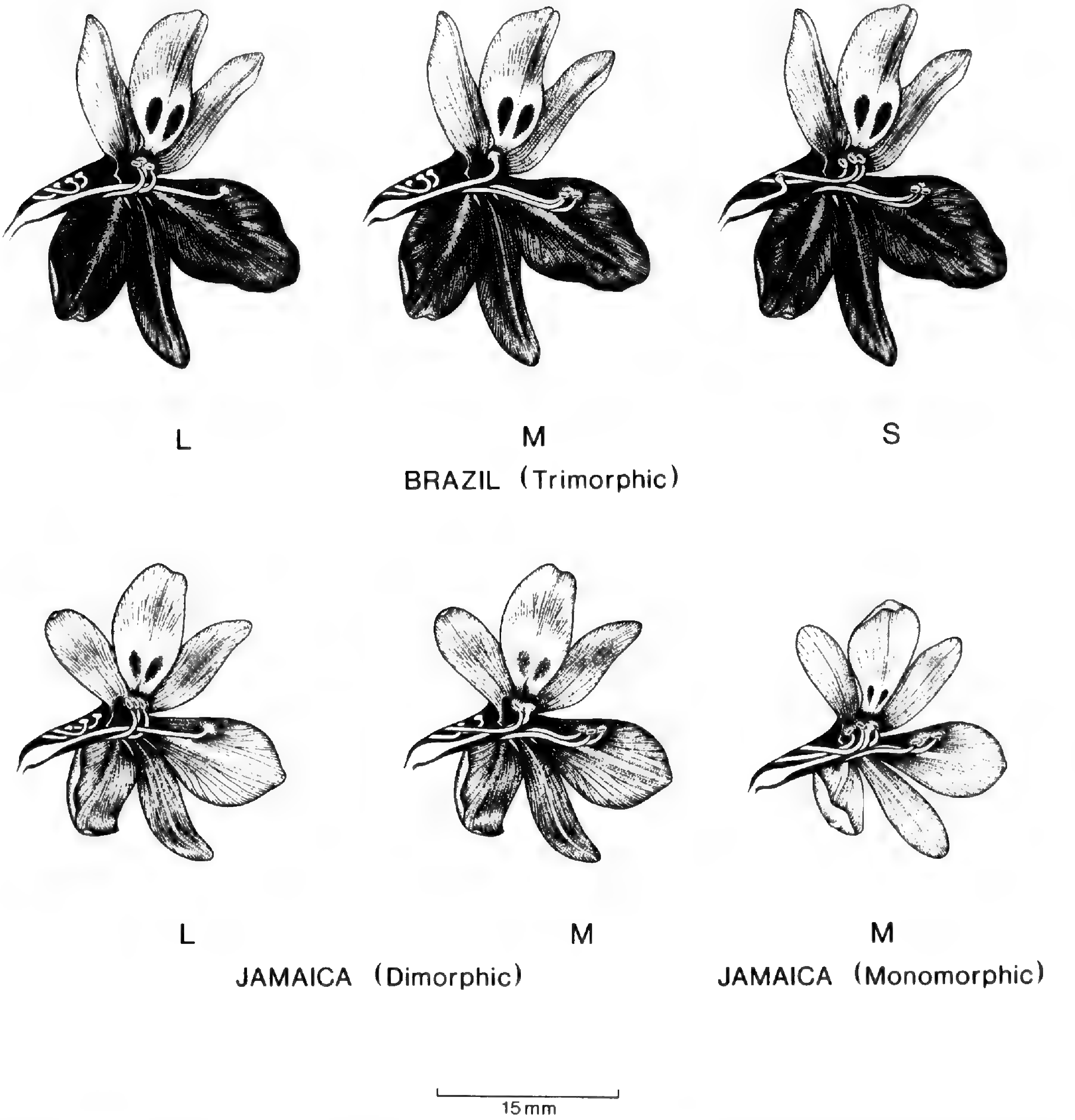

FIGURE 6. *The evolutionary breakdown of tristyly to semi-homostyly in* Eichhornia paniculata. *Flowers of the L, M, and S morphs from an outcrossing trimorphic population (B5) are contrasted with two semi-homostylous M variants from Jamaica (dimorphic J15, monomorphic J3). The semi-homostylous M variants differ from one another in the number of short-level stamens (1 versus 3) that are adjacent to the mid-level stigma. No stamen modifications of the L morph occur in dimorphic populations from Jamaica. For further details see Barrett (1985a) and Glover & Barrett (1986a).*

is not clear but may be associated with differences in the development and floral architecture of the morphs. In the Lythraceae and Oxalidaceae, semi-homostyly also appears to occur more commonly in the M morph (Stout, 1925; Ornduff, 1972).

The establishment of semi-homostyly in tristylous species of *Eichhornia* demonstrates that when selection pressures that maintain outcrossing are relaxed or changed in direction, the complex syndrome of traits that constitute the tristylous syndrome can rapidly break down towards increased self-fertilization. Furthermore, the wide range of semi-homostylous variants that occur in *E. paniculata* suggests that the processes responsible for the dissolution of floral polymorphism are still active in contemporary populations. This provides an opportunity to investigate directly the selection pressures acting on the mating system and to determine the ecological and genetic conditions that favor the evolution of self-fertilization. *Eichhornia paniculata* is particularly favorable for such studies because it possesses a short life

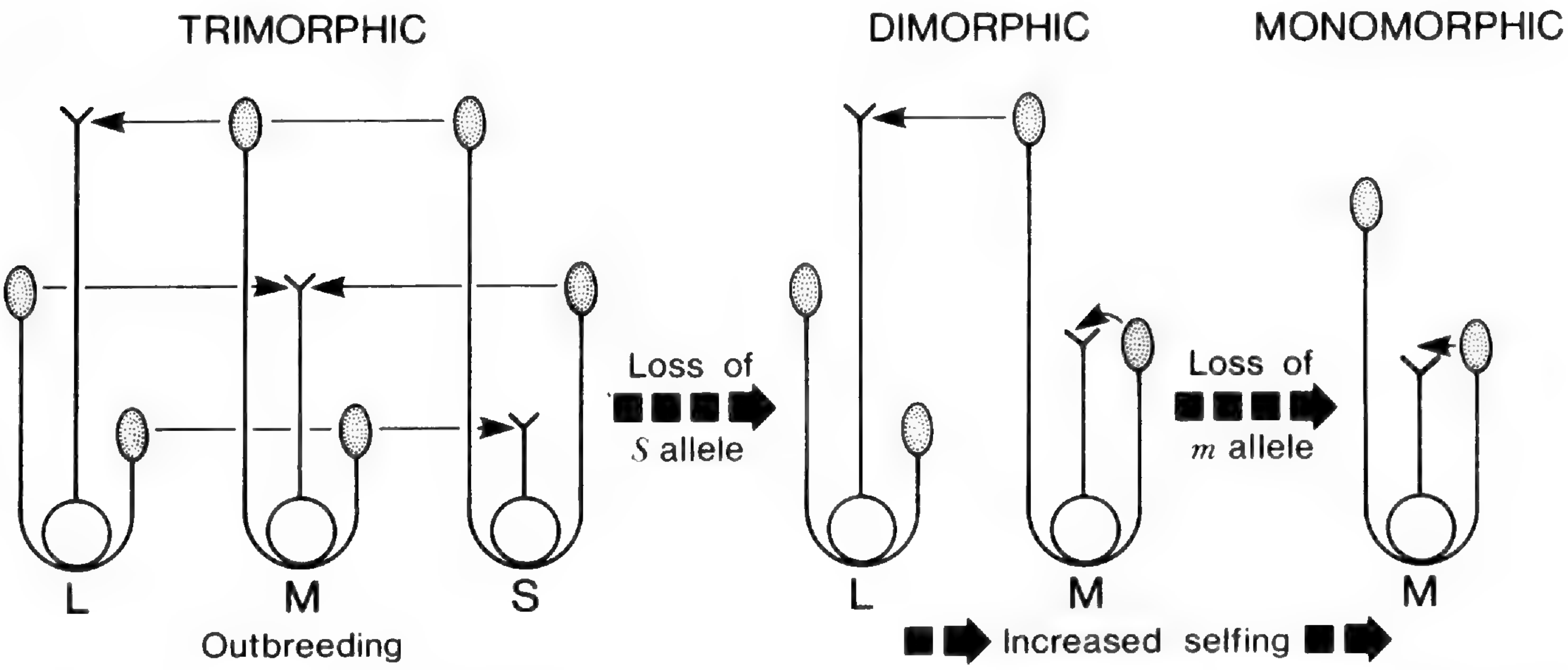

FIGURE 7. *Model of the breakdown of tristyly to semi-homostyly in* Eichhornia paniculata. *Arrows indicate predominant matings. Note the modifications in short-stamen position of the M morph in dimorphic and monomorphic populations. After Barrett (1985b).*

cycle, and population turnover is rapid due to the unpredictable nature of its habitats. These features increase the likelihood of detecting microevolutionary changes. This situation contrasts with that in *E. azurea* and *E. crassipes* where, because of heavy emphasis on clonal propagation, evolutionary changes in the breeding system of populations are more difficult to measure.

The breakdown process in Eichhornia paniculata. Surveys of the patterns of floral-morph frequency in populations of *E. paniculata* in conjunction with studies of their reproductive ecology and genetics have enabled the formulation of a model of the breakdown process (Barrett, 1985b; Glover & Barrett, 1986a, 1987). Figure 7 illustrates the major stages in the breakdown of tristyly to semi-homostyly in the M morph of *E. paniculata*. The model emphasizes two key stages: loss of the *S* allele and hence the S morph, and second, loss of the *m* allele and thus the L morph. Stochastic influences on population size, as discussed above, are thought to be largely responsible for the disappearance of the S morph from populations. However, because of its concealed stigma, a loss of specialized long-tongued pollinators in small populations may also reduce the maternal fitness of the S morph and hence its representation in founding populations. Comparisons of the fecundity of floral morphs in populations serviced by either long-tongued bees (*Florilegus festivus* and *Ancyloscelis* spp.) or generalist bees (*Trigona* spp. and *Apis mellifera*) provide evidence in support of this suggestion (S. C. H. Barrett, unpubl. data).

Loss of the L morph and fixation of the M morph in populations of *E. paniculata* are associated with the spread of mating system modifier genes and the evolution of semihomostyly. The genes that modify the short-level stamens of the M morph have no significant phenotypic effects when carried by the L and S morphs. As a result, in dimorphic populations, plants of the M morph frequently display altered stamen positions, whereas the L morph remains unmodified (e.g., fig. 3 in Glover & Barrett, 1986a, and Fig. 6). This pattern is also evident in *E. crassipes* (e.g., fig. 2 in Barrett, 1979). This phenotypic difference between the floral morphs of *E. paniculata* has a profound effect on their mating systems. Unlike tristylous populations where each morph is highly outcrossed, in dimorphic populations the M morph often experiences a high level of self-fertilization, whereas the L morph remains largely outcrossing (Glover & Barrett, 1986a; Barrett et al., 1987; Barrett, 1988a). With this mating asymmetry, and no major fitness differences between progeny arising from them, the M morph will likely replace the L morph. This is because the genes that cause an increased rate of self-fertilization have an "automatic advantage," since the maternal parent will transmit genes via both pollen and ovules to selfed progeny and thus evade the "cost of meiosis" (Maynard Smith, 1978).

An additional advantage that modified M plants possess over other floral morphs is their facility for automatic self-pollination in the absence of pollinating agents. Frequent colonizing episodes resulting in periods of low density are more likely to favor establishment of semi-homostylous variants, and this likely accounts for the predominance of populations monomorphic for the M morph in Ja-

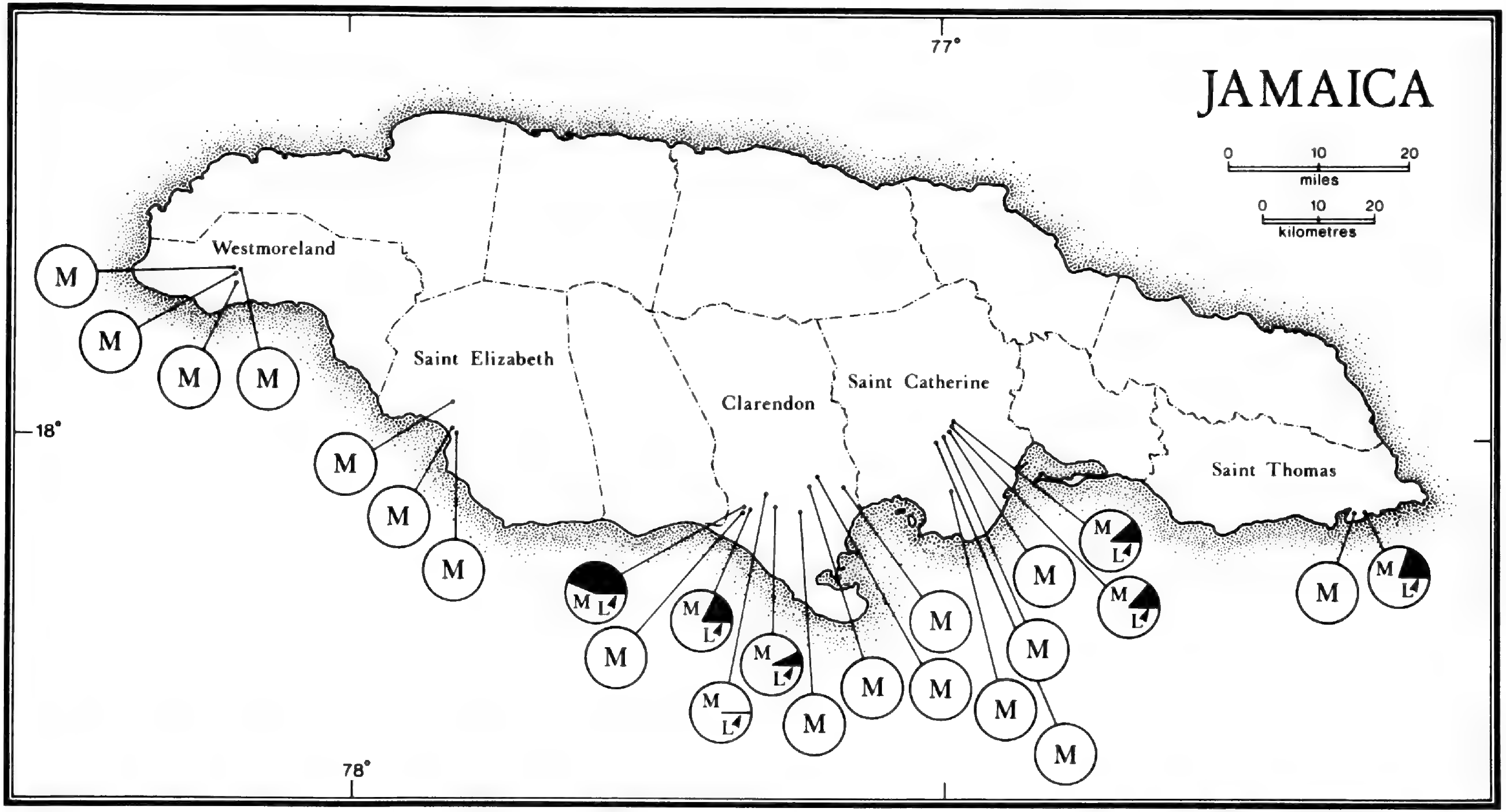

FIGURE 8. *Pattern of style-morph distribution in* Eichhornia paniculata *populations from Jamaica. Surveys were conducted in January 1979, 1984, and 1987. All plants of the M morph in Jamaica exhibit modified short-level stamens and are highly autogamous.*

maica (Fig. 8). The fecundity advantage of semi-homostylous variants of the M morph over the L morph has been demonstrated in Jamaican populations of *E. paniculata* (Barrett, 1988a) as well as in a dimorphic (L, M) population of *E. crassipes* (Barrett, 1979). The reproductive assurance of homostyly under conditions of low density and uncertain pollinator service has been used to explain the geographic patterns of floral variation in several other heterostylous groups (Baker, 1953, 1959; Ganders, 1975; Barrett & Shore, 1987).

FLORAL HETEROMORPHISMS IN SELFING TAXA

A second source of evidence in support of the derived nature of selfing in *Eichhornia* comes from investigation of the patterns of variation in floral traits within and among populations of predominantly autogamous taxa. As we have seen, in monomorphic and dimorphic populations of *E. paniculata*, residual floral heteromorphisms that were originally components of the ancestral tristylous syndrome remain in populations despite their largely selfed mating systems. Although the expression of these traits may be considerably modified from their original form, their occurrence in selfing species of *Eichhornia* is direct evidence that these taxa are descended from tristylous ancestors via evolutionary breakdown of tristyly.

Intrapopulation variation. Over most of the range of *E. heterosperma* and *E. diversifolia*, populations are composed of a single floral phenotype with a mid-length style and one set of anthers positioned just above the stigma and another below (Figs. 9 and 10, respectively). Because flower size is reduced in both species, the distance separating the reproductive organ levels is often small. In some populations this makes it difficult to determine the homologous positions of an ancestral tristylous condition and thereby infer the morphs from which the phenotypes descended. In most populations the phenotypes are best interpreted as semi-homostylous M plants in which elongation of the short stamen level into the mid position has occurred. Although this origin seems most plausible, based on analogy with semi-homostyle formation in outcrossing *Eichhornia* species, the possibility that some phenotypes are modified S plants with elongated styles cannot be ruled out.

Field studies of *E. heterosperma* in Venezuela and *E. diversifolia* in northeast Brazil have revealed a different pattern of floral variation. In both species a second floral phenotype can be found in populations in addition to the phenotype described above. The two phenotypes differ in style length, style coloration, pollen size, and the relative positions of their reproductive parts (Table 5). The expression of traits in the second phenotype indicates that it is a semi-homostyle derived from the L morph. The two semi-homostyles in *E. diversifolia* are illustrated in Figure 10. A trait of particular value in determining the origin of these floral phenotypes is style coloration. In tristylous *Eichhornia* species the three floral morphs differ in the degree of pigmentation of their styles. For example, in *E. crassipes* the L morph has a purple style, the M morph a lavender style, and the S morph a white style (Barrett, 1977a). In *E. diversifolia* and *E. heterosperma* the styles of the two semi-homostyles are pigmented to different degrees with the semi-homostylous L phenotype being either purple (*E. diversifolia*) or pink (*E. heterosperma*) and the semi-homostylous M phenotype light pink or white. In *E. heterosperma*, the two morphs can also differ in perianth color, with the semi-homostylous L phenotype possessing dark blue tepals and the M phenotype pale blue tepals. Differences in perianth color among the floral morphs of *Eichhornia crassipes* have also been reported, although this is not a universal feature of the species throughout its range (Müller, 1883; Haigh, 1936; Barrett, 1977a).

Populations of *E. diversifolia* and *E. heterosperma* that contain the two semi-homostylous phenotypes are largely self-pollinating, and it seems unlikely that the residual polymorphisms have any functional significance. If this is true, we might expect that mutation pressure will eventually break down the discontinuities that currently exist between the forms. Further field studies are required, however, to establish the overall distribution patterns of the morphs and to determine whether fitness differences that relate to floral phenotype exist. A recent survey of *E. diversifolia* populations in Ceará, northeast Brazil, provided no evidence that the two semi-homostylous phenotypes exhibit nonrandom distributions (S. C. H. Barrett, unpubl. data).

The rarity of *E. paradoxa* has restricted our investigations of its floral biology to surveys of herbarium specimens and to experimental studies of two natural populations from Paraiba and Sergipe, northeast Brazil. Even in this small sample several distinct patterns have emerged. The two field populations were each composed of a uniform but different self-pollinating semi-homostylous phenotype. One of these is illustrated in Figure 1B. The arrangement of reproductive parts and style coloration in the phenotypes is similar to the two semi-homostylous forms described above. It there-

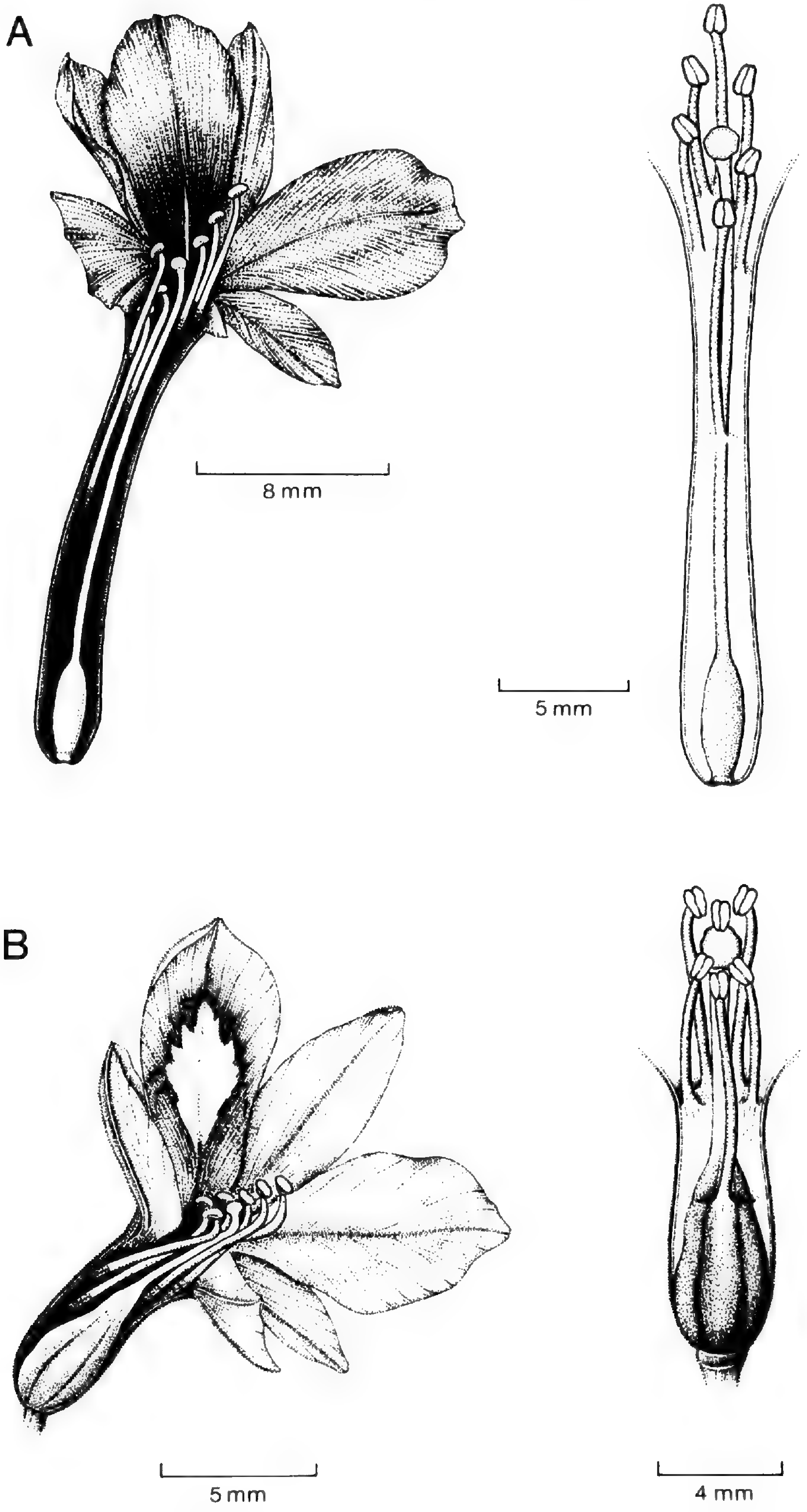

FIGURE 9. *Flowers and reproductive organs of semi-homostylous species of* Eichhornia.—*A.* E. heterosperma *(from Ceará, northeast Brazil).—B.* E. meyeri *(from Nueva Asunción, Paraguay). Note the close proximity of stigmas and anthers in the two species. A second floral phenotype occurs in parts of the range of* E. heterosperma *(see text).*

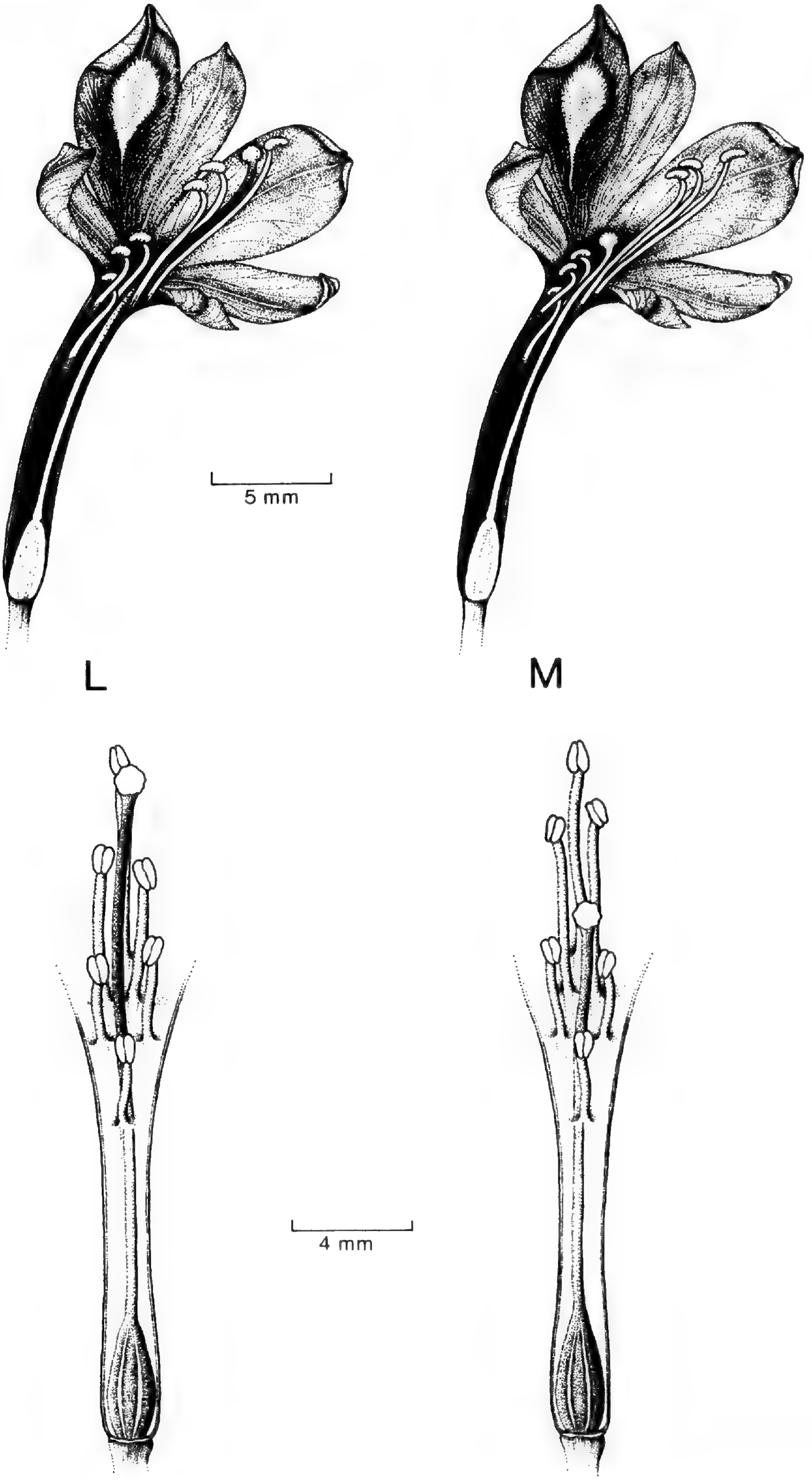

FIGURE 10. *Semi-homostylous L and M morphs of* Eichhornia diversifolia *from a population in Ceará, northeast Brazil. Note the differences in style length and pigmentation in the floral morphs.*

TABLE 5. *Mean style lengths and stamen heights (in mm) in semi-homostylous morphs of* Eichhornia diversifolia *and* E. heterosperma. *Measurements were made on field-collected flowers from populations at Croata, Ceará, northeast Brazil (N = 24 flowers per morph) and Calobozo, Guárico, Venezuela (N = 10 flowers per morph), respectively.*

Trait	*E. diversifolia* Semi-homostylous L		*E. diversifolia* Semi-homostylous M	*E. heterosperma* Semi-homostylous L		*E. heterosperma* Semi-homostylous M
Mean style length	26.3 ± 0.8	***	21.1 ± 0.9	23.7 ± 0.7	**	22.8 ± 0.6
Mean height of upper stamens	24.1 ± 0.9	***	25.8 ± 1.2	22.4 ± 0.7	***	24.1 ± 0.7
Mean height of lower stamens	18.4 ± 0.8	ns	18.8 ± 1.2	17.7 ± 0.8	***	20.0 ± 0.8

*** $P < 0.001$, ** $P < 0.01$, ns = not significant following Student's *t*-tests.

fore seems reasonable to assume that they are semi-homostylous L and M morphs. This can be confirmed by controlled crosses between the phenotypes, followed by genetic analysis of F_1 and F_2 variation.

Herbarium collections of *E. paradoxa* from a population in Bahia (*Harley 21401* (K), Bahia, Brazil) appear to contain three floral phenotypes that correspond to the L, M, and S morphs of a tristylous system. These plants possess inflorescences that contain many large flowers, and it is possible that the population retains a functionally tristylous breeding system. If this is true, *E. paradoxa* would resemble *E. azurea* and *E. paniculata* in displaying both outcrossing and selfing population systems. Because of its rarity and markedly disjunct distribution, it is probable that the species possesses considerable interpopulation differentiation, with individual populations displaying different stages in the breakdown of tristyly. Further studies of this interesting taxon are planned.

Floral monomorphism. Studies of the remaining two *Eichhornia* species (*E. natans* and *E. meyeri*) have as yet provided no evidence of polymorphisms in floral traits associated with the heterostylous syndrome. Both species exhibit mid-length styles and two stamen levels positioned very close to the stigma, one above and one below (Fig. 9B for *E. meyeri*). *Eichhornia natans* has highly reduced uniform blue flowers, and it is possible that the species is "quasi-homostylous" rather than semi-homostylous (see Ornduff, 1972). In quasi-homostyly the close juxtaposition of anthers and stigmas results from the reduced size of flowers rather than from genetic modifications in the relative positions of reproductive parts. Glasshouse studies of *E. meyeri* material collected from Paraguay (*Billiet & Jadin 3211* (BR), Nueva Asunción, Paraguay) indicate that the species is self-compatible, highly autogamous, and without residual pollen-size heteromorphism. The flowers of this collection are illustrated in Figure 9. Further work on both species is required to establish firmly the relationships of their breeding systems to an ancestral tristylous condition. This may be difficult if both species have lost all of the polymorphic variation associated with the tristylous syndrome. In *E. natans* this could have occurred through a genetic bottleneck during dispersal and establishment on the African continent. In *E. meyeri* progressive extinctions leading to its current rarity may have had a similar effect.

CONCLUSIONS

Studies of intraspecific and interspecific patterns of variation in the breeding systems of *Eichhornia* species indicate that tristyly has broken down repeatedly in the genus to give rise to predominantly selfing population systems. This conclusion rests on two lines of evidence: 1) the evolution of semi-homostylous forms within each of the three primarily tristylous species (*E. azurea*, *E. crassipes*, *E. paniculata*), and 2) the occurrence of residual floral heteromorphisms in several of the largely autogamous semi-homostylous species (*E. diversifolia*, *E. heterosperma*, *E. paradoxa*). The pathway of evolution from outcrossing to selfing in *Eichhornia* appears to be the only major shift in breeding system in the genus. This contrasts with the Lythraceae and Oxalidaceae, where, in addition to semi-homostyle formation, stable distylous breeding systems have evolved from tristyly (Mulcahy, 1964; Ornduff, 1972; Lewis & Rao, 1971; Weller, 1976; Charlesworth, 1979).

The selective pressures responsible for the change from outbreeding to inbreeding are always difficult to identify (Jain, 1976); however, ecological and genetic studies of *Eichhornia* populations have provided some insights into the conditions that foster the breakdown of tristyly. Genetic bottlenecks resulting from long-distance dispersal, as well as colonization of unpredictable habitats with uncertain moisture regimes play major roles in disrupting the maintenance of tristyly. Two features of *Eichhornia* species make them particularly prone to these effects: 1) their small-seeded habit favoring bird dispersal, and 2) their occurrence in tropical aquatic habitats that are susceptible to frequent droughts. These aspects of *Eichhornia* ecology result in frequent colonizing episodes and periodic fluctuations in population size. Under these influences, ecological and genetic conditions are likely to favor the establishment and spread of selfing genotypes. In small newly founded populations, serviced by unreliable generalist pollinators, semi-homostylous variants are likely to be at a selective advantage because of the reproductive assurance that autonomous self-pollination provides. In addition, the genetic load of populations may be sufficiently low, owing to frequent bottlenecks (see Lande & Schemske, 1985), that inbreeding depression may not be a serious obstacle to the spread of semi-homostylous variants.

Our discussion of the breakdown of tristyly in *Eichhornia* has focused primarily on details of the ecology and genetics of natural populations. However, for a comprehensive model of the breakdown process to be obtained, information from morphology and development needs to be integrated with studies from population biology. This is of particular importance in heterostylous groups, because the floral morphs can respond differently to selection and drift as a result of their particular floral morphologies and inheritance patterns. While in *Eichhornia* mutations affecting floral structure and mating system can arise in each morph, the available evidence indicates that the M morph is more susceptible to evolutionary modification. This may be because developmental constraints restrict the range of floral modifications that can occur in the L and S morphs. In addition, the S morph is frequently lost from populations through stochastic processes and may rarely encounter the selection pressures operating in small populations that favor the evolution of self-fertilization. Thus loss of the S morph may simply reflect a genetic constraint imposed by the two-locus system of inheritance of tristyly. While frequent colonizing episodes and ecological radiations into temporary aquatic habitats appear to be the major driving forces responsible for the evolution of breeding systems in *Eichhornia*, constraints imposed by the morphology and genetics of the polymorphism have guided the nature of the floral modifications that have occurred.

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DISTYLY AND MONOMORPHISM IN *VILLARSIA* (MENYANTHACEAE): SOME EVOLUTIONARY CONSIDERATIONS[1]

Robert Ornduff[2]

ABSTRACT

Distyly occurs in four of the five genera of the Menyanthaceae, as do breeding systems such as dioecy, gynodioecy, and homostyly that are believed to be derived from distyly. Most species of the largely Australian genus Villarsia *are distylous, but the Western Australian* V. albiflora *has monomorphic (nonheterostylous) flowers and appears to be homostylous. Despite this, individuals of this species are self-incompatible, although most members of the four populations studied are intercompatible. The incompatibility system of* V. albiflora *appears to be controlled by multiple alleles. Another Western Australian species,* V. parnassiifolia, *has distylous flowers and strong self-incompatibility. Long × Long crosses of this species fail to produce seeds, but Short × Short crosses commonly produce a full complement of seeds. Thus, this species possesses a self-incompatibility system, but Shorts have an unexpectedly high degree of intramorph intercompatibility, suggesting that the incompatibility system of this morph likewise is controlled by multiple alleles. Five of eight natural populations sampled of* V. parnassiifolia *showed Short-dominated morph ratios, suggesting that offspring of Short × Short pollinations may constitute a portion of these Short-dominated natural populations.* Villarsia albiflora *may represent a recombinant homostyle, a true-breeding Short morph derived from a distylous ancestor with a breeding system similar to that of* V. parnassiifolia, *or a species possessing a floral morphology and breeding system ancestral to the distyly that occurs widely in the Menyanthaceae. A scheme for the origin of distyly in* Villarsia *is presented.*

The Menyanthaceae consist of five genera of wetland or aquatic herbs. *Menyanthes* and *Fauria* (*Nephrophyllidium*) are monotypic north-temperate genera, both of which bear distylous flowers. *Nymphoides* is widely distributed in tropical and temperate regions of both hemispheres; distyly is common in this large genus, as are derivative breeding systems such as dioecy, gynodioecy, and autogamy associated with homostyly (Ornduff, 1966, 1970b, 1973; Vasudevan Nair, 1975). *Liparophyllum* is a monotypic genus restricted to New Zealand and Tasmania; its flowers are monomorphic and the species is self-compatible (Ornduff, 1973). *Villarsia* occurs in southeastern Asia, South Africa, and Australia, with the largest concentration of species in southwestern Western Australia. Several Australian *Villarsia* species have distylous flowers and an associated self- and intramorph incompatibility system (Ornduff, 1974, 1982, 1986, 1988; Fig. 1). My recent work has revealed that some species of *Villarsia* with distylous flowers have various altered incompatibility systems; one of these species, the Western Australian *V. parnassiifolia* (Labill.) R. Brown, is discussed in this paper. Another species, *V. albiflora* F. Muell., is a Western Australian species which has nonheterostylous flowers (Fig. 1), a self-incompatibility system, and essentially full intercompatibility among members of a population. This species is thus not the self-compatible homostyle of the type that commonly occurs in various other predominantly distylous genera (Richards, 1986). This paper documents the nature of the incompatibility systems of *V. parnassiifolia* and *V. albiflora* and discusses the possible relationships between the unique breeding system of *V. albiflora* and those that occur in other species of *Villarsia*. Since work on these two species, as well as others of the genus, is still in progress, this report is preliminary.

MATERIALS AND METHODS

Seeds were collected in 1983 from four populations of *Villarsia albiflora* in Western Australia:

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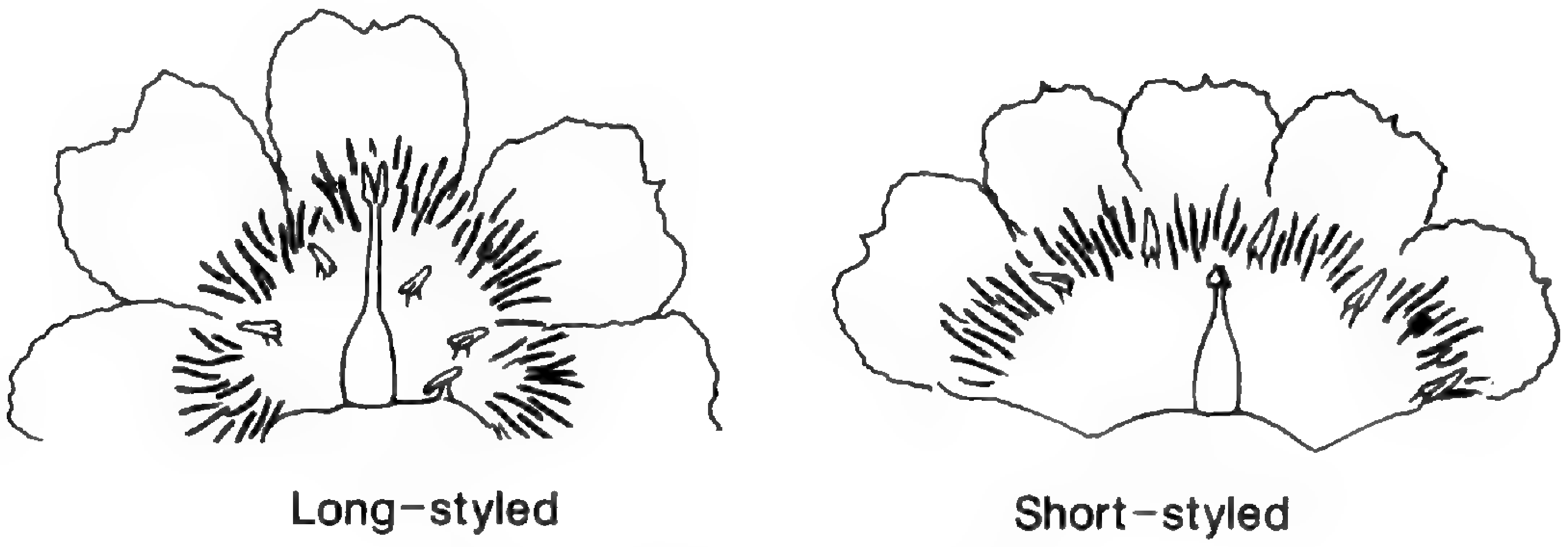
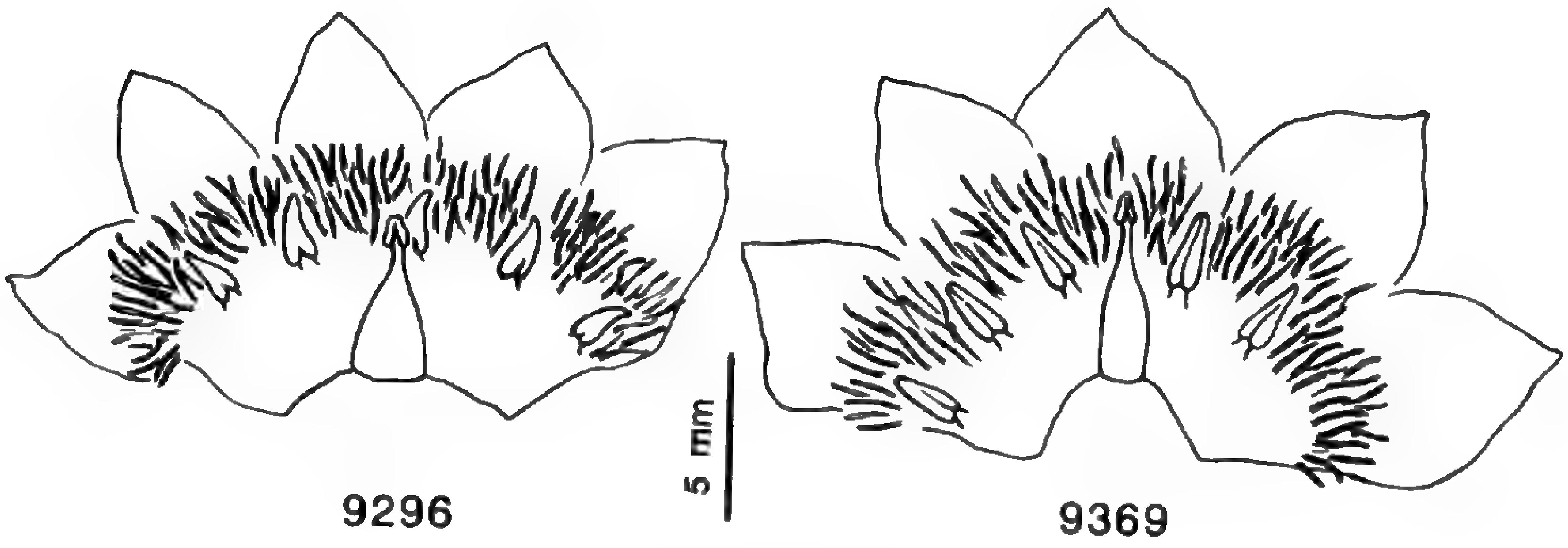


Villarsia parnassiifolia (9404)



Villarsia albiflora

FIGURE 1. *Dissections of distylous flowers of* Villarsia parnassiifolia *and of monomorphic flowers of* V. albiflora.

9296, Gnangara Lake, near Perth; 9365, Medina, near Perth; 9369, the Capel-Boyanup area; and 9397, near Mount Chudalup. This sampling encompasses most of the geographical range of this species, which is diploid (Ornduff & Chuang, in press). At the same time, seeds were also collected from two populations of *V. parnassiifolia*: 9404, a diploid population near Walpole, and 9413, a tetraploid population at Parry Beach, near Denmark (Ornduff & Chuang, in press), both occupying central positions in the range of this species along the southern coast of Western Australia. Plants were grown from these seeds in the greenhouses at the University of California, Berkeley. Thirty-eight individuals of *V. albiflora* and 10 long-styled plants (Longs) and 13 short-styled individuals (Shorts) of *V. parnassiifolia* were used in the crossing program. Each individual in a progeny was assigned a plant number for reference purposes. Each plant was self-pollinated and crossed with as many other individuals in the population as possible during the spring and summer of 1986 and 1987. At least six pollinations for each type of cross were performed. Nearly mature capsules were collected individually in seed envelopes, and the number of seeds counted. Flowers of self- and cross-pollinated plants of both species were collected 24 hours after pollination, the gynoecium excised, mounted, stained, and observed under ultraviolet light to observe the behavior of pollen and pollen tubes following various types of pollinations (using the method of Martin, 1959). Seeds of intra- and intermorph crosses of *V. parnassiifolia* (population 9413) were sown in a greenhouse, the seedlings grown to flowering, and the style lengths of each individual recorded.

RESULTS

All seed-set figures were assigned arbitrarily to one of three categories (Figs. 2, 3). "High" seed production refers to crosses in which all pollinations produced capsules with large numbers of seeds; "intermediate or variable" seed production includes crosses in which seed production was markedly lower than the "high" category of that seed parent, or in which some crosses failed to produce seed; and "low" seed production refers to crosses producing few or no seeds. These categories will not be quantified in this paper because of high variances in the first two categories and the small number of pollinations (a minimum of six) con-

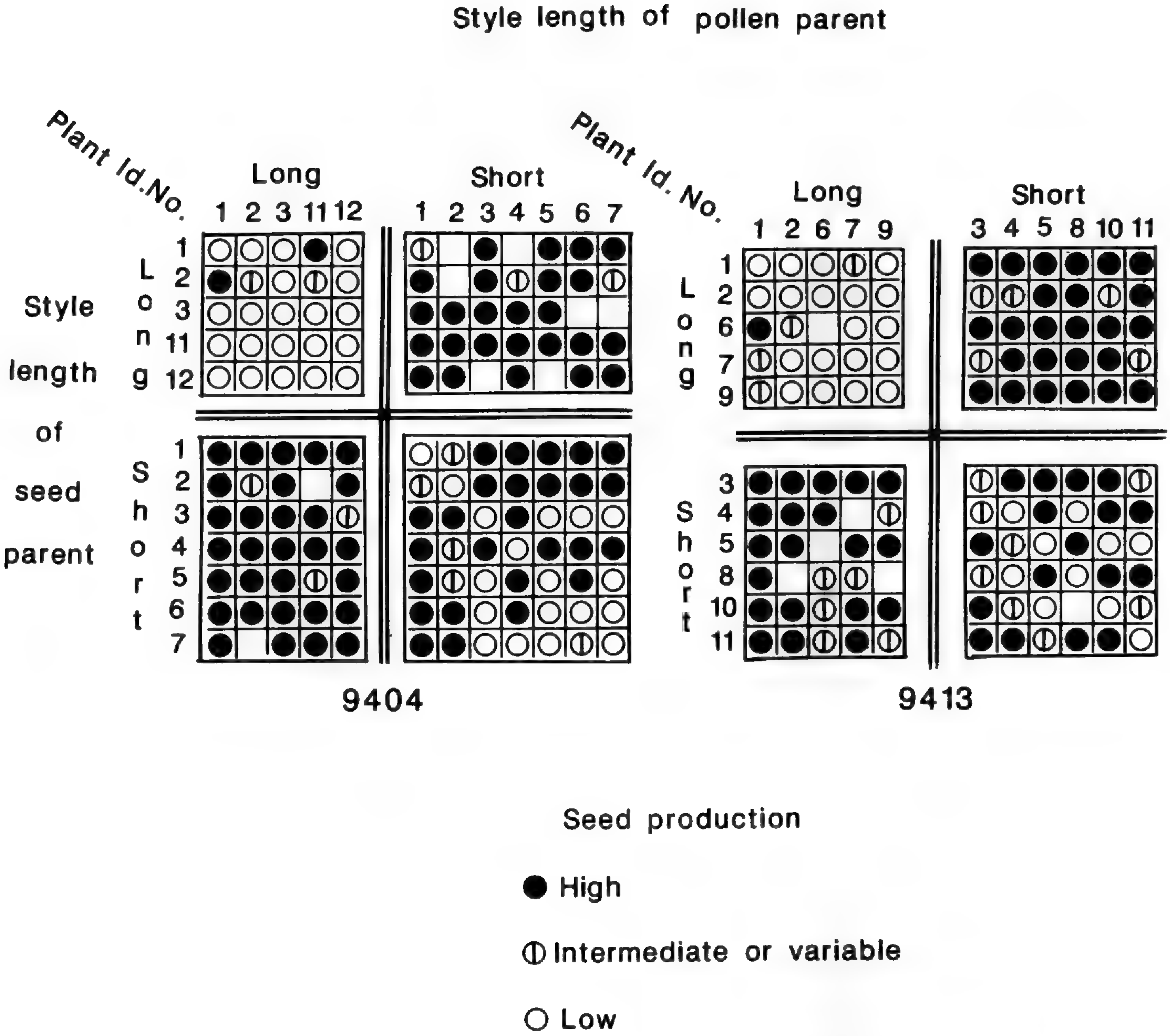
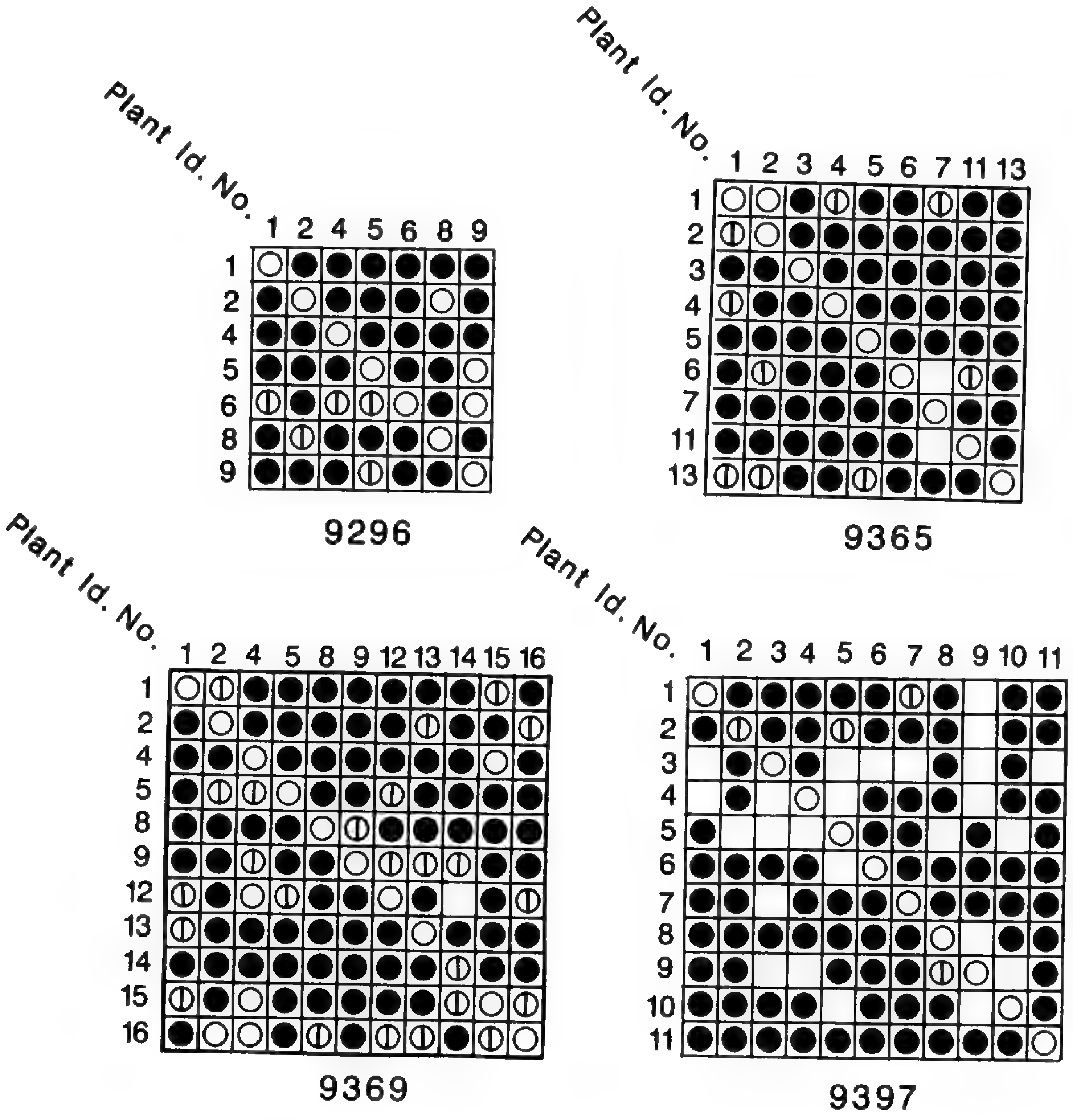


FIGURE 2. *Seed production following artificial self- and cross-pollinations of the two morphs of the distylous* Villarsia parnassiifolia, *using two greenhouse-grown populations. The vertical and horizontal series of numbers refer to individual plants in each population. Seed production figures are described in text.*

ducted for each cross. Additional work is planned to increase the sample sizes. However, I am confident that the "high" and "low" categories represent two distinct types of results and provide a meaningful and relatively consistent basis on which to discuss the nature of the breeding systems in the two *Villarsia* species discussed in this paper. Whether the "intermediate or variable" category represents something other than a procedural artifact awaits additional data.

Villarsia parnassiifolia. Longs and Shorts of this species are strongly self-incompatible; only one of the nine selfed Longs and one of the 13 selfed Shorts produced any seeds following selfing (Fig. 2). Intermorph pollinations produced generally high seed-sets: 50 of the 58 Long × Short pollinations and 51 of the 60 Short × Long pollinations produced high seed-sets. Only three of the 40 Long × Long crosses produced a high seed-set, and an additional six of these crosses produced some seeds, indicating a high level of intramorph incompatibility of Longs. In contrast, 43 of the 71 Short × Short crosses produced high seed-sets, and an additional 13 of the crosses produced some seed, indicating a high level of intramorph compatibility of Shorts. Each Short in the two populations was fully compatible with at least one other Short in that population, and a few Shorts were compatible with most other Shorts in the same population. Most successful Short × Short crosses were successful in both directions, and most that failed did so in both directions. No differences were noted in behavior between the diploid and the tetraploid populations of *V. parnassiifolia*.

Crosses between four Longs and four Shorts of tetraploid population 9413 all produced both Longs



Plant Id. No.	1	2	4	5	6	8	9
1	○	●	●	●	●	●	●
2	●	○	●	●	●	○	●
4	●	●	○	●	●	●	●
5	●	●	●	○	●	●	○
6	⦶	●	⦶	⦶	○	●	○
8	●	⦶	●	●	●	○	●
9	●	●	●	⦶	●	●	○

9296

Plant Id. No.	1	2	3	4	5	6	7	11	13
1	○	○	●	⦶	●	●	⦶	●	●
2	⦶	○	●	●	●	●	●	●	●
3	●	●	○	●	●	●	●	●	●
4	⦶	●	●	○	●	●	●	●	●
5	●	●	●	●	○	●	●	●	●
6	●	⦶	●	●	●	○		⦶	●
7	●	●	●	●	●	●	○	●	●
11	●	●	●	●	●	●		○	●
13	⦶	⦶	●	●	⦶	●	●	●	○

9365

Plant Id. No.	1	2	4	5	8	9	12	13	14	15	16
1	○	⦶	●	●	●	●	●	●	●	⦶	●
2	●	○	●	●	●	●	●	⦶	●	●	⦶
4	●	●	○	●	●	●	●	●	●	○	●
5	●	⦶	⦶	○	●	●	⦶	●	●	●	●
8	●	●	●	●	○	⦶	●	●	●	●	●
9	●	●	⦶	●	●	○	⦶	⦶	⦶	●	●
12	⦶	●	○	⦶	●	●	○	●		●	⦶
13	⦶	●	●	●	●	●	●	○	●	●	●
14	●	●	●	●	●	●	●	●	⦶	●	●
15	⦶	●	○	●	●	●	●	●	⦶	○	⦶
16	●	○	○	●	⦶	●	⦶	⦶	●	⦶	○

9369

Plant Id. No.	1	2	3	4	5	6	7	8	9	10	11
1	○	●	●	●	●	●	⦶	●		●	●
2	●	⦶	●	●	⦶	●	●	●		●	●
3		●	○	●				●		●	
4		●		○		●	●	●		●	●
5	●				○	●	●		●		●
6	●	●	●	●		○	●	●	●	●	●
7	●	●		●	●	●	○	●	●	●	●
8	●	●	●	●	●	●	●	○		●	●
9	●	●			●	●	●	⦶	○		●
10	●	●	●	●		●	●	●		○	●
11	●	●	●	●	●	●	●	●	●	●	○

9397

Seed production

● High

⦶ Intermediate or variable

○ Low

FIGURE 3. *Seed production following artificial self- and cross-pollinations of the monomorphic* Villarsia albiflora, *using four greenhouse-grown populations. The vertical and horizontal series of numbers refer to individual plants in each population.*

and Shorts in each progeny. Five Shorts of this population used in five Short × Short crosses produced Longs only in one progeny, Shorts only in two progenies, and Longs and Shorts in two progenies. Two 9413 Shorts selfed produced Longs and Shorts in each progeny. Two Long × Long crosses produced only Longs in their progenies. Although the progeny sizes are small, these results make it likely that the Shorts carry a dominant allele and Longs are homozygous recessive.

Villarsia albiflora. Results of pollinations using 38 individuals in four populations of *V. albiflora* provided relatively consistent results. All individuals proved to be self-incompatible, producing few or no seeds upon self-pollination (Fig. 3). Pollen grains on selfed stigmas either failed to germinate or germinated with growth of the pollen tube into stigmatic tissue but not further. Most individuals produced high seed-sets when crossed with other individuals in the population. Most crosses that failed in one direction were successful in the other direction, or provided seed-sets in the "intermediate or variable" category in that direction. Only one instance was found of apparent bilateral incompatibility (between plants 4 and 16 of population 9369). Thus, the nonheterostylous *Villarsia albiflora* has a pronounced self-incompatibility system, but most members of each population are intercompatible.

DISCUSSION

Villarsia parnassiifolia has morphologically distylous flowers and a strong self-incompatibility system. Although Long × Long crosses generally failed to produce seeds, most Short × Short crosses were fully compatible, producing high seed-sets. No differences were observed in the behavior of diploids and tetraploids. Self- and intramorph incompatibility are commonly associated with distyly, and in most examples where intramorph compatibility exists, as in some species of *Hedyotis* (Rubiaceae), *Melochia* (Sterculiaceae), and *Amsinckia* (Boraginaceae), it is associated with self-compatibility as well (Ganders, 1979).

The occurrence of self-incompatibility but intramorph compatibility in distylous species is rare. It has been reported in the borages *Anchusa hybrida* Ten. (Dulberger, 1970) and *A. officinalis* L. (Philipp & Schou, 1981). I am reluctant to consider the examples of *Narcissus tazetta* L. and *Mirabilis froebelii* (Behr) Greene cited by these authors to represent heterostyly. In *Anchusa officinalis*, Schou & Philipp (1984) demonstrated that the morphological features of distyly are controlled by a single diallelic locus, with Longs homozygous recessive and Shorts with one or two dominant alleles, which is the common genetic basis of distyly (Ganders, 1979). However, as Dulberger (1970) suggested is the case for *Anchusa hybrida*, the incompatibility system of *A. officinalis* is controlled by at least two alleles, and these segregate independently from those controlling the morphological features of distyly (Schou & Philipp, 1984).

The condition described in *Villarsia parnassiifolia* resembles that of the two *Anchusa* species but differs in that the Long but not the Short morph of *V. parnassiifolia* possesses intramorph- as well as self-incompatibility. It would appear that in the Long morph of this species the incompatibility alleles are linked to the "morphological" locus, but in the Short morph they are not. How this is accomplished (if it is) is unclear.

Style lengths of the few small progenies obtained by self- and intramorph pollinations of the tetraploid population of *Villarsia parnassiifolia* are consistent with the notion that the Short morph of this species carries a dominant allele with Longs thus homozygous recessive, but exact interpretation of the scant data may be obscured by tetrasomic inheritance. Short-dominated morph ratios occur in five of the eight field populations sampled of this species (Ornduff, 1986; $P = <0.05$ with the Wilcoxon's signed-ranks test), suggesting that under field conditions Short × Short crosses commonly participate in contributing to the composition of natural populations.

The floral morphology of *Villarsia albiflora* suggests that it is a homostyle, but this tentative conclusion requires examination. In genera or families with both distyly and homostyly, the homostylous condition is usually viewed as the result of genetic recombination in the S "supergene," leading to production of flowers combining carpel characters of one morph with stamen characters of the other morph. Commonly, such homostyles are Long-homostyles, although Short-homostyles are also known. Homostyly has been recorded in diverse genera such as *Armeria* (Plumbaginaceae; Baker, 1966), *Gelsemium* (Loganiaceae; Ornduff, 1970c), *Limonium* (Plumbaginaceae; Baker, 1953), *Nymphoides* (Menyanthaceae; Ornduff, 1970a), *Oldenlandia* (Rubiaceae; Bir Bahadur, 1970), *Piriqueta* (Turneraceae; Ornduff, 1970a), *Primula* (Primulaceae; Darwin, 1877; Ernst, 1955), *Turnera* (Turneraceae; Urban, 1883; Barrett & Shore, 1987), *Villarsia* (Menyanthaceae; Ornduff, 1974), and *Waltheria* (Sterculiaceae, Bir Bahadur, 1977). Because a single homostyle flower usually bears a combination of pollen of one morph with carpels of the other morph, such homostyles are generally self-compatible and sometimes largely autogamous. Other types of homostyles occur in *Amsinckia* (Boraginaceae; Ray & Chisaki, 1957), *Hedyotis caerulea* (Rubiaceae; Ornduff, 1977), *Mitchella repens* (Rubiaceae; Ganders, 1975), and *Primula* (Primulaceae; Ernst, 1955). The nature and placement of anthers and stigmas of these homostyles vary, but cannot be attributed to genetic recombination alone and must involve the additional action of modifier genes. Such homostyles may be self-compatible (as in *Amsinckia* and some species of *Primula*) or self-incompatible (as in *Mitchella repens*, *Hedyotis caerulea*, and some species of *Primula*). In the latter examples, self-incompatible homostyles appear to be very rare or known only from cultivated material (Ganders, 1975). Once homostyly has developed, even as a result of simple genetic recombination, carpel, stamen, and other floral traits may subsequently be altered by modifier genes to accommodate the homostyly in the direction of greater autogamy (as apparently is the case in *Piriqueta cistoides*, Ornduff, 1970a) or in the direction of greater xenogamy (as apparently is the case for some races of *Turnera ulmifolia*; Barrett, 1988).

The nature and origin of the floral monomorphism of *Villarsia albiflora* are not clear. If we assume for purposes of discussion that this species represents a recombinant homostyle, its self-incompatibility and essentially full intercompatibility are consistent with the idea that style-length and incompatibility reactions are not uniformly controlled by sets of linked alleles in distylous *Villarsia* species. However, since incompatibility of Short pollen but not Long pollen appears to be unlinked to style length, this may require that the putative homostyly of *V. albiflora* is Long-homostyly (i.e., the style of Longs combined with anther position and incompatibility behavior of Shorts in one flower) rather than Short-homostyly. Whether this supposition will survive the scrutiny of further study remains to be seen.

A second, perhaps more attractive (or at least potentially less flawed) hypothesis is that the monomorphism of *V. albiflora* represents a situation in which the flowers of this species are fundamentally Shorts, and in which the Longs of a presumed distylous ancestor have been lost. The anther position and stylar morphology of *V. albiflora* resemble those of Shorts of *V. parnassiifolia* more closely than they do those of Longs of that species (Fig. 1). Short × Short pollinations of *V. parnassiifolia* are mostly compatible ones that produce vigorous offspring under artificial and, apparently, natural conditions. It is possible that in the evolution of *V. albiflora*, a postulated distylous ancestor lost the *s* allele and thus the Long morph, leading ultimately to a condition where populations consist of true-breeding homozygous Shorts carrying only the dominant *S* allele. If this postulated ancestor possessed the breeding system and Short-dominated morph ratios characteristic of *V. parnassiifolia* today, periodic severe reductions in population size as a consequence of the cyclic fluctuations in annual rainfall that have characterized southwestern Western Australia since mid or late Tertiary times (Hopper, 1979) might have resulted in the loss of the *s* allele and thus the loss of Longs. This would result in true-breeding homozygous Shorts as the exclusive components of surviving populations. Since *Villarsia* typically occurs in mesic to aquatic circumstances, recurrent xerothermic periods could have had strong effects on population sizes and distribution of species in this genus.

Because of the occurrence of distyly in four of the five genera of Menyanthaceae, it is natural to assume that the floral condition and incompatibility system of *V. albiflora* are derivative ones from a distylous antecedent. A third evolutionary scenario contrary to this directionality in evolution is that the floral monomorphism of *V. albiflora* is primary in the genus and that distyly elsewhere in *Villarsia* has been derived from this type of monomorphism. Starting with a self-incompatible nonheterostylous species similar to *Villarsia albiflora* (which today shows some interpopulation variability in position of stigmas relative to anthers, Fig. 1; Ornduff, 1986), selection might operate to favor increased distance between stigmas and anthers as a means of reducing pollen wastage by selfing. One means of achieving this could be via style-length dimorphism associated with a slight shifting of anther position (the positions of anthers in the two morphs of the distylous *V. parnassiifolia* are not very different; Fig. 1). Initially, the alleles controlling floral dimorphism would be unlinked to those multiple alleles controlling the incompatibility reaction (as in *Anchusa*). Gradually, linkage between these two sets of alleles would develop with a concomitant decrease in the number of incompatibility alleles; in *Villarsia parnassiifolia* such a linkage appears to occur in Longs but not in Shorts. Ultimately, the alleles controlling floral dimorphism would be tightly linked to those controlling incompatibility, the latter having been reduced to a pair of alleles at a single locus. At this point, distyly of the conventional type that occurs in a variety of unrelated genera would have been achieved. In *Villarsia*, such "conventional" distyly and incompatibility occur in *V. capitata* Nees (Ornduff, 1982) and *V. congestiflora* F. Muell. (Ornduff, 1988).

Assuming this latter scheme represents an approximation of the sequence of events in the evolutionary history of *Villarsia*, it would explain an apparent anomaly that I commented on many years ago, namely that *V. capitata* and *V. congestiflora* "possess an unusual combination of highly advanced characters" with the "primitive" one of distyly (Ornduff, 1982). If distyly is indeed a condition that has developed from monomorphism within *Villarsia*, this anomaly is resolved, since distyly is thus viewed as advanced and not primitive.

This last suggested series of events is highly speculative. When more information becomes available on the breeding systems of other species of *Villarsia*, this third scenario should be evaluated in the context of different suggestions concerning the mode of origin of distyly proposed or discussed by Charlesworth & Charlesworth (1979), Ganders (1979), Muenchow (1982), and Gibbs (1986).

Clearly, breeding systems in the Menyanthaceae merit further experimental work and theoretical consideration.

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WIND POLLINATION IN AQUATIC ANGIOSPERMS

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ABSTRACT

Aquatic angiosperms have evolved from terrestrial ancestors several times. About 79 angiosperm families and 380 genera contain aquatic species; 119 genera (31.3%) are wind pollinated. Among these wind-pollinated aquatics, 100 genera have obvious terrestrial relatives that are also wind pollinated. Sixteen genera (4.2%) have no obvious terrestrial relatives but belong to exclusively anemophilous families; the anemophily, however, could be associated with life in water. In only two genera (0.5%), Brasenia *(Cabombaceae) and* Limnobium *(Hydrocharitaceae), is it likely that the evolution from entomophily to anemophily has taken place in the aquatic environment. In* Hydrilla *(Hydrocharitaceae) the pollen grains are heavy and are propelled through air from the male to the female; although this mechanism almost certainly evolved in water, it is not considered to be true anemophily where buoyant grains are carried by air movements. Wind pollination is not considered an important feature especially associated with life in the aquatic environment.*

Crane (1986) suggested that the seeming simplicity of wind pollination has deflected interest in a process that is, in fact, far from straightforward. However, combining the detailed pioneer work on pollen dimensions and pollen production by Pohl (1937a, b) with the physical approaches by Whitehead (1969) and Niklas (1985) and with the renewed morphological approach of Crane (1986), a better view of wind pollination in gymnosperms and terrestrial angiosperms is emerging. Wind pollination and associated characteristics have rarely been studied in aquatic angiosperms.

The main purpose of this review is to collect information bearing on the question of which aquatic plants are pollinated by wind. By comparing these with their terrestrial ancestors it should be possible to find out which of them have modified their pollination mechanisms. In turn, this should give insight into the question: is wind pollination especially associated with the aquatic environment? Perhaps the highest development of aquatic angiosperms is the use of water for the transfer of pollen (hydrogamy). It is also an aim of this review to see if wind pollination is a prerequisite to hydrogamy.

The term aquatic is used in the sense described by Cook et al. (1974); it includes plants whose photosynthetically active parts are submerged in water or floating on the water surface permanently or, at least, for several months each year. Within the angiosperms the aquatics have evolved from terrestrial ancestors several times, as Sculthorpe (1967) pointed out. It is important to appreciate that most aquatic angiosperms resemble terrestrial flowering plants, not only in gross features of floral morphology, but also in exhibiting similar trends of floral specialization. The aquatic members of predominantly anemophilous families Centrolepidaceae, Cyperaceae, Hydatellaceae, Juncaceae, and Poaceae from the point of view of their pollination biology resemble the terrestrial members and are thus not described in detail here.

The first angiosperms were almost certainly insect pollinated, so anemophily is a derived state (for example, see Crane, 1986). It is also clear that wind pollination has originated several times from diverse stocks. Anemophily has evolved at different times from different morphological backgrounds with differing degrees of efficiency. It is not surprising that it is sometimes difficult to make a clear-cut distinction between wind-pollinated plants and those pollinated by other means. Many predominantly wind-pollinated species may be regularly visited by pollen-eating insects (particularly syrphid flies) and may occasionally be pollinated by insects. For such plants Stelleman (1984) used the term ambophily.

Quantitative data on the efficiency of wind pollination or even direct observations are lacking among aquatics. The decision of whether a species is wind pollinated or not is often based on morphological criteria. This is justifiable since there is a whole complex of characters associated with anemophily. The following list attempts to summarize the most important features of this wind pollination syndrome.

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1. The characteristics of wind-borne pollen grains are well summarized by Crane (1986): size 20–40(–60) μm diam., Reynolds number around 0.1 at a terminal velocity of 5 cm sec.$^{-1}$, spread singly, powdery and nonsticky (lipids absent, chemically altered or hidden within the wall), surface relatively smooth, resistant to changes in temperature and to desiccation (size and/or number of apertures reduced).
2. The flowers are usually unisexual: the male must dispense pollen, and the female must catch pollen.
3. The amount of pollen is increased: this is usually achieved by an increase in anther size and is often associated with a decrease in number of anthers in each flower and an increase in number of male flowers.
4. The flowers are usually separated from the leaves (temporally or spatially) and held above the water on specialized structures.
5. The perianth and bracts are reduced (to increase aerodynamic efficiency).
6. There are sometimes special arresting or explosive mechanisms to ensure that pollen gets into the airstream.
7. The number of ovules in each flower is usually reduced; the reason for this is not clear.
8. The stigmas are often specialized to increase "capture" efficiency.

I. Aquatics Previously Considered Anemophilous but Probably Entomophilous

Details of the pollination mechanisms of many aquatic angiosperms are unknown. Many with small and insignificant flowers have been considered to be wind or even water pollinated. The following, which have been thought to be wind pollinated, are probably pollinated by other means; all are illustrated in Cook et al. (1974).

ALISMATACEAE

Ten of the eleven genera have large showy petals; some are scented and have septal nectaries and are clearly insect pollinated. *Wiesneria*, a genus with two African and one Asian species, recently redescribed by Sivadasan (1986), has whorled, subsessile, unisexual flowers with small and reflexed perianths. The male flowers, which are borne above the females, have three stamens, the lowest number in the family. The carpels are reduced to three or four in each female flower. These characters may suggest anemophily, but the inflorescences are shorter than and partly hidden by the leaves; the petals, though small, are cream-colored and relatively conspicuous; the anthers are small (ca. 1 mm long); the filaments are short (ca. 0.5 mm long); the pollen grains are echinate, have numerous apertures (Fig. 6), and are somewhat sticky. These characters strongly suggest insect pollination. It is not known if *Wiesneria* is scented or if it produces nectar.

APONOGETONACEAE

Aponogeton, the only genus, sometimes has catkinlike inflorescences. A few species have unisexual flowers, and sometimes the perianth is reduced. These features suggest wind pollination. However, the pollen has supratectal spines in all species (see Bruggen, 1985) and most species investigated to date have septal nectaries and are strongly scented. *Aponogeton* is insect pollinated, but in some species some pollen may be transferred by wind. This is unlikely, however, as the pollen grains stick together in clumps.

ARACEAE

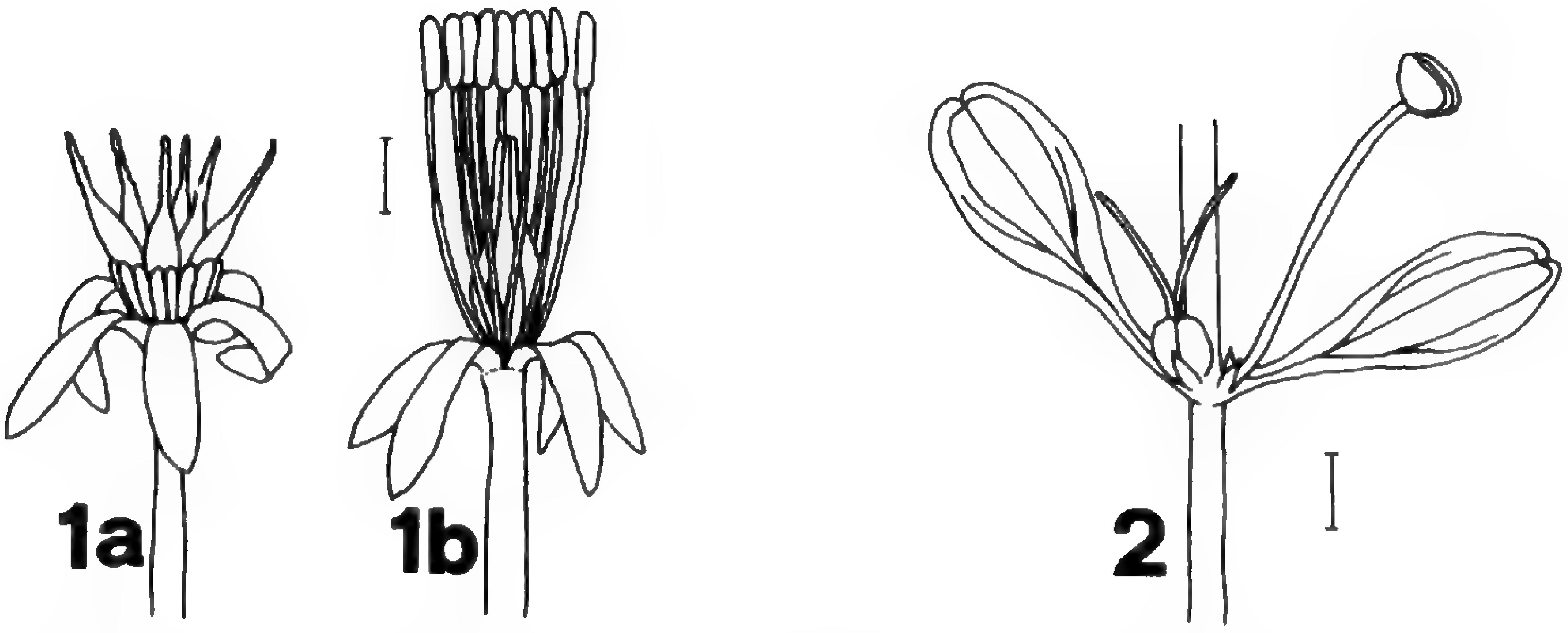
It has been suggested that *Acorus* and *Orontium* are wind pollinated. A considerable amount of work has been published on both genera, cited by Cook et al. (1974), but I have found no observational data on pollination. From their morphology (mostly bisexual flowers, relatively large perianth segments, small anthers, sticky pollen) they are probably entomophilous.

ERIOCAULACEAE

Because the flowers are small, rather insignificant, often unisexual, and apparently dry, they have been considered to be wind pollinated. However, the flowers are structurally complex and elaborate. In the few species examined, they secrete nectar, have sticky pollen, and are thus most likely insect pollinated or autogamous (see Stützel, 1981, 1984).

HANGUANACEAE

The flowers are small and unisexual with long slender filaments, which suggests anemophily (see Dahlgren et al., 1985). However, the pollen grains are spinulose, the male flowers have conspicuous fleshy bodies, and the stigmas are not exposed beyond the perianth, all of which suggests zoogamy. No direct observations on pollination have yet been reported.



FIGURES 1, 2. *1. Diagram of flowers of* Brasenia schreberi. *(a) Female phase. (b) Male phase. Scale bar = 6 mm.—2. Diagram of flowers of* Callitriche obtusangula. *Left, female flower. Right, male flower. Scale bar = 1 mm.*

LEMNACEAE

The flowers are unisexual, very small (stamens ca. 1 mm long, stigma ca. 0.5 mm above the carpel) and not obviously showy. Wind and water have been suggested as pollen vectors, but as Landolt (1986) pointed out, this is unlikely, as the pollen grains are spiny, sticky, often less than 20 μm in diameter, and sometimes only 20 grains develop in each locule; these characters all suggest zoogamy. Although water movements may bring flowers on different fronds in contact, the pollen is probably mostly transferred on the legs of different kinds of arthropods (flies, aphids, mites, small spiders). At least some races of *Lemna minor* and *Wolffiella oblonga* are self-incompatible, while many other species are self-compatible, although some of these are not autogamous and require a pollinator (for details see Landolt, 1986).

PODOSTEMACEAE

This family has about 45 genera, of which some, such as *Mourera* and *Tulasneantha*, are clearly insect pollinated. The majority, however, have very small, almost naked flowers (see Cook et al., 1974). Of these, some are probably autogamous, while others may well be wind pollinated (see Philbrick, 1984b). It is a shame that so little is known about the floral biology of this rather extraordinary family.

II. FAMILIES WITH WIND-POLLINATED SPECIES

CABOMBACEAE (sometimes included within the NYMPHAEACEAE)

Cabomba is insect pollinated, and *Brasenia* is wind pollinated (Fig. 1; see Osborn & Schneider, this volume: 778–794). *Brasenia* has most likely evolved to anemophily from entomophily in the aquatic milieu.

CALLITRICHACEAE

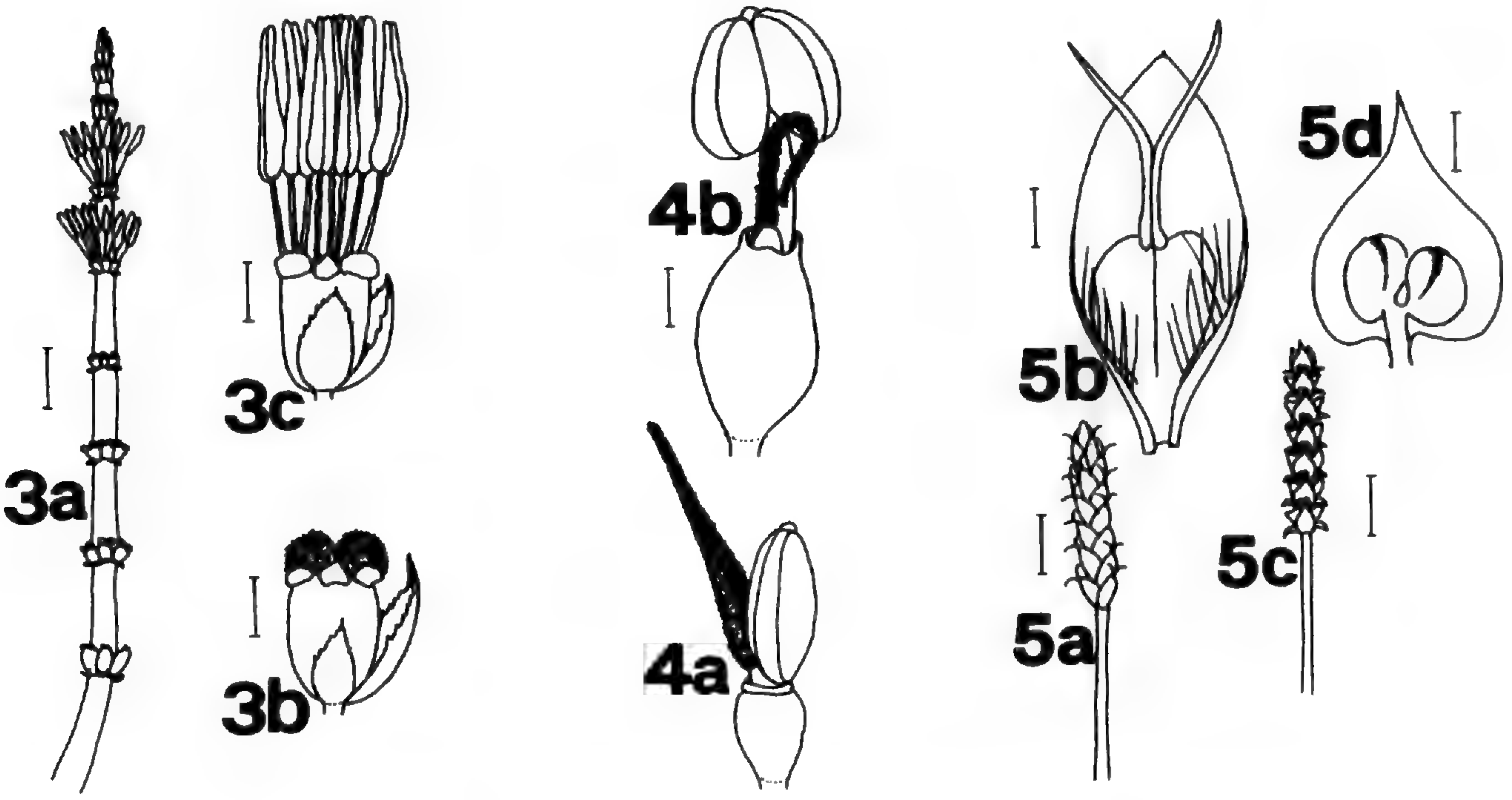
This monotypic family is wind pollinated (Fig. 2) or shows an extreme kind of autogamy above or below the water surface, described by Schotsman (1982, 1985) and Philbrick (1984a). It is doubtful that true hypohydrogamy (transfer of wet pollen through water to wet stigmas) takes place. It is also unlikely that epihydrogamy, with floating pollen, is an effective means of pollen transfer since the stigmas are usually either submerged or aerial.

HALORAGACEAE

Haloragis, *Laurembergia*, *Myriophyllum*, *Proserpinaca*, and *Vinkia* have aquatic species, all of which are well adapted to wind pollination. All have flowers with reduced and often caducous perianths (Fig. 3) and dry, powdery pollen liberated from long-filamented anthers. There is a trend from bisexual to unisexual flowers culminating in dioecy. Patten (1956) suggested without quantitative data that significant quantities of pollen may be transferred by insects in *Myriophyllum spicatum*.

HIPPURIDACEAE

This monotypic family has highly reduced bisexual or sometimes unisexual flowers. The stamens are reduced to one with a relatively massive anther, and the ovary is reduced to a virtually naked, one-seeded carpel (Fig. 4). The pollen is anemophilous-like. No published data on pollination have been found, but from personal observations it is strongly protogynous (Fig. 4), and seed-set is usually good. I can only assume it is wind pollinated.



FIGURES 3–5. *3. Diagrammatic representation of* Myriophyllum spicatum. *(a) Inflorescence, male above, female below. Scale bar = 1 cm. (b) Female flower. (c) Male flower. Scale bar = 1 mm.—4. Diagram of flowers of* Hippuris vulgaris. *(a) Female phase. (b) Male phase. Scale bar = 0.75 mm.—5. Diagrammatic representation of* Hydrostachys perrieri. *(a) Female inflorescence. Scale bar = 1 cm. (b) Female flower. Scale bar = 1 mm. (c) Male inflorescence. Scale bar = 1 cm. (d) Male flower. Scale bar = 1 mm.*

HYDROCHARITACEAE

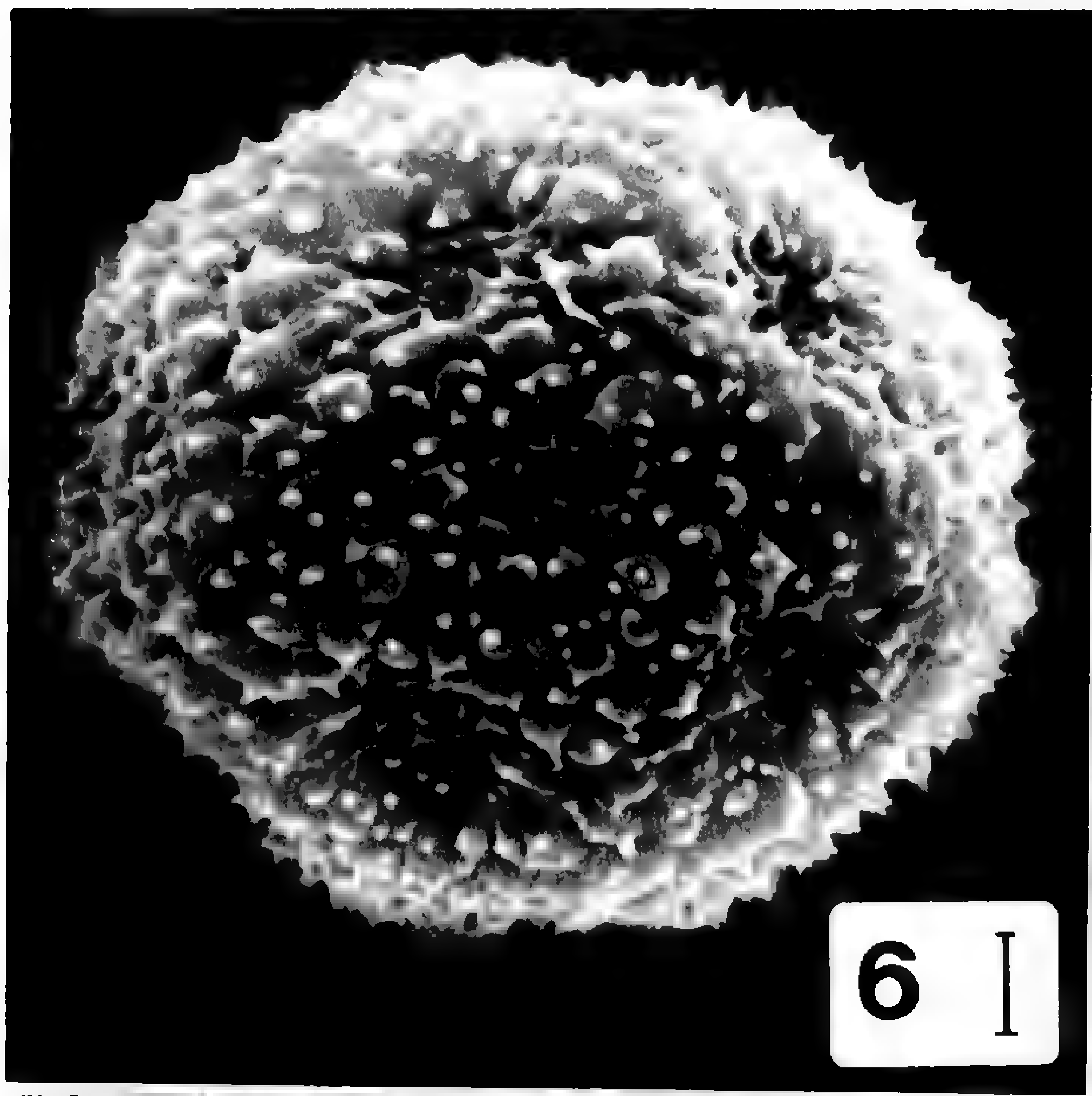
This exclusively aquatic family with 16 genera is extraordinary in its spectrum of floral structures, showing entomophily, anemophily, epi- and hypohydrophily (see Cook, 1982, for a general review). In *Appertiella, Enhalus, Lagarosiphon* (Figs. 7, 11), *Maidenia, Nechamandra,* and *Vallisneria* (Fig. 8) the male flowers become detached from the mother plant and are dispersed by wind or water currents; in these genera the pollen is sticky and transferred directly from anther to stigma. In *Elodea* the pollen is liberated on the surface of the water (Fig. 12) and is dispersed by wind or water currents to the stigma (Cook & Urmi-König, 1985). Although wind plays an important role in pollination, this kind of pollination is usually classified as epihydrophilous, since part of the pollen is in contact with water; however, it must be stressed that the pollen and stigma remain dry.

In pollination biology *Hydrilla* is remarkable, as shown by Cook & Lüönd (1982). The male flowers are liberated from the mother plant as buds, which then open explosively, shooting pollen grains through the air. The pollen of *Hydrilla* is inaperturate (the furrow illustrated by Yeo et al., 1984, is an artifact), spherical, 93 ± 5.7 μm in diameter, and densely covered with baculae 2 μm long, each bearing a small flamelike process (Fig. 9a, b). This pollen is too large and rough to "fit" in the wind pollination syndrome. The stigmas are rather small and borne at the base of a wineglasslike perianth (Fig. 10) exposed to the air but below the surface of the water. For effective pollination the pollen should not get into the airstream, as in other anemophilous plants, but must drop almost vertically to reach the stigmas, and it must stick and not bounce out again. The pollen is propelled through the air, but wind, as such, plays an unimportant role; I hope it is not necessary to create a new term for this unique pollination mechanism.

Described in detail by Cook & Urmi-König (1983), pollination in *Limnobium* is "normal" when compared with other genera of the Hydrocharitaceae. The sepals of the male flowers act as pollen-arresting organs (Fig. 13). The pollen is then "picked up" off the petals by the wind. The arched petals were suggested by Cook & Urmi-König (1983) to have an aerodynamic function, but after observations in the field it seems clear that their function is to keep the pollen dry when waves come or when it rains; when the flowers are immersed in water the sepals come to rest on the petals, thus enclosing an air bubble.

The marine genera *Halophila* and *Thalassia* have wettable pollen and stigmas and are pollinated underwater (hypohydrogamous).

Within the Hydrocharitaceae, *Limnobium* is the only genus with dry, powdery, and buoyant pollen that is transported to the stigmas by movements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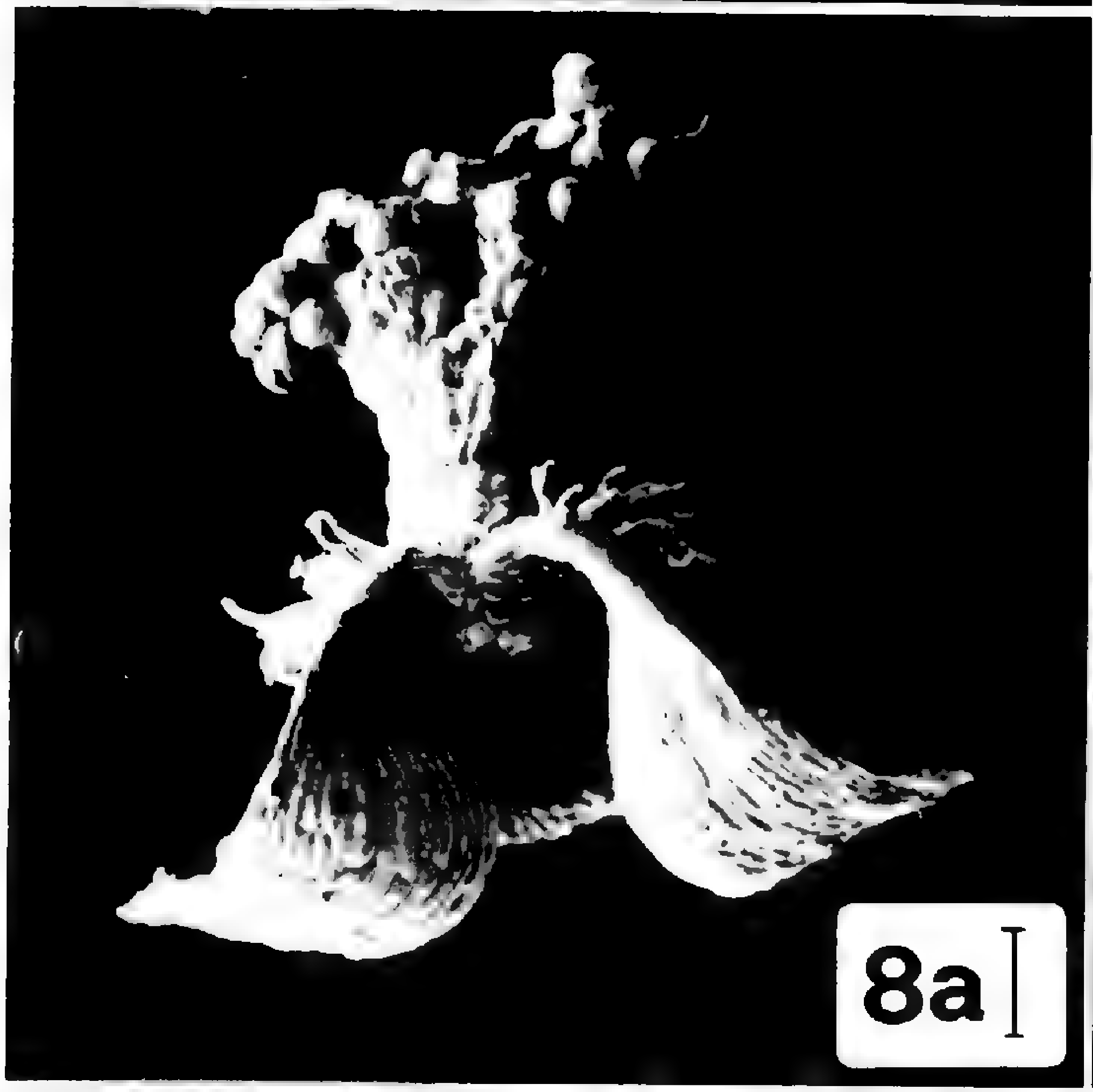
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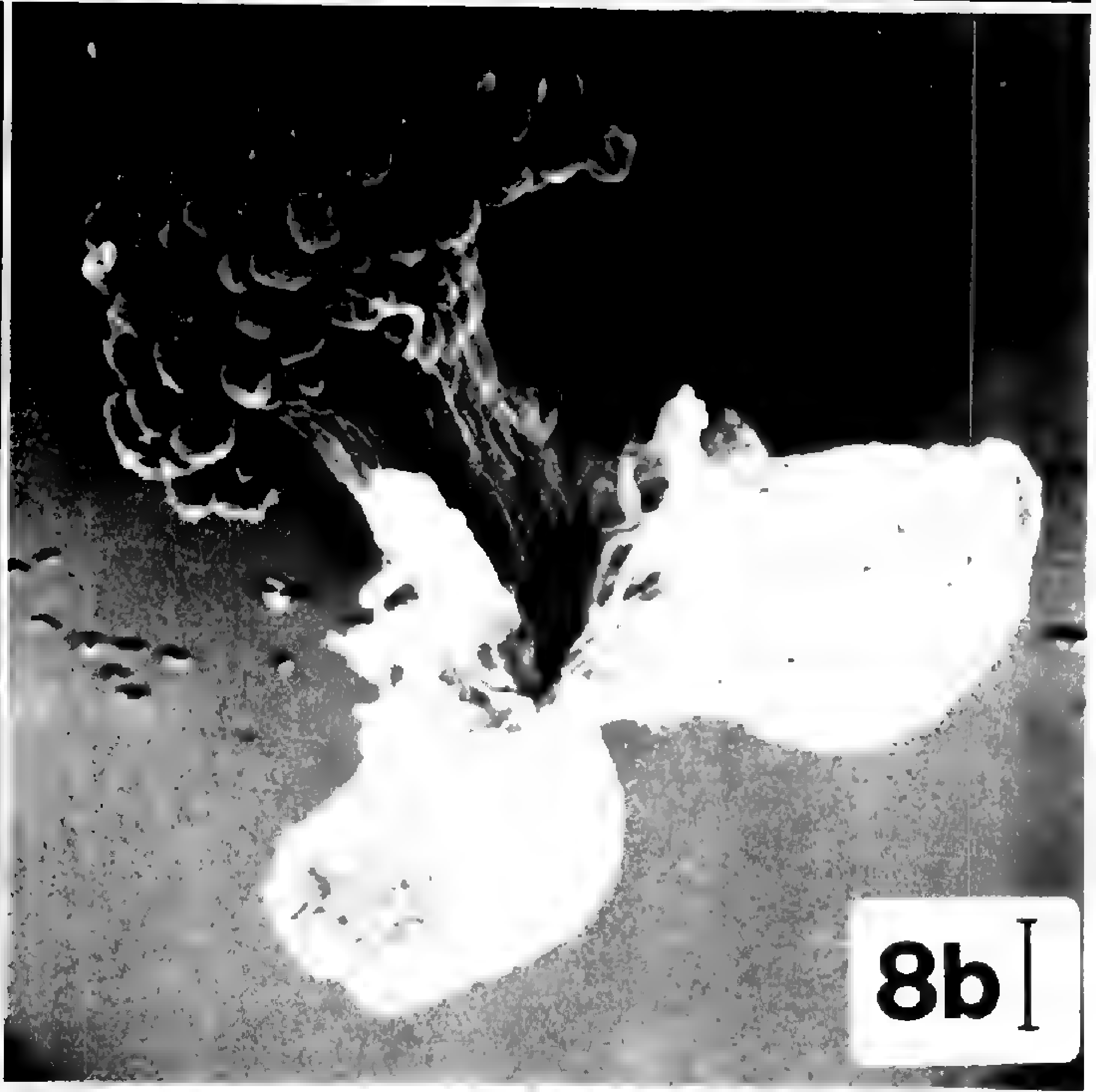
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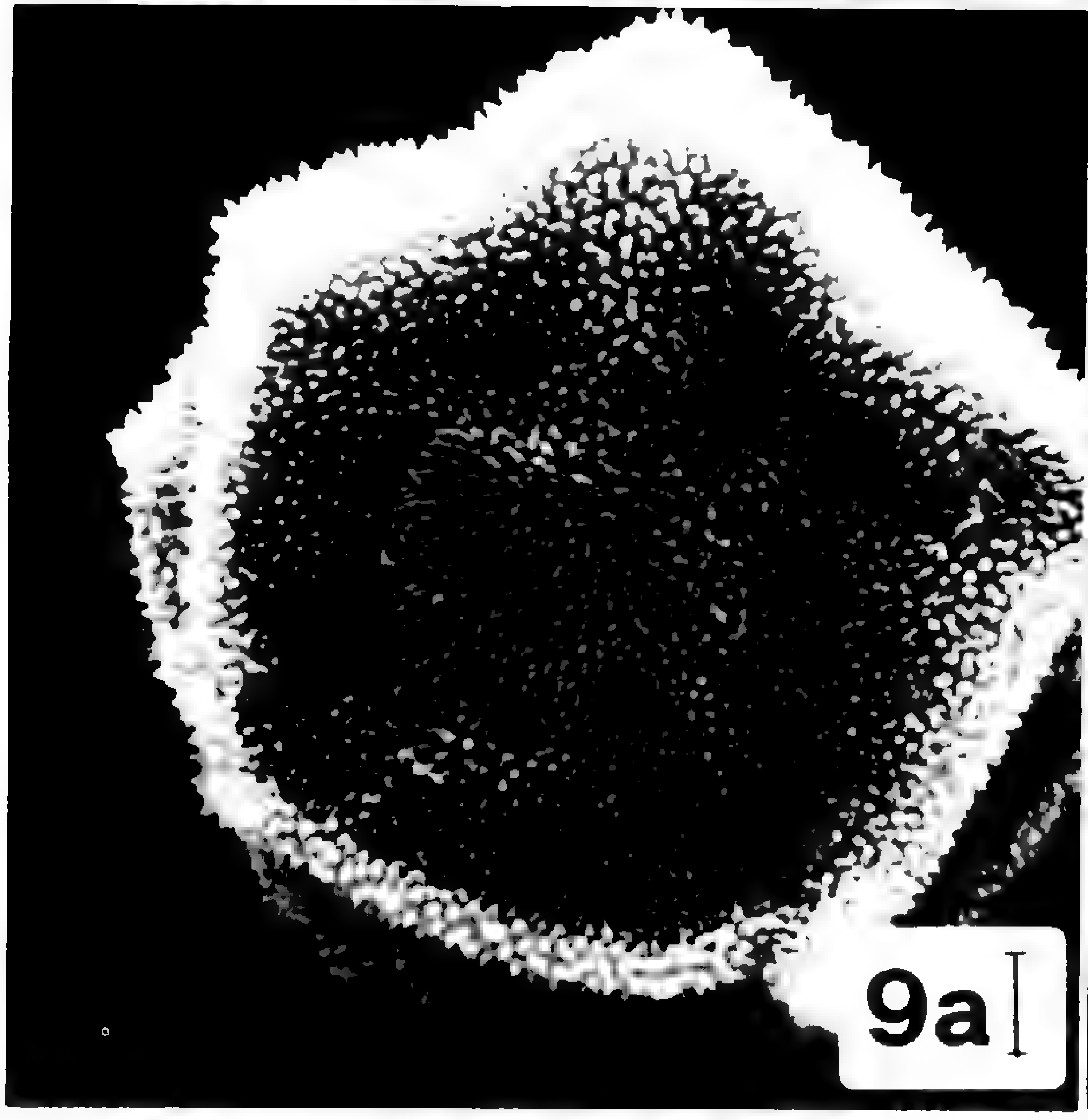
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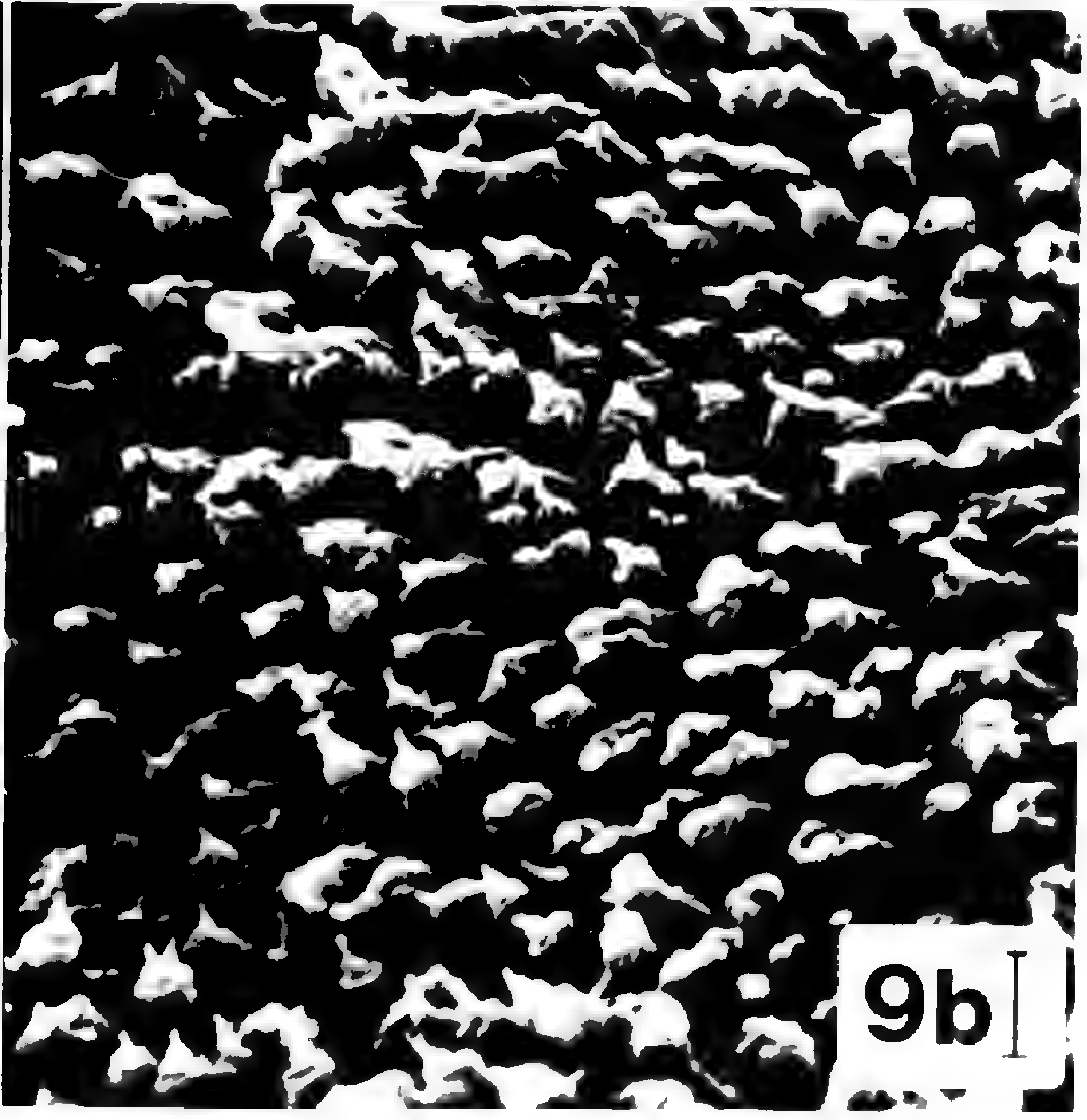
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of air and thus can be called anemophilous. *Hydrilla* has heavy pollen actively propelled through the air and is not dependent on air movements; it is, therefore, not strictly speaking "wind pollinated." Morphological and anatomical evidence indicates that the patristic relationships of *Limnobium* are to exclusively entomophilous genera *Hydrocharis*, *Ottelia*, and *Stratiotes*. The epi- and hypohydrogamous genera (within the framework of the Hydrocharitaceae) are not patristically close to *Limnobium* and are probably derived from a *Blyxa*-like ancestor. The genus *Blyxa* is essentially entomophilous or highly autogamous (Cook et al., 1981; Cook & Lüönd, 1983).

The evolution from entomophily to anemophily in *Limnobium* has most likely taken place within the aquatic environment. The expanded sepals, which hold pollen until wind carries it off, and the arched petals, which protect the pollen from waves and submergence, may be considered as elaborations connected with wind pollination and with the aquatic environment.

HYDROSTACHYDACEAE

This extraordinary monotypic family, reviewed by Cusset (1973), has about 22 species. The morphology of the flowers suggests anemophily (Fig. 5). The perianth is absent and a bract arrests the pollen, analogous to *Limnobium*. The carpel contains numerous seeds, an unusual feature in anemophily. No direct observations on pollination have been published.

JUNCAGINACEAE and LILAEACEAE

These two families are sometimes united. From the floral morphology they are wind pollinated, but I know of no direct observations. Some species have pollen-arresting mechanisms very like those in *Potamogeton*, and others have highly heteromorphic flowers (Fig. 14) (Posluszny et al., 1986).

PLANTAGINACEAE

The aquatic genus *Littorella* has obvious affinities to the terrestrial genera *Bougneria* and *Plantago*. Some species of *Plantago* show tendencies toward entomophily, but most are anemophilous. *Littorella*, however, shows further anemophilous specialization in having stalked male flowers and sessile, uniovulate female flowers.

POTAMOGETONACEAE and RUPPIACEAE

These two families are sometimes united. Most of the species of *Potamogeton* are wind pollinated, with erect, many-flowered spikes, spherical pollen grains, bisexual flowers with strong protogyny, and organs generally known as connective appendages to arrest the pollen and liberate it in the airstream after the female receptive phase (Fig. 15). *Potamogeton filiformis*, *P. pectinatus*, and others are pollinated below the water surface. This kind of pollination is described by Philbrick in this volume (pp. 836–841).

The pollination mechanism of *Groenlandia* has not, I believe, been critically described, but my own observations revealed that in spite of having rather short-stalked, two-flowered inflorescences, it is either autogamous or pollinated by wind and does not seem to be, as sometimes supposed, pollinated by floating pollen (epihydrogamous).

Ruppia is better known than the other genera; Verhoeven (1979) described the pollination in *R. cirrhosa* and *R. maritima* in detail. Both have curious elongated 'v'-shaped pollen grains (Fig. 16) that sometimes form chains. This might suggest hypohydrogamy, but the pollen is nonwettable and is liberated in bubbles; the stigmas are protected by the same bubbles. *Ruppia cirrhosa* is usually pollinated at the surface like *Elodea*, while *R. maritima*, in Europe, is usually pollinated in bubbles under water like *Potamogeton pectinatus*.

SPARGANIACEAE

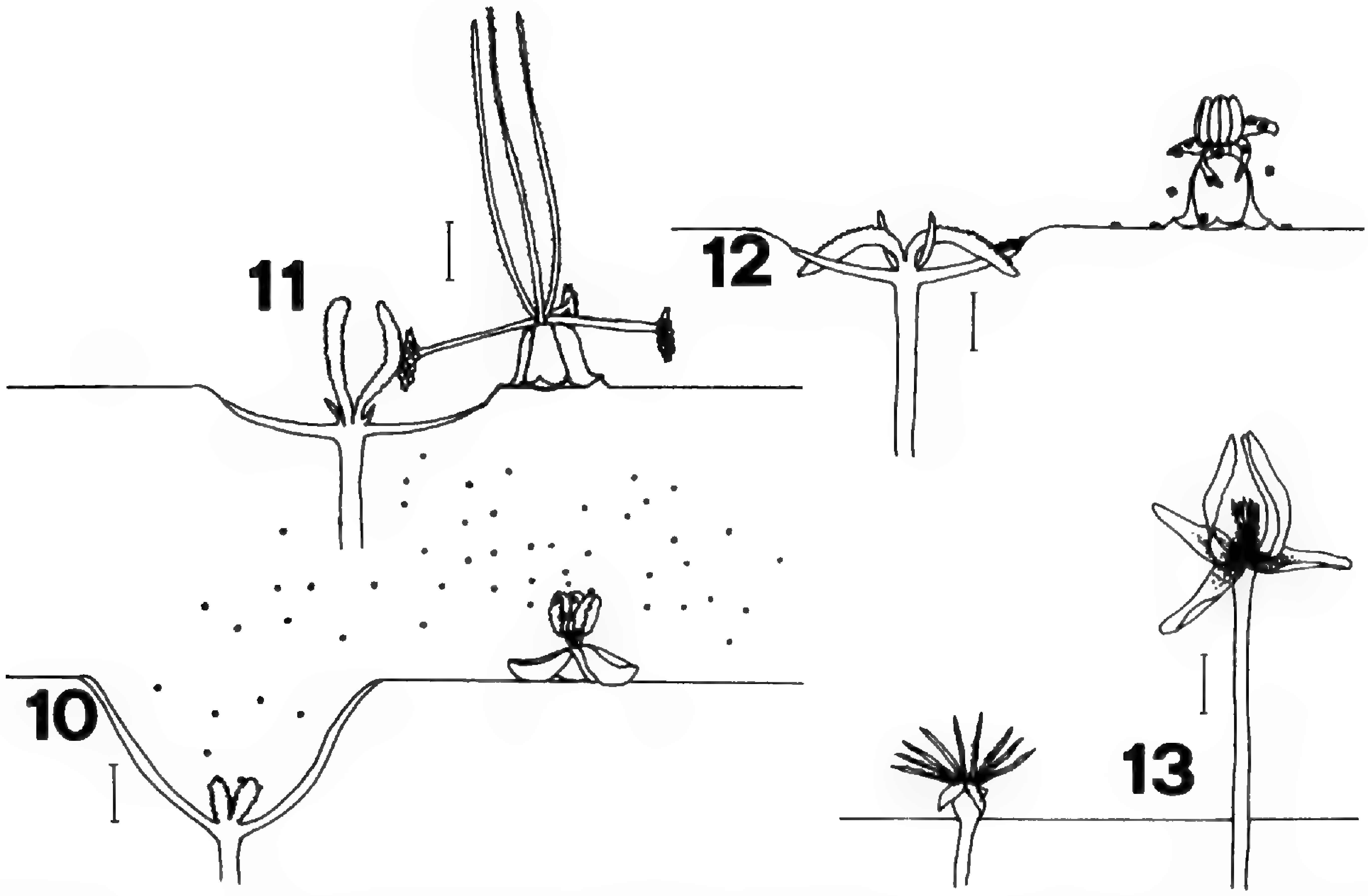
A monotypic family having flowers arranged in unisexual heads with male heads above females (Fig. 17). All species are clearly wind pollinated (Cook & Nicholls, 1986, 1987), in spite of the fact that some syrphid flies specialize on *Sparganium* pollen as a source of food.

THURNIACEAE

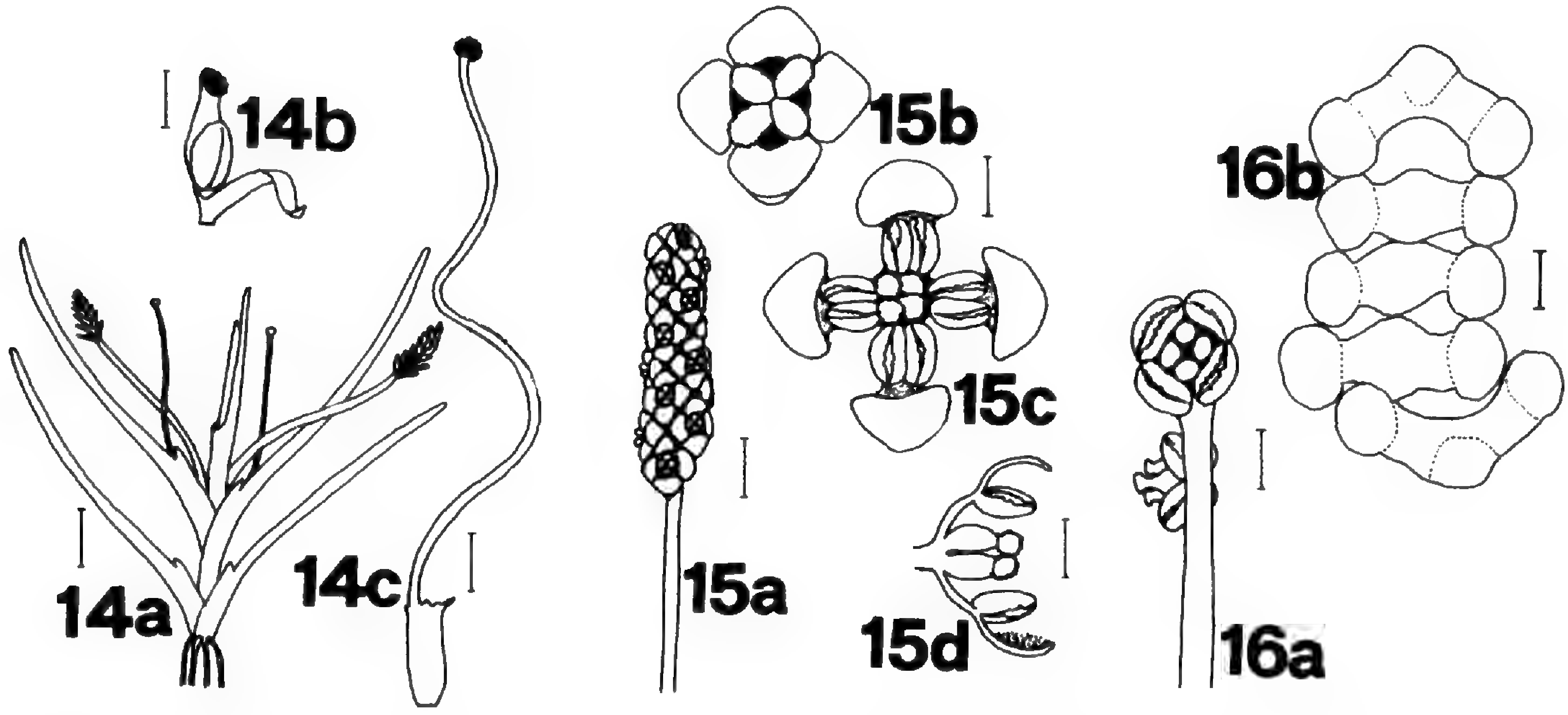
It is not certain that this monotypic family deserves to be called aquatic. The floral structure suggests pollination by wind (Fig. 18) but no observations have been published.

←

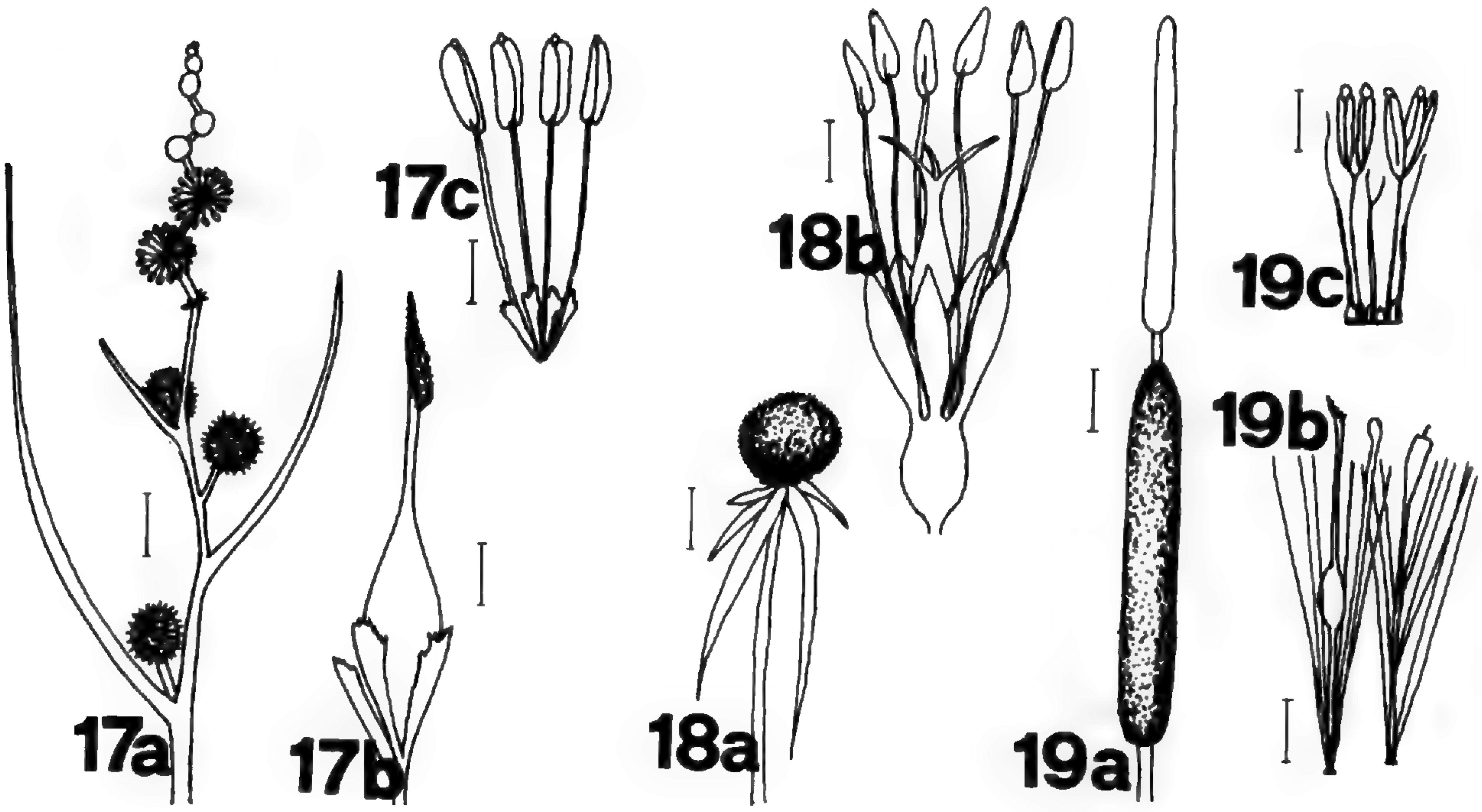
FIGURES 6–9. *6. Pollen grain of* Wiesneria triandra. *Scale bar = 5 µm.—7. Young male flower of* Lagarosiphon muscoides, *filaments and staminodes not fully extended and some pollen grains missing. Scale bar = 200 µm.—8. The male flower of* Vallisneria americana. *(a) Showing branched stamen. (b) The same from the other side, showing tepal. Scale bar = 100 µm.—9. Pollen of* Hydrilla verticillata. *(a) A somewhat shrunken grain; when fresh they are spherical. Scale bar = 10 µm. (b) Detail of surface showing baculae. Scale bar = 2 µm.*



FIGURES 10-13. *10. Diagram of pollination in* Hydrilla verticillata. *Left, female. Right, male. Scale bar = 0.8 mm.—11. Diagram of pollination in* Lagarosiphon muscoides. *Left, female. Right, male. Scale bar = 1.2 mm.—12. Diagram of pollination in* Elodea nuttallii. *Left, female. Right, male. Scale bar = 2 mm.—13. Diagram of the flowers of* Limnobium laevigatum. *Left, female. Right, male. Scale bar = 3 mm.*



FIGURES 14-16. *14. Diagrammatic representation of* Lilaea scilloides. *(a) Whole plant with inflorescences. Scale bar = 8 mm. (b) Bisexual flower. Scale bar = 3 mm. (c) Long-styled, female flower. Scale bar = 5 mm.—15. Diagrammatic representation of* Potamogeton polygonifolius. *(a) Inflorescence during female phase. Scale bar = 1 mm. (b) Flower at female phase. Scale bar = 1 mm. (c) Flower at male phase. Scale bar = 1 mm. (d) Longitudinal section of flower at male phase, showing the connective appendages as pollen arresting organs. Scale bar = 1 mm.—16. Diagram of* Ruppia maritima. *(a) Inflorescence. Scale bar = 1 mm. (b) Chain of five pollen grains. Scale bar = 20 μm.*



FIGURES 17–19. *17. Diagrammatic representation of* Sparganium emersum. *(a) Inflorescence; male flowers above, females below. Scale bar = 2 cm. (b) Female flower. Scale bar = 1 mm. (c) Male flower. Scale bar = 1.5 mm.—18. Diagram of* Thurnia sphaerocephala. *(a) Inflorescence. Scale bar = 1 cm. (b) Flower. Scale bar = 0.8 mm.—19. Diagrammatic representation of* Typha angustifolia. *(a) Inflorescence; male above, female below. Scale bar = 2 cm. (b) Female flowers; left fertile, right sterile. Scale bar = 2 mm. (c) Male flowers. Scale bar = 1 mm.*

TYPHACEAE

This monotypic family is relatively well documented and is clearly wind pollinated (Fig. 19; see Krattinger, 1975), even though syrphid flies may collect pollen adhering to the female inflorescence.

All species have single ovules in each flower; some species, however, have pollen in tetrads. This contradicts all previous theoretical predictions regarding the function of pollen tetrads in pollination. Nicholls & Cook (1986) found that pollen tubes from tetrads are capable of traversing from the stigma of one flower through air to the stigma of another (Fig. 20) and fertilizing neighboring flowers. This results in increased efficiency of gametes in effecting fertilization (measured as seed-set) compared with other species of *Typha* having single pollen grains.

CONCLUSIONS

About 79 angiosperm families and 380 genera contain aquatic species. Most of the data are to be found in Cook et al. (1974). Excluding the Podostemaceae, because its floral biology is so poorly known, 31.6% of the families and 42% of the genera are pollinated abiotically.

Of the abiotically pollinated genera, 18 (or 19 including *Potamogeton*) have wettable pollen and are pollinated under water; about seven genera are pollinated at the water surface. This leaves 119 genera (35.5%) exclusively wind pollinated. I have tried without success to find geographical correlations between pollination and distribution of aquatics; it seems that about one-third wind pollinated remains reasonably constant when one compares the Old and New worlds, Northern and Southern hemispheres, and Tropics and Temperate zones. Within particular plant communities or associations there are enormous differences in the proportion of wind-pollinated species as also found by Kugler (1971). Reedswamp and sedge-dominated communities are mostly made up of wind-pollinated plants. Also the plants of deep and permanent water are mostly abiotically pollinated; all the marine angiosperms, for example, are hydrogamous. Nevertheless, about two-thirds of all aquatic genera (and this probably also applies at the level of species) are biotically pollinated.

So little is known about the breeding systems of aquatic species that it is not possible to generalize on in- or outbreeding within the context of the mode of pollination.

Aquatic angiosperms have evolved from terrestrial ancestors. All available evidence suggests that the aquatic members of at least six families (Centrolepidaceae, Cyperaceae, Hydatellaceae, Juncaceae, Plantaginaceae, and Poaceae) have evolved from anemophilous ancestors. This translates to an

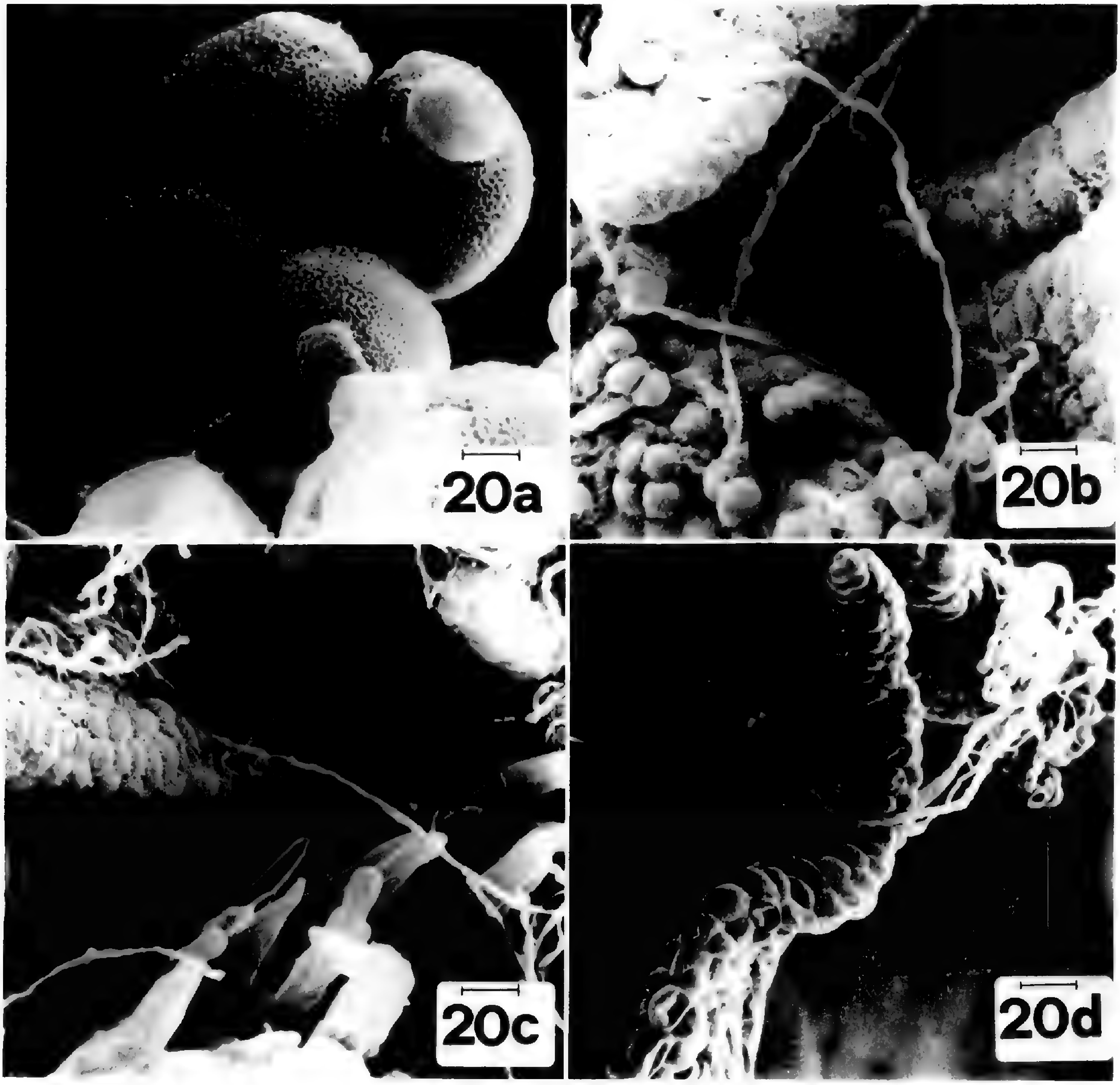


FIGURE 20. Typha latifolia.—*a. Pollen tetrad, two grains germinating. Scale bar = 5 μm.—b–d. Pollen tubes crossing from one stigma to another. b, scale bar = 3 μm; c, d, scale bar = 50 μm.*

estimate of at least 100 genera that brought anemophily with them into the aquatic milieu. This leaves a mere 19 genera where the anemophily may have evolved subsequent to the invasion of the aquatic habitat. When these 19 genera are examined a little closer, although they do not have any obvious terrestrial relatives, they mostly belong to exclusively anemophilous families (Callitrichaceae, Haloragaceae, Hippuridaceae, Hydrostachydaceae, Lilaeaceae, Potamogetonaceae, Ruppiaceae, Sparganiaceae, Thurniaceae, and Typhaceae).

In only *Brasenia* (Cabombaceae) and *Limnobium* (Hydrocharitaceae) is it very likely that the evolution from entomophily to anemophily has taken place in the aquatic environment. The genus *Hydrilla* (Hydrocharitaceae) is not strictly "wind" pollinated, because heavy pollen grains are actively propelled from the male flowers to the females. This mechanism relies on water and therefore probably evolved in water. However, it shows an alternative pathway to the evolution of anemophily.

From a total of 380 aquatic angiosperm genera, a minimum of two and a maximum of 19 may have evolved from entomophily to anemophily subsequent to the invasion of the aquatic habitat. From these numbers alone it does not seem likely that pollination by wind is a feature that is especially associated with life in the aquatic environment like, for example, the presence of gas spaces (lacunae) and hydropoten or the absence of lignin and/or stomata. Many aquatics clearly evolved from terrestrial groups that were already anemophilous; there is no evidence that any of these aquatics have returned to biotic pollen transfer. Taken as a whole, it is not possible to say that anemophily is particularly beneficial or detrimental to plants living in water. However, it is remarkable, when the different floral types illustrated in this contribution are compared, how many different strategies are adopted to guarantee transference of pollen by means of wind. There are no obvious trends among the wind-pollinated aquatics that indicate the pathway to hydrogamy. "Aquatic" anemophily is not different from "terrestrial" anemophily.

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MORPHOLOGICAL STUDIES OF THE NYMPHAEACEAE SENSU LATO.
XVI. THE FLORAL BIOLOGY OF *BRASENIA SCHREBERI*[1]

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ABSTRACT

Observations conducted in East Texas on the pollination biology of Brasenia schreberi *J. F. Gmel. confirm that anthesis is diurnal, with individual flowers opening and closing for two consecutive days. First-day flowers are morphologically and functionally pistillate. They are characterized by short, undehisced stamens and elongated, papillate stigmas that radiate outward over the perianths, providing an expanded surface area for pollen adherence. Second-day flowers are morphologically and functionally staminate. Staminal filaments are elongated, elevating the dehiscent anthers to a position above the centrally aggregated stigmas. Although self-pollination occurs, dichogamy prevents individual flowers from self-fertilizing.* Notiphila *cf.* cressoni *(Diptera; Ephydridae) was the most frequent insect visitor. Based on behavior and pollen loads, insect pollination is insignificant. The expanded stigmatic surface area, exserted stamens, and additional floral and vegetative features are adaptations for wind pollination. Data from pollen dispersal experiments indicate that anemophily is the primary mechanism of pollen transfer. This pollination mechanism is unique in the Nymphaeaceae sensu lato. Evidence from pollination biology, floral anatomy, seed anatomy, and embryology indicates a close evolutionary relationship between the Cabombaceae and Nymphaeaceae sensu stricto. Genera of the Nymphaeaceae s. str. and Nelumbonaceae exhibit a phyletic elaboration of the flower, whereas the Cabombaceae represent a phyletic reduction.*

Brasenia schreberi J. F. Gmelin is a monotypic genus with a wide but sporadic distribution in lakes, ponds, and slow streams. It occurs in eastern Asia, Australia, Africa, the West Indies, and South, Central, and North America. In North America the species ranges from Florida to East Texas, north to Prince Edward Island, southern Quebec, southern Ontario, and Minnesota. It also occurs in Idaho, California, north to British Columbia, and Alaska (Wood, 1959). Although *Brasenia* does not presently occur in Europe, fossil specimens are known (Srodon, 1935; Tralau, 1959; Jessen et al., 1959; Hall, 1978; Collinson, 1980). *Brasenia* is commonly known as water-shield, water-target, purple bonnet, and purple wen-dock and is a cultivated food source in Japan (Matsuda & Hara, 1985).

Brasenia is one of eight genera within the Nymphaeaceae sensu lato as circumscribed by Bentham & Hooker (1862). Subsequent workers have grouped the nymphaeaceous genera into various orders, families, and tribes (for review see Goleniewska-Furmanowa, 1970; Takhtajan, 1980; Cronquist, 1981). The opinions that the genera should be divided among three subfamilies or three families (Nymphaeaceae, Nelumbonaceae, and Cabombaceae) within the order Nymphaeales has been widely advocated on the basis of available data. A ninth genus, *Ondinea*, was described by den Hartog (1970) and placed within the Nymphaeaceae sensu stricto. This taxonomic alignment is supported based by studies of seed anatomy, floral morphology, and floral biology (Schneider, 1978, 1983).

In all systematic treatments, *Brasenia* has been allied with *Cabomba* on the basis of such shared morphological features as long, slender, sympodial stems; peltate floating leaves; small hypogynous flowers with apocarpous gynoecia, and few floral parts. Moseley et al. (1984), comparing anatomical

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and morphological features of the vegetative axes and flowers in *Cabomba* and *Brasenia*, suggested that the two genera are more distant taxonomically than envisioned by earlier workers (Vinogradov, 1967; Goleniewska-Furmanowa, 1970; Bukowiecki et al., 1972, 1974), a view also shared by Collinson (1980). Moseley et al. emphasized, however, that the taxonomic distance was not adequate to warrant dismantling the Cabombaceae. Richardson (1969) concluded that the floral vascular system (and by inference, the flower) of *Brasenia* exhibits a phylesis toward condensation and reduction from a more primitive, larger-flowered ranalian ancestor. Ito (1986a) determined that the ontogeny and anatomical construction of the receptacular vascular plexus, a feature common to all water lily genera, differs in the Cabombaceae from those found in the Nymphaeaceae s. str. Ito also considered the floral vasculature of *Cabomba* to be derived (via reduction in the number of stamens and carpels) from the type of vasculature found in the flower of *Brasenia*.

Numerous studies of *Brasenia* involving a diversity of features have been conducted including: seed anatomy and embryology (Weberbauer, 1893, 1894; Chifflot, 1902; Cook, 1906, 1909; Melikyan, 1964; Khanna, 1965; Corner, 1976); pollen morphology (Wodehouse, 1932; Ikuse, 1955; Ueno & Kitaguchi, 1961; Ueno, 1962; Meier, 1964; Walker & Doyle, 1975; Walker, 1976a, b; Clark & Jones, 1981; Batygina & Shamrov, 1983); xylem anatomy (Kosakai, 1968); karyology (Langlet & Söderberg, 1927; Okada & Tamura, 1981); chemical analyses (Nakahara, 1940; Riemer & Toth, 1970; Goleniewska-Furmanowa, 1970; Kakuta & Misaki, 1979; Sevilla et al., 1984); leaf development and anatomy (Goleniewska-Furmanowa, 1970; Kaul, 1976; Chen & Zhang, 1986); floral anatomy (Troll, 1933; Moseley, 1958; Khanna, 1965; Richardson, 1969; Moseley et al., 1984; Ito, 1986a); paleobotany (Hall, 1978; Collinson, 1980; Dorofeev, 1984); and general morphology and taxonomy (Lawson, 1888; Schrenk, 1888; Caspary, 1891; Keller, 1893; Raciborski, 1894; Schilling, 1894; Gwynne-Vaughn, 1897; Hill, 1900; Chrysler, 1938; Wood, 1959; Adams, 1969; Kristen, 1974; Ogden, 1974; Rao & Banerjee, 1979; Matsuda & Hara, 1985). Little attention, however, has been given to the floral (pollination) biology of the genus. Tokura (1937) investigated the blooming of *Brasenia* in Japan and was the first to record the movements of floral parts during the two-day anthesis period. Tokura suggested that flowers on the first day of anthesis are pistillate, while on the second day staminate, during which time large quantities of pollen are released. Tokura noted the importance of the increased height of second-day, pollen-releasing flowers above those of the first-day, pollen-receptive flowers from the standpoint of pollen transfer but did not suggest the vector(s) for pollination. Schneider & Jeter (1982) reported "*Notiphila*-like" flies functioning as pollinators in populations of *Brasenia* growing in East Texas.

This investigation is part of a continuing series of studies designed to contribute new evidence for determining relationships among water lily genera. It is the objective of this study to: (1) confirm and amplify observations on floral morphology and floral behavior during anthesis of *Brasenia*; (2) elucidate the mechanism(s) of pollen transfer and relate floral morphology to pollination syndrome(s); and (3) compare the pollination biology of *Brasenia* with other genera of Nymphaeaceae s.l. This may contribute to a better understanding of the phylogeny of this angiosperm family, which occupies a basal, pivotal systematic position in many old and modern classification schemes.

MATERIALS AND METHODS

SITE DESCRIPTION

Observations on the floral biology of *Brasenia* were conducted during the summers of 1986 and 1987 in Toledo Bend Reservoir, Sabine County, Texas. Extensive populations of *Brasenia* exist in numerous coves throughout the reservoir. This study was conducted in a cove of six surface hectares adjacent to the Willow Oak Recreation Area. The water level within the reservoir fluctuated widely throughout the study period. The depth of water in which *Brasenia* grew ranged from 0.5 to 2.5 m.

FLORAL CYCLE

Ten flowers in various stages of anthesis were tagged with numbered fluorescent orange corks by securing them to peduncles with nylon fishing line. Heights of the floral structure above and below water level were measured over four consecutive days. Measurements were made from the base of the receptacle to the water level. In addition, sepal, petal, staminal, and stigmatal positions were observed.

CAGING TREATMENTS

Exclusion treatments were accomplished by placing floating cages over emergent flowers for the duration of anthesis. Flowers were tagged with fluorescent corks attached to the peduncle for fruit retrieval. Different experiments were identified by color-coded survey ribbons stapled to corks. Cages consisted of 950-ml styrofoam and plastic drinking cups mounted inversely on 21-cm^2 styrofoam sheets. The center portion of the styrofoam base was removed to allow placement of cages over flowers. Two types of cages were used: one to exclude all abiotic and biotic pollen vectors, and a second to exclude only biotic vectors. Abiotic and biotic exclusion cages were made from clear plastic cups (transparent cages). Biotic exclusion cages were produced using styrofoam cups with four rectangular windows cut out around their circumferences. Windows were covered with 1-mm^2 fiberglass mesh screen glued to the styrofoam cups (mesh cages). Transparent cups were mounted on 2.5-cm-thick styrofoam, while mesh cups were mounted on 1.3-cm-thick styrofoam sheeting to maximize flower exposure through the mesh windows above the styrofoam base. Both types of cups were mounted to the styrofoam bases with water-insoluble glue.

Three control groups, each consisting of 25 second-day flowers, were tagged during intervals throughout the study period to determine natural seed set. An additional control group, consisting of 25 flowers that had morphologically short stigmas, was also tagged. Each exclusion treatment involved various floral manipulations of 25 first-day flowers and their subsequent seed production to check for the following:

Parthenocarpy (Group A). Flowers were covered prior to anthesis with transparent cages and emasculated. Emasculation involved the removal of undehisced anthers on the first day of anthesis. Cages were observed periodically throughout anthesis to check flower position and condition.

Autogamy (Group B). Flowers were covered with transparent cages and left undisturbed.

Stigmatic receptivity (Group C). (1) Flowers were covered with transparent cages and emasculated. First-day stigmas were dusted copiously with pollen transferred mechanically from uncaged pollen-releasing flowers. (2) Flowers were covered with transparent cages and emasculated. Pollen was transferred mechanically to second-day stigmas.

Allogamy (Group D). (1) Geitonogamy. Flowers were covered with transparent cages and mechanically cross-pollinated on the first day with pollen from uncaged flowers from the same plant. (2) Xenogamy. Flowers were covered with transparent cages and cross-pollinated on the first day with pollen from uncaged flowers from different plants.

Anemophily (Group E). (1) Flowers were covered with mesh cages and left undisturbed. (2) Flowers were covered with mesh cages and emasculated.

POLLEN DISPERSAL AND TERMINAL SETTLING VELOCITY

The presence of wind-borne *Brasenia* pollen was determined using an Andersen 0101 particle-size air sampler (Andersen, 1958). In addition, dispersed pollen was quantified by measuring distance and angle of dehiscence from pollen-releasing flowers. Measurements were made using calibrated poster boards 71.5 × 56 cm. Black poster boards (pollinometers) were marked in increments of 10 cm and 20° from the midpoint of one edge (Fig. 1). Circles equal in size to an average stigmatic surface area of a first-day flower were drawn into distance-angle segments. Boards were laminated and mounted on 2.5-cm-thick styrofoam.

Individual pollinometers were placed downwind from single pollen-releasing flowers with the peduncle at the 0° mark between 0800–1200 hours. All additional pollen-releasing flowers from the surrounding 3-m radius were removed. Pollinometers were retrieved after total anther dehiscence, and the number of pollen grains within each circle was quantified using a hand lens. Samples were taken on two separate days, six trials per day. Wind-speed measurements were taken using a Taylor anemometer. Results were analyzed using Student's *t*-test and regression analyses.

Stigmas were viewed with a dissecting microscope to detect the presence of pollen. These included stigmas on uncaged first-day flowers in close proximity and downwind of pollen-releasing flowers and uncaged first-day flowers not adjacent to pollen-releasing flowers. Comparisons were made of pollen quantity on stigmas of flowers in each condition. Additionally, pollen distribution was observed (e.g., more grains on leeward or windward surfaces).

The terminal settling velocity of freshly collected *Brasenia* pollen was determined utilizing the stroboscopic photography techniques of Niklas (1984).

POLLEN–OVULE RATIOS AND POLLEN VIABILITY

The number of pollen grains/flower was determined by suspending all pollen from 10 anthers in a 0.5-ml solution of aniline-blue in lactophenol and counted using a hemacytometer (Cruden, 1977). Pollen–ovule ratios were calculated assuming a mean number of 28 anthers and 12 carpels (24

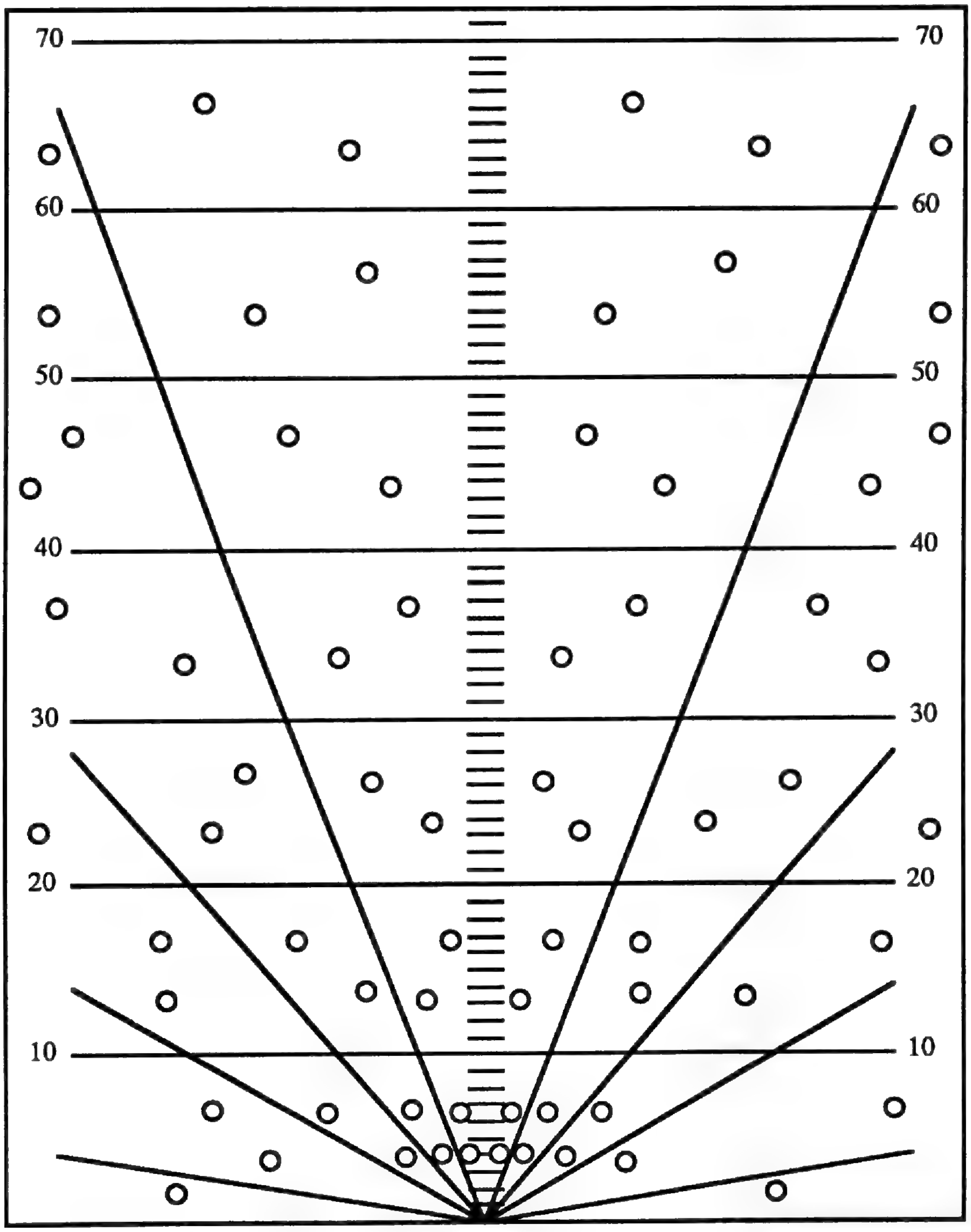

FIGURE 1. *Pollinometer. Circles represent the average stigmatic surface area of first-day flowers. Seventy cm scale.*

ovules) per flower. Pollen viability was determined using aniline-blue in lactophenol staining.

FLORAL DENSITY

The distributional density of flowers was determined by counting the total number of first- and second-day flowers within ⅛-m frames in a random stratified design.

FLORAL SECRETIONS

The presence of floral secretory tissues was determined using neutral red stain as an indicator (Esau, 1965; Vogel, 1966). Fresh first- and second-day flowers were placed in neutral red for three to six hours. After excess stain was removed by lightly washing with water, the flowers were examined using a dissecting microscope.

ULTRAVIOLET REFLECTANCE AND ABSORPTION

Ultraviolet (UV) photographs using black and white Kodak Plus X film, 125 ASA, and a Kodak Wratten ultraviolet filter No. 18A were made of first-day and second-day flowers and leaves in sunlight. Second-day flowers were photographed prior and subsequent to anther dehiscence.


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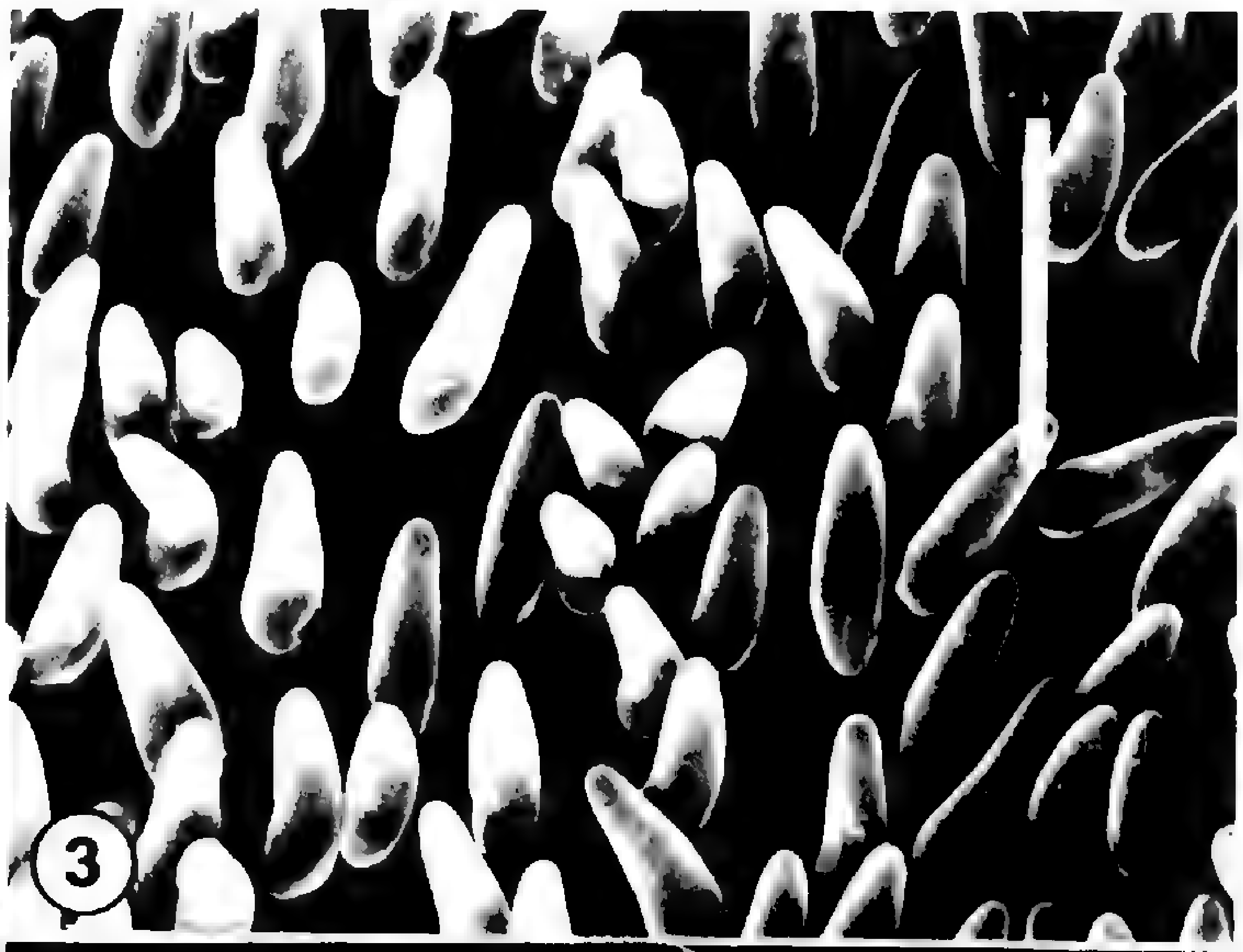
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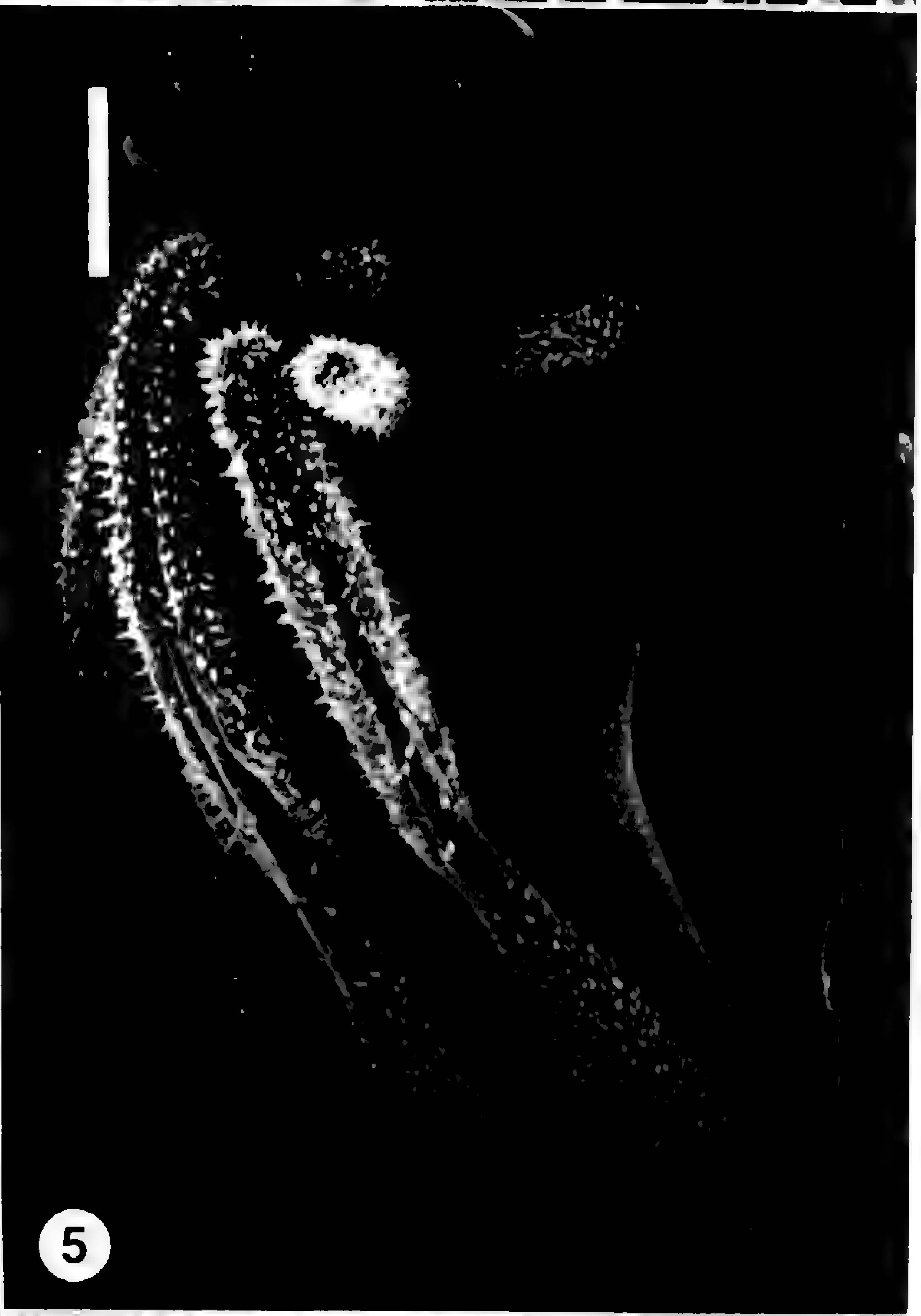
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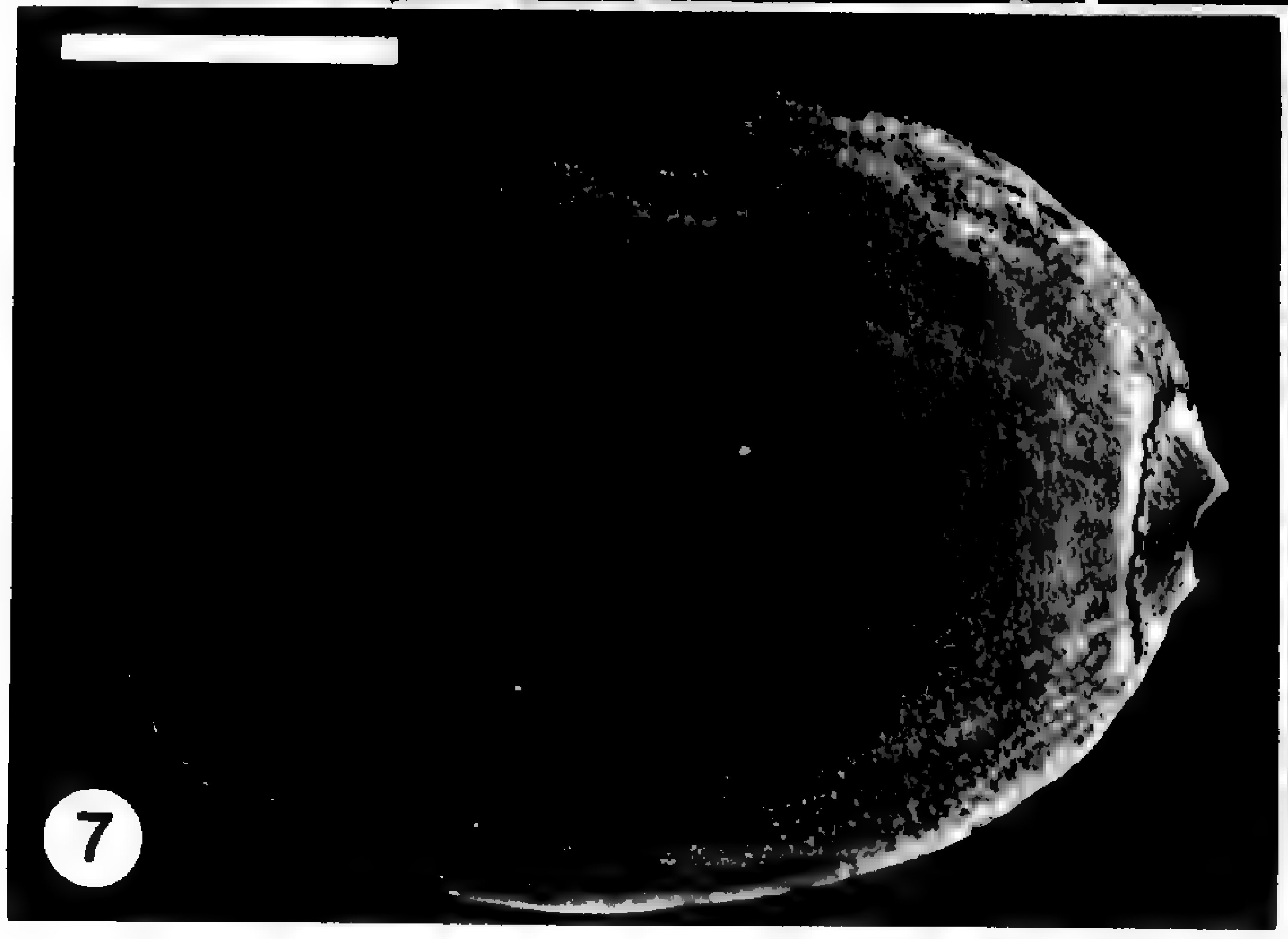
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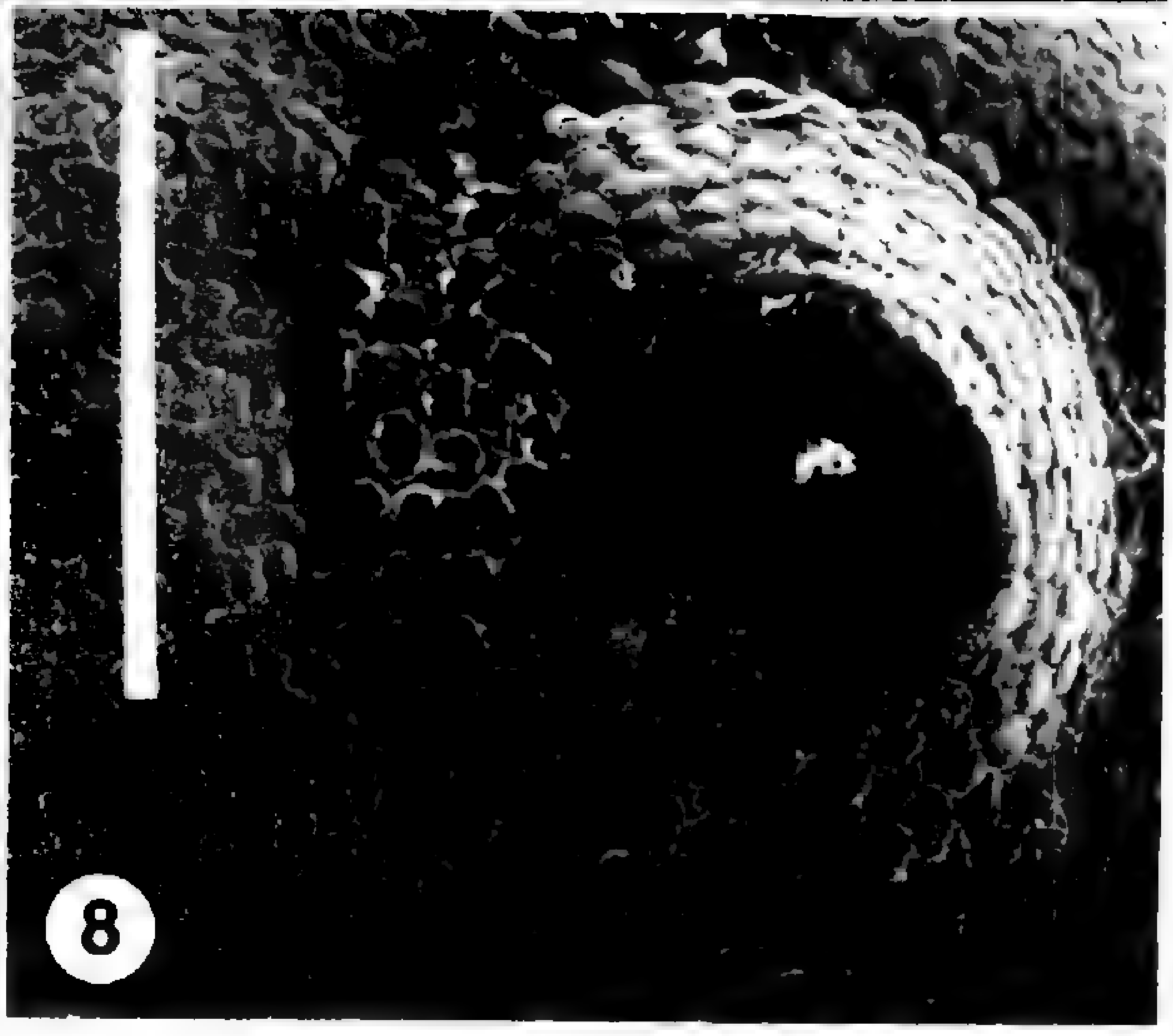
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ANTHOPHILOUS VISITORS

Observations were made to determine diversity, frequency, behavior, and extent of pollen loads of various insect visitors. Insects on flowers and leaves were collected using kill jars with ethyl acetate and were preserved in 70% ethanol. Voucher specimens are housed at SWTSU.

SCANNING ELECTRON MICROSCOPY

Floral and fruit specimens were investigated with a Cambridge S90 scanning electron microscope (SEM). Tissues were fixed for 24 hours in 2% glutaraldehyde in 0.1 M cacodylate buffer, pH 7.2. Samples were washed with the buffer and postfixed in 1% osmium tetroxide for three hours, then stored in the buffer. Floral specimens were dehydrated in acidified dimethoxypropane (Postek & Tucker, 1976; Linn et al., 1977) and critical-point dried. Seeds were immersed in acetone and placed in an ultrasonicater for five minutes and air dried. Pollen grains were pipetted onto filter paper and air dried. Floral and seed specimens were sputter-coated with gold or gold–palladium and then mounted on aluminum stubs with colloidal graphite. Pollen grains were mounted by inverting finely polished stubs covered with Mikrostik® onto filter papers with the dried pollen and then sputter-coated.

OBSERVATIONS

HABIT

Brasenia is a rhizomatous, aquatic perennial. The rhizomes bear axillary buds, adventitious roots, and leaves at each node. Leaves are alternate, long-petioled, and centrally peltate. Young leaves are involute in bud. Mature leaf blades are floating and oval to elliptic with entire margins. Submerged stems, petioles, and abaxial leaf surfaces are heavily coated with a layer of transparent mucilage, as are young plant parts such as axillary buds and juvenile leaves (Fig. 2).

Flowers of *Brasenia* are about 2 cm in diameter, dull purple, and emergent. They are borne singly on long, mucilage-coated peduncles and possess linear-lanceolate perianth parts with three petaloid sepals and three petals. All perianth members bear antrorse, adaxial trichomes (Fig. 3).

The androecia of flowers within the study site are composed of 24–33 stamens with filiform filaments and four apical microsporangia. Dehiscence is latrorse in the study populations. Pollen grains are elliptic, monosulcate, and have faintly scabrate ornamentation (Fig. 4). The pollen–ovule ratio of *Brasenia* is 9,238 ± 625 (95% C.I., N = 11), and 98% of the pollen is viable.

Flowers are hypogynous with apocarpous gynoecia of 10–14 carpels in Toledo Bend populations. These are characterized by relatively short styles and by linear, extremely papillate stigmas with abaxial stigmatic crests (Figs. 5, 6). Ovaries contain one or two anatropous and crassinucellate ovules. Placentation ranges from laminar to dorsal (Richardson, 1969) to median (Ito, 1986a).

Fruits are aggregate and subtended by a persistent perianth. Each simple fruit is indehiscent, one- or two-seeded, and surrounded by a leathery pericarp. Peduncles bearing aggregate fruits abscise, float to the surface, and drift. Eventually, simple fruits detach from the receptacle, float on the water's surface where they are carried by wind and wave actions, and then sink to the pond bottom.

The seeds are ovoid (Fig. 7) and at their apex possess a pyramidal structure with a central micropyle (Fig. 8). The seed coat surface is composed of irregularly digitate cells. Seeds contain small amounts of endosperm, copious perisperm, and haustorial tubes. Embryos are minute, with two broad hemispherical cotyledons (Fig. 9).

FLORAL CYCLE

The floral structure of *Brasenia* is diurnally emergent over a three-day period. On the first day of emergence, the flower is in bud and covered with mucilage (Fig. 10). Individual flowers bloom for two consecutive days. On the first day, flowers are morphologically pistillate; they are characterized by short, undehisced stamens and elongate, papillate stigmas radiating outward over the re-

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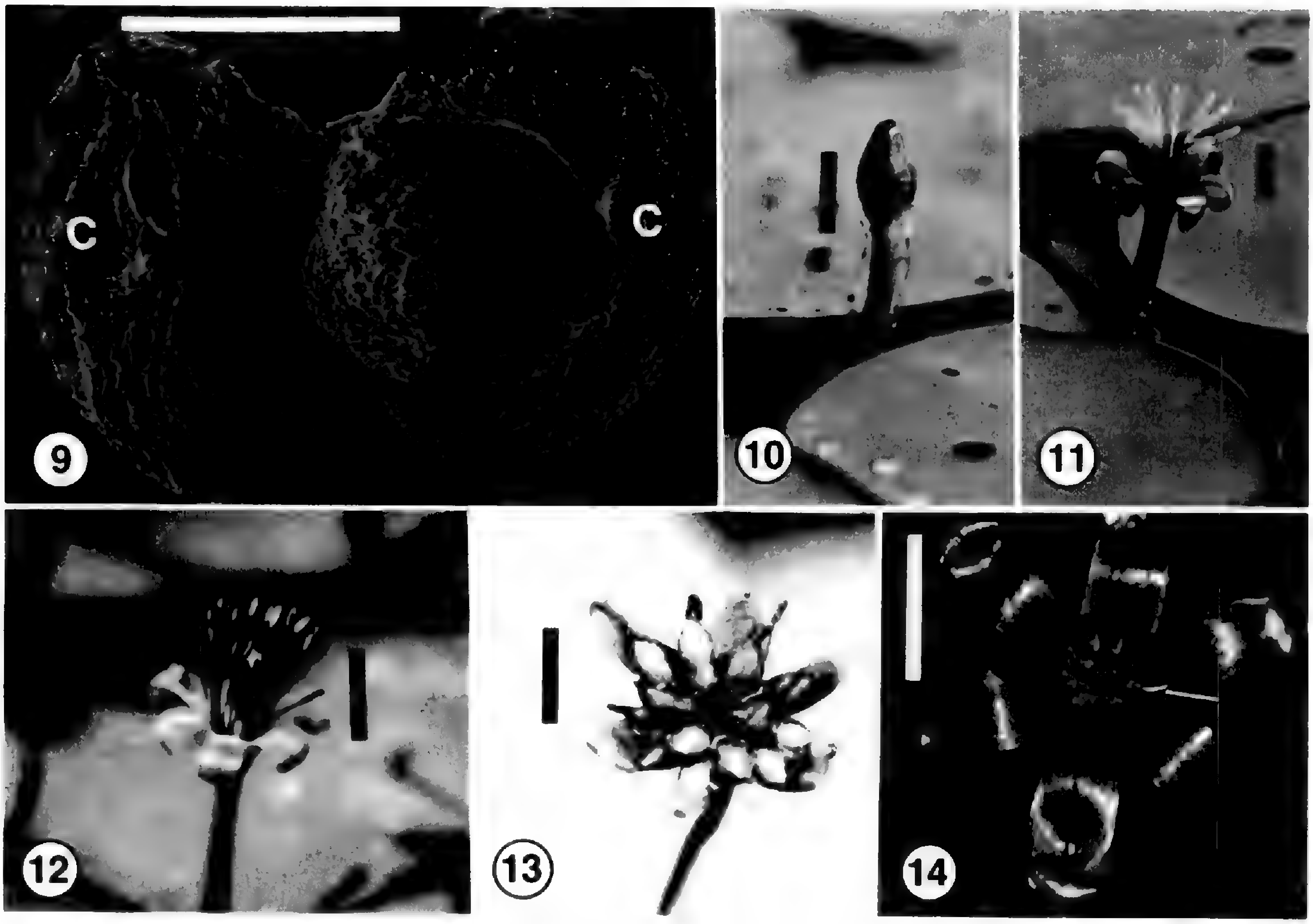
FIGURES 2–8. *Morphological and anatomical features of* Brasenia.—*2. Axillary bud and juvenile leaves; note abundant mucilage covering entire apex and abaxial surface of older leaf. Scale bar = 1 cm.—3. SEM of adaxial surface of sepal; note numerous antrorse trichomes. Scale bar = 1 mm.—4. SEM of monosulcate pollen grain. Scale bar = 20 µm.—5. SEM of second-day flower showing carpel morphology; note linear stigmas with abundant papillae and stigmatic crests. Scale bar = 1 mm.—6. SEM of papillate stigma; note abaxial stigmatic crest (SC). Scale bar = 500 µm.—7. SEM of seed. Scale bar = 1 mm.—8. SEM of seed apex; note digitate cells of seed surface and polygonal cells of apex surface. Scale bar = 500 µm.*



FIGURES 9–14. *Embryo and flowers of* Brasenia.—*9. SEM of embryo with hemispherical cotyledons (C). Scale bar = 250 µm.—10. Floral bud; note mucilage-covered peduncle.—11. First-day flower showing short, undehisced anthers and radiating stigmas.—12. Second-day flower showing elongated filaments, dehiscent anthers, and centrally aggregated stigmas.—13. Aggregate fruit.—14. First-day flower of* Brasenia *showing variation in lengths of stigmas. (Figures 10–14, scale bars = 1 cm.)*

flexed perianth (Fig. 11). Flowers submerge at the end of the first day. On the second day, the flowers are morphologically staminate; the filaments have elongated, elevating the dehiscent anthers to a position at or above the now centrally aggregated stigmas (Fig. 12). The perianth occupies a position similar to that of first-day flowers. At the end of the second day, flowers again submerge. Third-day flowers remain submerged but occasionally occur at the water surface. These flowers are nonfunctional, characterized by closed perianth parts with protruding senescent anthers. Aggregate fruits develop below the water surface (Fig. 13). Fruit development occurs in four to six weeks early in summer and as quickly as two weeks in the late summer.

During the course of fieldwork, morphological variation was observed among flowers. Aside from typical features described above, several *Brasenia* flowers had short stigmas which did not conspicuously radiate over the perianth (Fig. 14).

Individual flowers vary in position above and below the water level. General trends of the floral cycle can be identified, however (Fig. 15). Anthesis begins at 0630–0730 hours on both the first and second days. First- and second-day flowers reach maximum height above water at 1300–1400 hours. Second-day flowers are generally elevated to a higher position, with anther dehiscence occurring at 0830–1100 hours.

As first-day flowers close, the gynoecia and perianths gradually change position. When flowers are at peak height, stigmas begin to arch centrally until they completely aggregate at the time flowers close and submerge. Perianth members begin to close gradually at 1300–1400 hours, with the corolla closing prior to the calyx.

CAGING TREATMENTS

Results from caging experiments are reported as percentage seed set (Table 1). The percentage values are conservative because they were calculated assuming two ovules (seeds) per carpel (simple fruit) within carpels remaining on aggregate fruits at time of retrieval. They do not take into account

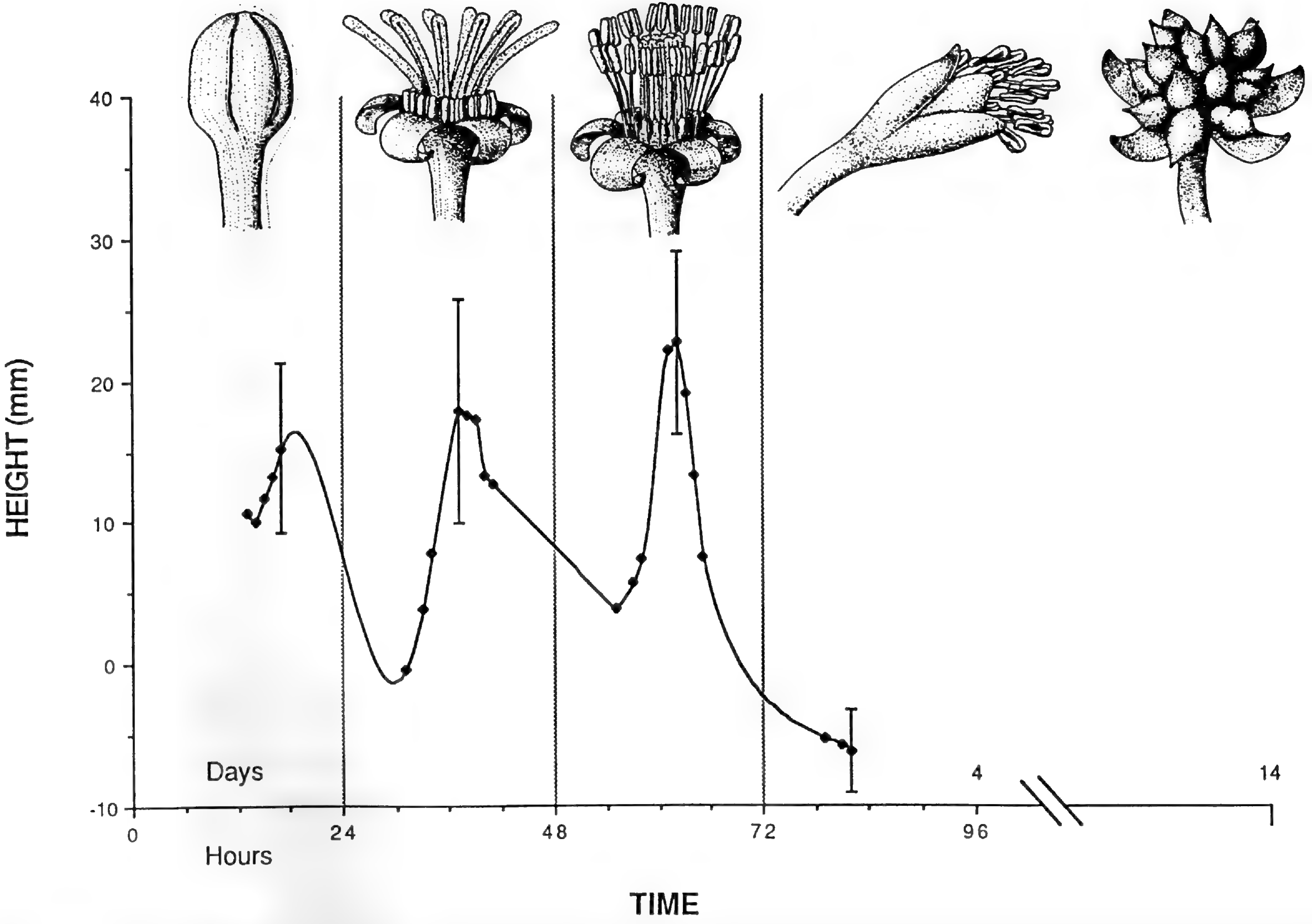


FIGURE 15. *Floral cycle of* **Brasenia** *illustrating changes in floral morphology and position above or below water level. Error bars represent average 95% confidence intervals of all values from each day; buds C.I. = 6.06, first-day flowers C.I. = 7.92, second-day flowers C.I. = 6.41, and third-day flowers C.I. = 2.83. Best-fit curve was computer generated.*

TABLE 1. *Percentage seed set from caging treatments conducted on separate trial dates.*

Experiment (N = 25)	5/23/86	6/19/86	7/03/86	7/31/86	5/18/87
Control					
1. Typical flowers	18.2%	6.1%	—	—	28.7%
2. Flowers with short stigmas	—	—	—	—	1.1%
Group A—Parthenocarpy					
(Transparent cages, emasculated)	—	0%	—	—	—
Group B—Autogamy[1]					
(Transparent cages, left undisturbed)	—	0%	—	—	—
Group C—Stigmatic receptivity					
1. Transparent cages, emasculated, cross-pollinated first-day	—	—	12.7%	—	—
2. Transparent cages, emasculated, cross-pollinated second-day	—	—	0.5%	—	—
Group D—Allogamy[1]					
1. Geitonogamy (transparent cages, cross-pollinated first-day with pollen from same plant)	—	—	—	—	48.0%
2. Xenogamy (transparent cages, cross-pollinated first-day with pollen from different plant)	—	—	—	—	41.4%
Group E—Anemophily					
1. Mesh cages, left undisturbed	—	0%	—	1%	—
2. Mesh cages, emasculated	—	—	0%	—	—

[1] Terminology follows Faegri & van der Pijl (1979).

any carpels that had abscised prior to retrieval or carpels with only one ovule.

The results of exclusion treatments indicate that apomixis and autogamy did not occur (Groups A and B). Self-pollination did occur in treatment B, however, based on the observation of pollen on the stigmas. Flowers artificially pollinated on the first day and second day of anthesis (Group C) produced seeds. Flowers pollinated on the first day of anthesis exhibited greater seed set than those pollinated on the second day. These data indicate first-day flowers are receptive to pollen and should be considered functionally pistillate. Second-day flowers are functionally staminate. The results of experiment D, determination of allogamy, revealed that *Brasenia* is compatible with pollen of both geitonogamous and xenogamous origins. Only one of three trials from the mesh cage treatments (Group E) set seed. It is believed that minimal seed set in flowers subjected to this treatment occurred because the cages alter the aerodynamics of the floral structure (Niklas, pers. comm.) and the mesh screen probably inhibits the passage of pollen grains.

The three control groups of morphologically "typical" flowers yielded varying seed set (Table 1). This variation may be attributed to differences in wind speed and distributional density of flowers on each sample date. Flowers with short stigmas produced few seeds despite their occurrence in the same population as the "typical" control group.

POLLEN DISPERSAL AND TERMINAL SETTLING VELOCITY

Measurements with the Andersen particle sampler revealed that *Brasenia* pollen was airborne. Pollinometer experiments indicated the mean number of pollen grains dispersed from second-day (pollen-releasing) flowers decreases with distance. The numbers of grains at subsequent 10 cm intervals on each trial date were significantly different, with the exceptions of the 0–10 and 60–70 cm intervals. These differences can be attributed to wind velocity. Average wind speeds on respective sampling dates differed by a factor of five. Dispersion of pollen can be described exponentially (Fig. 16). A regression analysis of dispersed pollen grains exhibited correlation coefficients of $r = 0.99$ and $r = 0.85$ at 8 kph and 1.6 kph, respectively.

Pollen on the stigmas of a variety of flowers was also observed. First-day flowers that were downwind of and within 0.5 m of second-day flowers had abundant pollen on their stigmas. Those grains were primarily restricted to windward stigmas. Pol-

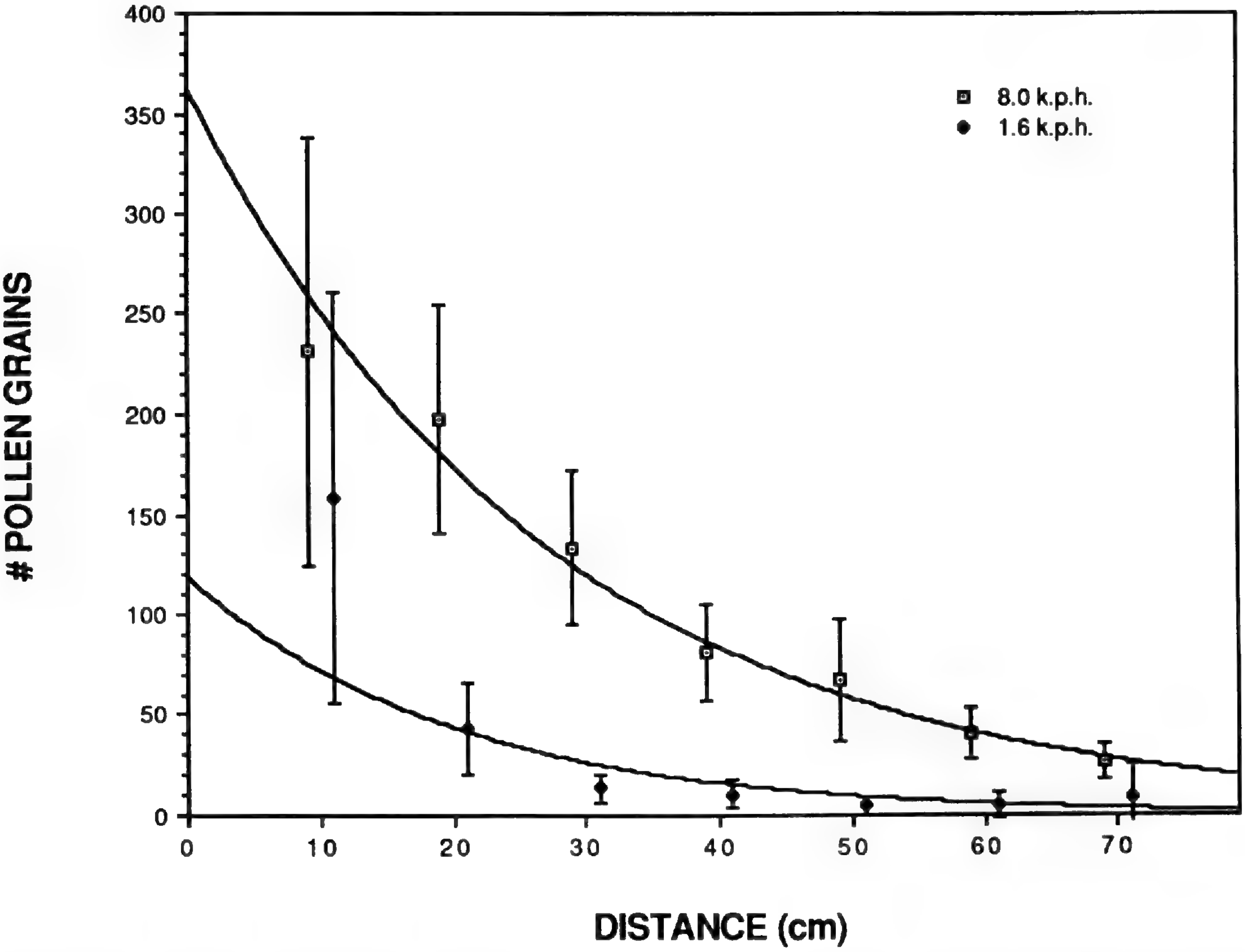


FIGURE 16. *Regression analysis of pollen grain deposition from pollinometer experiments. At 8 kph,* y = *367.9*10^ (0.02*x*),* r *value of 0.99; and at 1.6 kph,* y = *112.7*10^ (0.02*x*),* r *value of 0.85. Error bars represent 95% confidence intervals; best-fit curves were computer generated.*

len-receptive first-day flowers that were 2–3 m from second-day flowers exhibited very low quantities of pollen, if any, on their stigmas. The terminal settling velocity of *Brasenia* pollen was calculated to be 7.7 ± 0.8 (95% C.I., N = 21) cm/sec.

FLORAL DENSITY

Of four sample plots, the mean numbers of flowers/m^2 ± 95% C.I. were as follows: 110 ± 22; 82 ± 26; 73 ± 17; and 36 ± 14.

FLORAL SECRETIONS

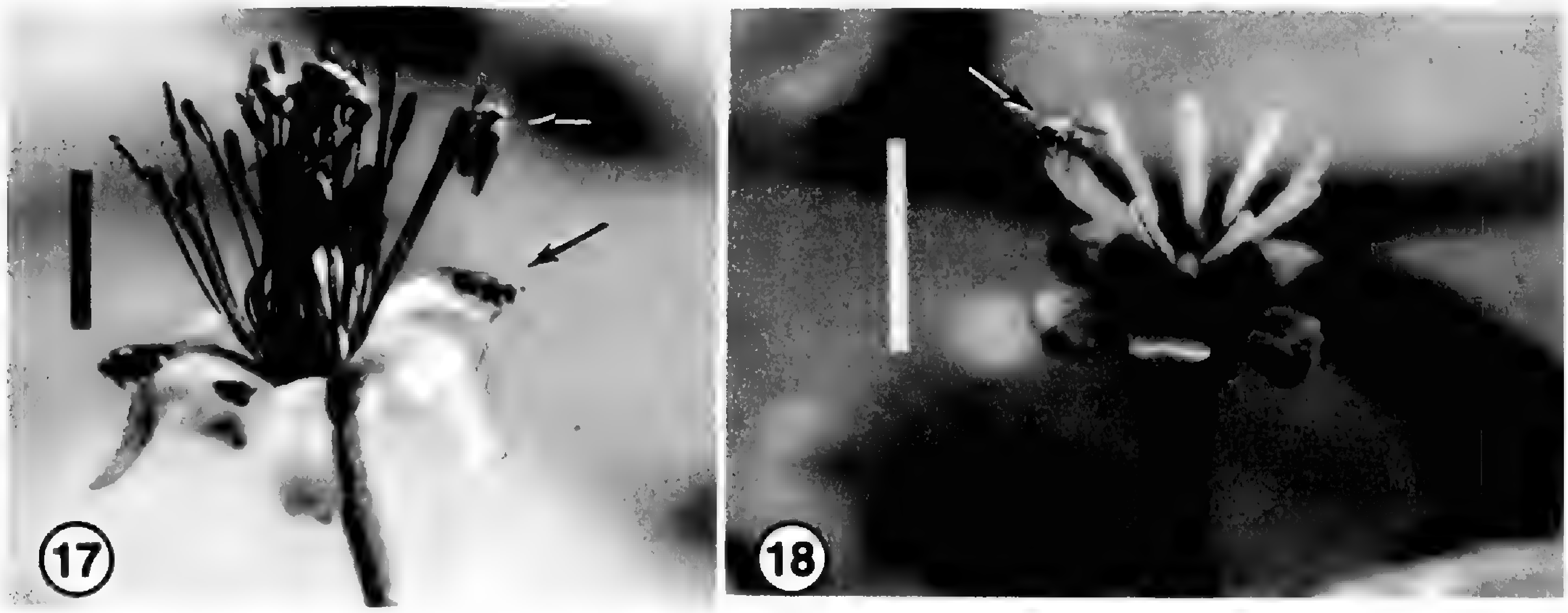
Neutral red staining revealed the absence of nectaries. The numerous perianth trichomes stained indicated a secretory role.

ULTRAVIOLET REFLECTANCE AND ABSORPTION

The inner surfaces of dehisced anthers are UV reflective. Adaxial (emergent) leaf surfaces are UV absorptive.

ANTHOPHILOUS VISITORS

A variety of insects visit flowers of *Brasenia*, including *Donacia cincticornis* Newman (Coleoptera; Chrysomelidae), *Perigaster cretura* Herbst (Coleoptera; Curculionidae), *Notiphila* cf. *cressoni* Cresson (Diptera; Ephydridae), *Apis mellifera* L. (Hymenoptera; Apidae), and various odonates. The most frequent and abundant visitor was *Notiphila* cf. *cressoni*. *Notiphila* primarily visited staminate flowers and there foraged for pollen either directly from the dehisced anther sacs or from the adaxial surface of the reflexed perianth where pollen accumulates (Fig. 17). Grooming and copulatory acts were also frequently observed. Pistillate flowers were rarely visited by flies, but upon their brief visitations, members of *Notiphila* would typically land on the elongated stigmas or reflexed perianth (Fig. 18). Additionally, flies commonly foraged for



FIGURES 17, 18. *Insect visitors of* Brasenia.—*17. Post-dehiscent second-day flower with* Notiphila *cf.* cressoni *foraging for pollen.*—*18.* Notiphila *on stigma of first-day flower. Scale bars = 1 cm.*

the abundant airborne pollen that had become deposited on the adaxial surfaces of leaves. Microscopic examinations of dipteran bodies indicated that pollen loads were minimal except around the bases of the legs where body hairs are more dense. The stickiness of *Brasenia* pollen was not determined. Other insects were only occasional floral visitors and cannot be considered pollinators.

DISCUSSION

FLORAL CYCLE

Field observations of *Brasenia* confirm that anthesis is diurnal, with individual flowers opening and closing for two consecutive days. First-day flowers are morphologically pistillate; second-day flowers staminate. Caging experiments (Table 1) indicate that stigmas of first-day flowers are receptive to pollen and those of second-day flowers generally are not. Thus floral structure and function are correlated. Caging experiments further reveal that *Brasenia* flowers set seed only with pollen from an allogamous origin (sensu Faegri & van der Pijl, 1979). Although individual flowers are self-pollinating, seeds are not produced. It is unlikely that a genetic mechanism of self-incompatibility is responsible for the lack of seed set. Abundant seed production from geitonogamous pollinations is indicative of self-compatibility. In the populations studied, self-fertilization (autogamy) is prevented by dichogamy.

WIND POLLINATION

In the populations studied, *Brasenia* is predominantly anemophilous. This conclusion is reached by correlating data and observations of the following: pollinometer experiments, floral densities, number of viable pollen grains produced, flower position above water level, terminal settling velocity of pollen, and floral morphology. The pollinometer experiments reveal that *Brasenia* pollen is dispersed over a relatively short distance. Therefore, for successful pollination by wind, the flowers must be closely grouped and produce a significant amount of viable pollen. As has been shown, floral density can exceed 100 flowers/m^2 and viable pollen production > 200,000 grains/flower. The elevated position of second-day flowers above first-day flowers, together with a pollen terminal settling velocity of 7.7 cm/sec., further enhances the dispersal distance of *Brasenia* pollen. Direct observations of pollen on stigmas of first-day flowers downwind of pollen-releasing flowers at distances of < 1 m and > 2 m support the above conclusion. Large pollen–ovule ratios, as discovered in *Brasenia*, are also characteristic of wind-pollinated taxa (Faegri & van der Pijl, 1979).

Whitehead (1983) identified several "idealized conditions" that need to be met by a plant species if wind pollination is to be successful. The floral and vegetative morphologies of *Brasenia* are adapted for anemophily. Table 2 summarizes those adaptations of *Brasenia* in comparison with other anemophilous plants. Floral anomalies (e.g., short stigmas), however, are not as well adapted for reception of wind-borne pollen. This accounts for the low seed set in flowers with short stigmas (Table 1) compared with typical flowers.

Additionally, observations of infrequent insect visitations between first-day and second-day flowers, despite insect abundance, and minimal pollen loads negate entomophily as a primary mechanism of pollen transfer in this study site.

TABLE 2. *Comparison of* Brasenia *adaptations with Whitehead's "idealized conditions" for anemophily.*

Whitehead	*Brasenia*
There is production of large numbers of pollen grains.	Greater than 221,700 pollen grains are produced per average flower.
Pollen grains possess appropriate aerodynamic characteristics, are typically 20–40 μm in size, and have terminal settling velocities of 2–6 cm/sec.	Pollen grains are elliptic, smooth, within "ideal" size range (36.3 × 47.6 × 36.9 μm),[1] and have a terminal settling velocity of 7.7 cm/sec.
The probabilty of pollen's entrainment in moving air is maximized due to flower and inflorescence structure and their location on the plant.	Second-day (staminate) flowers possess elongated filaments that elevate dehiscent anthers; perianth parts are reflexed and stigmas are centrally aggregated out of the path of ambient air.
Stigmatic surfaces are structured and positioned to maximize collection efficiency.	First-day (pistillate) flowers possess elongated, papillate stigmas which radiate outward over the perianth providing an increased surface area for pollen adherence.
Pollen release is timed within both the season and the day to maximize the possibility of pollen capture by receptive conspecifics downwind.	Pistillate flowers are fully open and generally elevated lower than staminate flowers at the time of anther dehiscence.
There is a relatively close spacing of compatible plants.	Flowers exhibit relatively dense distribution, up to 110/m² during peak anthesis, and are both geitonogamous and xenogamous.
Plants possess a vegetational structure that is relatively open to minimize filtration of pollen by nonstigmatic surfaces.	Vegetative organs are either submerged or floating; the only emergent structures are floral.
The range of wind velocities ensures pollen transport and minimizes its downwind dispersion.	Pollen can be dispersed at least 70 cm at wind speeds as low as 1.6 kph.

[1] Ueno & Kitaguchi (1961).

OCCURRENCE OF INSECTS

The frequency, abundance, and behavior of *Notiphila* flies on second-day flowers and leaves are related to their life history and association with the other nymphaeaceous genera, *Cabomba* and *Nymphaea* (Van der Velde et al., 1978; Van der Velde & Brock, 1980; Willmer, 1982), in the study site. Members of *Notiphila,* while foraging on nectar and pollen, function as the primary pollinators of *Cabomba* (Schneider & Jeter, 1982). In *Nymphaea* the flies forage on pollen and occasionally sponge stigmatic fluid, but native halictid bees are pollinators of the diurnal Toledo Bend species of this genus.

We view the relationship of *Notiphila* with *Brasenia* as one of herbivory in which flies mainly forage for pollen and utilize the flower to groom and mate. The flies forage for pollen in anther sacs only after the majority of pollen grains have been wind dispersed and the inner UV reflective walls, which aid in the attraction of the flies, are exposed. As the flies move about the dehiscent androecium and pollen-covered perianth surface, a small quantity of pollen accumulates on their legs. This minute pollen load can be attributed at least in part to the smooth walls of the *Brasenia* pollen. Occasional visits to pistillate flowers may facilitate transfer of minimal pollen; therefore, *Notiphila* should only be considered an incidental pollinator. The occurrence of flies and their role as incidental pollinators, together with floral variations such as shortened stigmas, suggest a possible evolutionary shift from anemophily to partial myophily (ambophily; Stelleman, 1984).

POLLINATION BIOLOGY OF THE NYMPHAEACEOUS SENSU LATO FAMILIES

This investigation provides the first documentation of anemophily in the Nymphaeaceae s.l. Traditionally, wind pollination has been interpreted as derived in the angiosperms (Whitehead, 1969; Faegri & van der Pijl, 1979). Dilcher (1979), Dilcher & Kovach (1986), and Crane & Dilcher (1984), however, have shown that several extinct lower- to mid-Cretaceous flowering plants had the reproductive morphology to accommodate pollination by both wind and insects. The occurrence of anemophily in the Nymphaeaceae s.l., a taxon traditionally viewed as primitive and entomophilous, dictates that the phylogeny of this group be re-examined.

Cabombaceae. Several studies (e.g., Kosakai, 1968; Goleniewska-Furmanowa, 1970; Bukowiecki et al., 1972; Okada & Tamura, 1981; Ito, 1986a, 1987) suggest *Cabomba* and *Brasenia* share sufficient characteristics to warrant maintenance of the Cabombaceae. From a classical viewpoint, it could be argued that the presence of perfect flowers, a perianth, the occurrence of foraging flies, and some UV reflectance in *Brasenia* are remnants of a former entomophilous condition which has more recently specialized for wind pollination. An alternative hypothesis, that anemophily is primitive, could also be argued. Support for this viewpoint comes from the fossil record in which Tertiary pollen of *Brasenia* exhibits the same morphological features as extant *Brasenia* pollen (Jessen et al., 1959). Although pollen alone is not a definitive indicator of pollination biology, modern *Brasenia* pollen is adapted for wind pollination (Table 2). Because fossil and extant pollen are morphologically similar, comparable functions can be postulated.

We do not view these two hypotheses as completely exclusive of each other. A third line of reasoning, that the cabombaceous ancestor had the reproductive morphology to facilitate both wind and insect pollination, could be advocated. An ancestor with dual pollination capabilities would explain the long anemophilous history as suggested by fossil pollen and the occurrence of the entomophilous features noted above. An extension of this third concept suggests that the pollination syndromes in extant *Brasenia* and *Cabomba* are specialized. Phylesis in *Cabomba*, therefore, would have involved a reduction and stabilization in the number of androecial and gynoecial members, as evidenced by the vasculature studies of Ito (1986a), and the appearance of a distinct, colorful perianth possessing nectaries to enhance a myophilous pollination syndrome (Schneider & Jeter, 1982). Here, pollination is achieved by the appropriate positions of the pollen-receptive stigmas in first-day flowers (Fig. 19L) and pollen-dehiscent anthers in second-day flowers (Fig. 19K) above the petaliferous nectaries where *Notiphila* flies sponge secretions. The elongated stigmatic surfaces which radiate above the recurved perianth in first-day flowers of *Brasenia* (Fig. 19N) enhance collection of airborne pollen. In second-day flowers (Fig. 19M), the elevation of anthers above the recurved perianth promotes pollen dispersal.

A recent cladistic analysis of the Nymphaeales by Ito (1987) indicates *Ceratophyllum* has association with *Brasenia* and *Cabomba*. Les (1986) has proposed that the hydrophilous pollination mechanism of *Ceratophyllum* (Jones, 1931) is derived from anemophily. The occurrence of wind pollination within the Cabombaceae warrants continued examination of the suggested relationships among *Ceratophyllum*, *Brasenia*, and *Cabomba*.

Nymphaeaceae s. str. Some investigations (Collinson, 1980; Moseley et al., 1984) indicate *Brasenia* shares more affinities with the Nymphaeaceae s. str. than with *Cabomba*. We do not support dismantling the Cabombaceae. It is our opinion that data from pollination biology, floral anatomy, anatomy of fossil and extant seeds, and embryology support a common ancestry hypothesis. The Nymphaeaceae s. str., unlike the Cabombaceae and Nelumbonaceae, possess completely syncarpous gynoecia. When correlated with an evolutionary shift from hypogyny in *Nuphar*, through perigyny in *Nymphaea*, to epigyny in *Barclaya*, *Euryale* (Kadono & Schneider, in press), and *Victoria*, flowers of this family exhibit an overall elaboration. This elaboration consists of an increase in size and number of floral parts and stigmatic surface area facilitated by radial extension of the carpels and by the appearance of specialized organs (e.g., staminodia and carpellary appendages). This family, like the Nelumbonaceae, is entomophilous except for the cleistogamous flowers of *Barclaya* (Fig. 19D), *Euryale* (Fig. 19C), and some species of *Nymphaea*.

The flowers of *Nuphar* (Fig. 19I, J) have a close relationship with beetles of the genus *Donacia*, which complete their life cycle in association with the plant, during which time they facilitate pollination (Schneider & Moore, 1977). Diurnal flowers of *Nymphaea* and *Ondinea* are specialized for washing pollen from the body of foraging native bees. This is accomplished by the production of stigmatic fluid on the first day of anthesis (Fig. 19F, H; Conard, 1905; Schmucker, 1933; Prance & Anderson, 1976; Schneider, 1979, 1982a, b, 1983; Meeuse & Schneider, 1980; Schneider & Chaney, 1981; Capperino & Schneider, 1985). The pollination biology of nocturnally flowering species of *Nymphaea* is largely unstudied, but cantharophily is known (Cramer et al., 1975; Wiersema, 1987).

Large, nocturnal flowers of *Victoria* are adapted for pollination by *Cyclocephala* beetles. Beetles

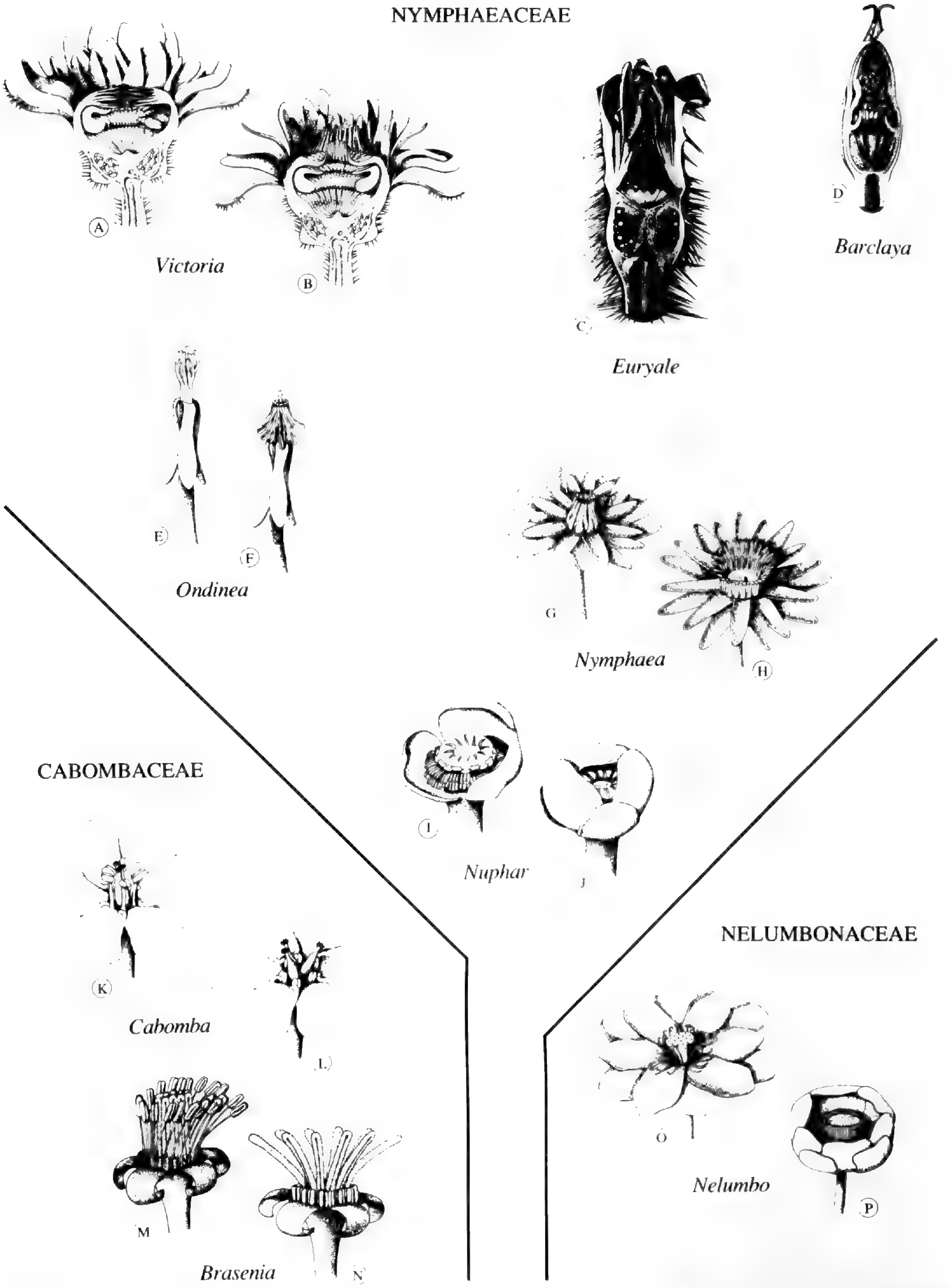


FIGURE 19. *Comparative morphologies of first-day (pistillate) and second-day (staminate) flowers of the Cabombaceae (first-day, L, N; second-day, K, M), Nymphaeaceae s. str. (first-day, B, C, D, F, H, J; second-day, A, E, G, I), and Nelumbonaceae (first-day, P; second-day, O). Note: flowers not drawn to scale.*

are attracted by the white color and fragrance of first-night flowers. The diffusion of fragrance is accelerated by a rise in floral temperature due to the thermogenicity of carpellary appendages (Fig. 19B). Pollination is achieved when pollen-covered beetles crawl about the inner stigmatic cup. While "trapped" within the flower, beetles forage on starch-rich carpellary appendages (Fig. 19A). As beetles emerge from second-evening flowers they become dusted with pollen from the now-dehiscent anthers and, once again, are attracted to first-evening flowers (Knoch, 1899; Valla & Cirino, 1972; Prance & Arias, 1975; Schneider, 1976; Lovejoy, 1978).

Nelumbonaceae. Separation of *Nelumbo* from the Nymphaeaceae s.l. into the Nelumbonaceae has been justified on numerous grounds, including seed anatomy (Collinson, 1980) and floral anatomy/morphology (Moseley & Uhl, 1985; Ito, 1986b, 1987). Despite this separation, *Nelumbo* displays a floral behavior similar to that of chasmogamous flowers of the Cabombaceae and Nymphaeaceae s. str. in which first-day flowers are pistillate (Fig. 19P) and second-day flowers are staminate (Fig. 19O). Flowers of *Nelumbo* are principally adapted for cantharophily (Schneider & Buchanan, 1980), although bees and flies (Sohmer & Sefton, 1978) also transfer pollen. Moseley & Uhl (1985) suggested that the flower of *Nelumbo* represents an evolutionary elaboration in response to cantharophily.

Comparative studies of the reproductive biology of Cabombaceae, Nymphaeaceae s. str., and Nelumbonaceae, when viewed in conjunction with structural aspects of the flower, suggest that evolution within these families has involved both floral reduction and elaboration as a result of adaptive evolution in response to abiotic and biotic vectors. This concept is consistent with other angiosperm taxa as indicated by the fossil record (Basinger & Dilcher, 1984).

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REPRODUCTIVE BIOLOGY OF *NYMPHAEA* (NYMPHAEACEAE)[1]

John H. Wiersema[2]

ABSTRACT

Several reproductive strategies have evolved within the genus Nymphaea. *Sexual reproduction is mostly protogynous; flowers are open two to several days (depending on the species), with pollen release usually commencing on the second day. The five subgenera of* Nymphaea *exhibit differences in floral biology. There is considerable variation in the timing of flower opening, floral odor, flower color, and the form and function of various flower parts. These differences may contribute to genetic isolation between species both through temporal separation of flowering and attraction of different pollinators. While sexual reproduction in many species is dependent on xenogamy or geitonogamy, other species have adaptations to promote autogamy. No species of* Nymphaea *is known to be agamospermous, but several other modes of asexual reproduction are exhibited: detachable tubers, stolon formation, and proliferations of floral and foliar tissue. Wide-ranging tropical species all avoid being totally reliant on pollinators by employing one or more reproductive alternatives to outcrossing; clearly some obligate outcrossers are limited in their colonizing by pollinator availability. The most important of these reproductive alternatives is autogamy. Wide-ranging temperate species, which mostly rely exclusively on outcrossing for sexual reproduction, probably avoid pollinator limitations by utilizing a broader range of pollinators.*

Nymphaea is the largest and most widely distributed genus in the Nymphaeales. About 40 species of waterlilies, as they are commonly known, are distributed on all continents except Antarctica. The classification of Conard (1905), still generally accepted, recognizes five subgenera: the north-temperate subgenus *Nymphaea*, neotropical subg. *Hydrocallis*, and paleotropical subg. *Lotos* of the syncarpous group and the Australian subg. *Anecphya* and pantropical subg. *Brachyceras* of the apocarpous group. The success of this genus as determined by number of species and distributional range is due to several factors. Its age, dating probably from mid Tertiary (Collinson, 1980), may be one factor; however, other nymphaeaoid genera of comparable age have not demonstrated the same degree of evolutionary divergence. Another factor is its specialized but widely available ecological niche. Waterlilies almost invariably inhabit still or gently flowing water over rich organic substrates. In stable aquatic habitats they root in water too deep for competing emergent vegetation. Their floating leaves, in addition, outcompete submersed leaves for light. A few other genera are competitors for this niche, including primarily nymphaeaceous genera such as *Nuphar*, *Brasenia*, and *Nelumbo*, and the distantly related genus *Nymphoides*. None of these, however, has attained the species radiation and global distribution of *Nymphaea*.

According to Gupta (1978, 1980) polyploidy, structural chromosome changes, and gene mutations have played important roles in the evolution of *Nymphaea*. The poor development of isolating mechanisms is also mentioned as being responsible for the high incidence of natural and artificial interspecific hybridization. However, such mechanisms are not altogether absent. Certainly ecological factors help isolate certain species from others, such as the alkaline-tolerant *N. tuberosa* Paine from the more acidophilic *N. odorata* Aiton, or the slightly halophilic *N. rudgeana* G. Meyer from less salt-tolerant species, or the riparian *N. potamophila* Wiersema from lacustrine species. Geographical isolation has also been a factor, such as separating *N. alba* L. of Europe from the North American *N. odorata*.

This paper, in discussing the reproductive biology of *Nymphaea*, focuses on several potential external mechanisms for reproductive isolation. Internal mechanisms (terminology from Grant, 1981) no doubt are important in promoting the hybrid breakdown and sterility often observed in *Nymphaea* (Gupta, 1978) but are outside the scope of this discussion. Differences within and among the

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subgenera with regard to floral odor, flower color, the timing of floral responses, and the form and function of various flower parts may contribute to genetic isolation between species. Isolating mechanisms are probably more important for tropical and subtropical species, since their densities tend to be greater than those in temperate areas. After focusing on these potential isolating mechanisms, several adaptations relating to asexual reproduction in *Nymphaea* will be discussed, thereby permitting an evaluation of the various reproductive strategies found among waterlilies.

FLORAL BIOLOGY

Some general aspects of floral biology in *Nymphaea* should be presented. The flowers consist of 4 sepals, 7–40 petals, 20–700 stamens, and 5–47 carpels, the latter forming a ring embedded in cup-shaped receptacular and appendicular tissue to which the appendicular organs are attached laterally. The upper surface of each carpel contributes a ray of stigmatic tissue to the stigmatic disk, which tops the ovary, and this ray usually terminates abaxially in a free appendage termed the carpellary appendage or carpellary style.

Sexual reproduction is mostly protogynous. First-day flowers generally open slightly less than on later days, with the stamens and carpellary appendages, if present, spreading to permit insect visitors access to the stigmatic region. The tips of the stamens form a circular wall or palisade around a central pool of stigmatic fluid. Although variable in quantity, I have observed this fluid in all species thus far examined. It reportedly contains a surfactant primarily responsible for washing pollen from the bodies of insect visitors, but also possibly contributing to their frequently observed drownings. In second-day flowers the sepals, petals, and most of the stamens reflex fully. Anther dehiscence occurs in second-day flowers, with the stigmatic fluid drying up at or by this time. Insects are generally free to forage for pollen due to the dryer nature of the stigma and the incurving of the inner stamens and carpellary appendages over the stigmatic region. Pollen-covered insects that subsequently visit first-day flowers effect pollination. In many species first-day flowers open slightly later than on subsequent days. This ensures that insect visitors will first visit pollen-releasing flowers prior to their entrance into pollen-receptive flowers (Schneider, 1979; Meeuse & Schneider, 1980; and pers. obs.).

Floral odor. Although numerous authors have commented on the differences in floral odor among various waterlily species (Conard, 1905; Cramer et al., 1975; Prance & Anderson, 1976; Meeuse & Schneider, 1980), which range from inodorous to lightly fragrant or strongly pungent, nothing is known of the chemistry of the odor-producing compounds or their potential in attracting certain taxa of pollinators. The importance of floral odor seems to be greatest for night-blooming species, which can rely less on flower color to attract pollinators. Most members of the night-blooming subg. *Hydrocallis* emit considerable odor that is detectable for some distance. These species are probably pollinated by Coleoptera (Cramer et al., 1975; Prance & Anderson, 1976; Prance, 1980; Wiersema, 1987), in contrast to members of the day-blooming subgenera *Anecphya*, *Brachyceras*, and *Nymphaea*, which appear to be pollinated by Hymenoptera or Diptera (Van der Velde et al., 1978; Schneider & Chaney, 1981; Schneider, 1982a, b; Capperino & Schneider, 1985). The latter group has typically far less odorous flowers, with odors appearing to differ qualitatively from those of subg. *Hydrocallis*. In subg. *Anecphya*, no odor is known (Conard, 1905; Schneider, 1982b). Strong odors have not been observed in *N. lotus* L. of the night-blooming subg. *Lotos*, although nothing is known regarding insect pollinators in this subgenus.

Schneider (1982a) has hypothesized that in subg. *Hydrocallis* the highly developed carpellary appendages may help volatilize odors. A darkening of these appendages and sometimes the staminal bases is frequently observed as flowering progresses, suggesting that chemical activity may be taking place. Olfactory tests with *N. jamesoniana* Planchon support this, but additional tests are needed. In the inodorous subg. *Anecphya*, carpellary appendages are absent.

Flower color. Considerable variation in petal coloration is evident among waterlily species. Flower color is, however, relatively constant among night-blooming species, with all species of subgenera *Hydrocallis* and *Lotos* having white or nearly white petals. An exception to this trend is found in the red-flowered *N. rubra* Roxb. ex Andrews, but recent evidence suggests that this is an apomictic "species" that may not undergo sexual reproduction (Mitra & Subramanyam, 1982). Certain species of the other syncarpous subgenus, the diurnally flowering subg. *Nymphaea*, have also yielded pink- to red-flowered forms under rare circumstances (Conard, 1905; Elkins, 1970; Erixon, 1980), white being the usual petal color in all species involved. However, *N. mexicana* Zucc. of this subgenus has yellow petals. The neotropical members of subg. *Brachyceras* are also primarily white-petaled (pale blue fading to white in *N. elegans* Hook.); those of the paleotropics are predominantly blue-petaled, although both white- and yellow-petaled species are known (Conard, 1905; Mendonça, 1960; Hutchinson & Dalziel, 1966).

Little evidence exists to evaluate the importance of flower color in *Nymphaea* in attracting different pollinators. The presence of blue and yellow color forms may be an adaptation favoring pollination by hymenopterans or dipterans, which pollinate similarly colored flowers in other plant groups (Proctor & Yeo, 1972). Schneider and colleagues have examined pollinators of the white-flowered *N. odorata* (Schneider & Chaney, 1981), the blue-flowered *N. elegans* (Schneider, 1982a), and the yellow-flowered *N. mexicana* (Capperino & Schneider, 1985). Insect visitors to all of these diurnally flowering species included Hymenoptera, Diptera, and Coleoptera, indicating that the same classes of pollinators appear to be attracted to all three flower colors. As all of these observations have come from Texas, more observations on pollinators throughout the ranges of these species, especially in situations where they coexist, are needed in order to evaluate better the importance of flower color as a factor in reproductive isolation. Valuable observations toward a resolution of this question could be made in south-central Africa where all three color forms occur.

Temporal responses. Timing of floral responses may be important in determining which pollinators are associated with a particular species, insofar as activity levels of potential pollinators may vary throughout the day or night. Species that utilize the same pollinators could still be reproductively isolated through temporal separation of flowering, which seems to provide a partial if not total barrier to gene flow between certain species. For day-blooming North American species of subg. *Nymphaea* (Fig. 1A), flowers of the widespread *N. odorata* open just after dawn and close around noon or shortly thereafter (Conard, 1905, Pennsylvania; Schneider & Chaney, 1981, Texas; Wiersema & Haynes, 1983, Alabama). In the northern portion of its range its distribution overlaps that of *N. tetragona* Georgi, whose flowers are open from just before noon to around 5:00 P.M. (Conard, 1905, cultivation in Pennsylvania).

The sequence of floral opening proceeds from the sepals and outer petals gradually inward to the inner stamens and requires ½–1 hour, as does floral closure. First-day flowers (pollen-receptive) generally open slightly later than those of subsequent days. The important times to consider are the periods when the stigmas of first-day flowers are accessible to potential pollen donors and the stamens of later flowers accessible to potential pollen acceptors. Allowing for the adjustments just mentioned, it is probable that complete temporal separation exists between *N. odorata* and *N. tetragona*, although field data are needed from areas of sympatry to support this assumption. Similarly, *N. mexicana*, whose flowers open ca. 11:00 A.M. and close ca. 4:00 P.M. (Conard, 1905, cultivation in Pennsylvania; Wiersema & Haynes, 1983, Alabama; Capperino & Schneider, 1985, Texas), achieves some degree of temporal separation from *N. odorata*, with which it is sympatric over parts of the southeastern United States. Less than an hour overlap appears to be present in the flowering schedules of these two species, which have different-colored flowers, and occasional natural hybrids occur (Ward, 1977, Florida and Georgia; Wiersema & Haynes, 1983, Alabama). On the other hand, the flowering schedules of *N. odorata* and the closely related *N. tuberosa* (Conard, 1905, Pennsylvania) overlap considerably (3–4 hours), and not surprisingly, their taxonomic relationship remains confused (Conard, 1917; Monson, 1960; Williams, 1970).

Available information on the day-flowering species of subg. *Brachyceras* in the New World (Conard, 1905; Prance & Anderson, 1976; Schneider, 1982a) indicates considerable overlap in the flowering schedules of the three species (Fig. 1B). Data are lacking for most Old World taxa of this subgenus.

Considerable information on flowering schedule in the nocturnally flowering, neotropical subg. *Hydrocallis* has been gathered from outdoor cultivation in Alabama (Wiersema, 1987). Cultivated samples of those species obtained from two or more regions exhibited little variation in flowering schedule. Among most species sufficient overlap in flowering time was observed to negate the importance of this feature as a barrier to genetic exchange between species (Fig. 1C). This is particularly true of species that complete flowering before midnight. Species, such as *N. amazonum* C. Martius & Zucc. and *N. prolifera* Wiersema, whose flowers remain open after midnight, are provided some degree of genetic isolation. In *N. prolifera* second-day flowers, although opening at dusk, remain mostly inaccessible to pollinators due to delayed reflexing of the inner petals and stamens until after midnight, when flowers of most other species have closed. In *N. amazonum* floral responses reach their greatest specialization. First-day flowers open fully and close during the two hours just preceding dawn. Second-day flowers open at dusk, remain open throughout

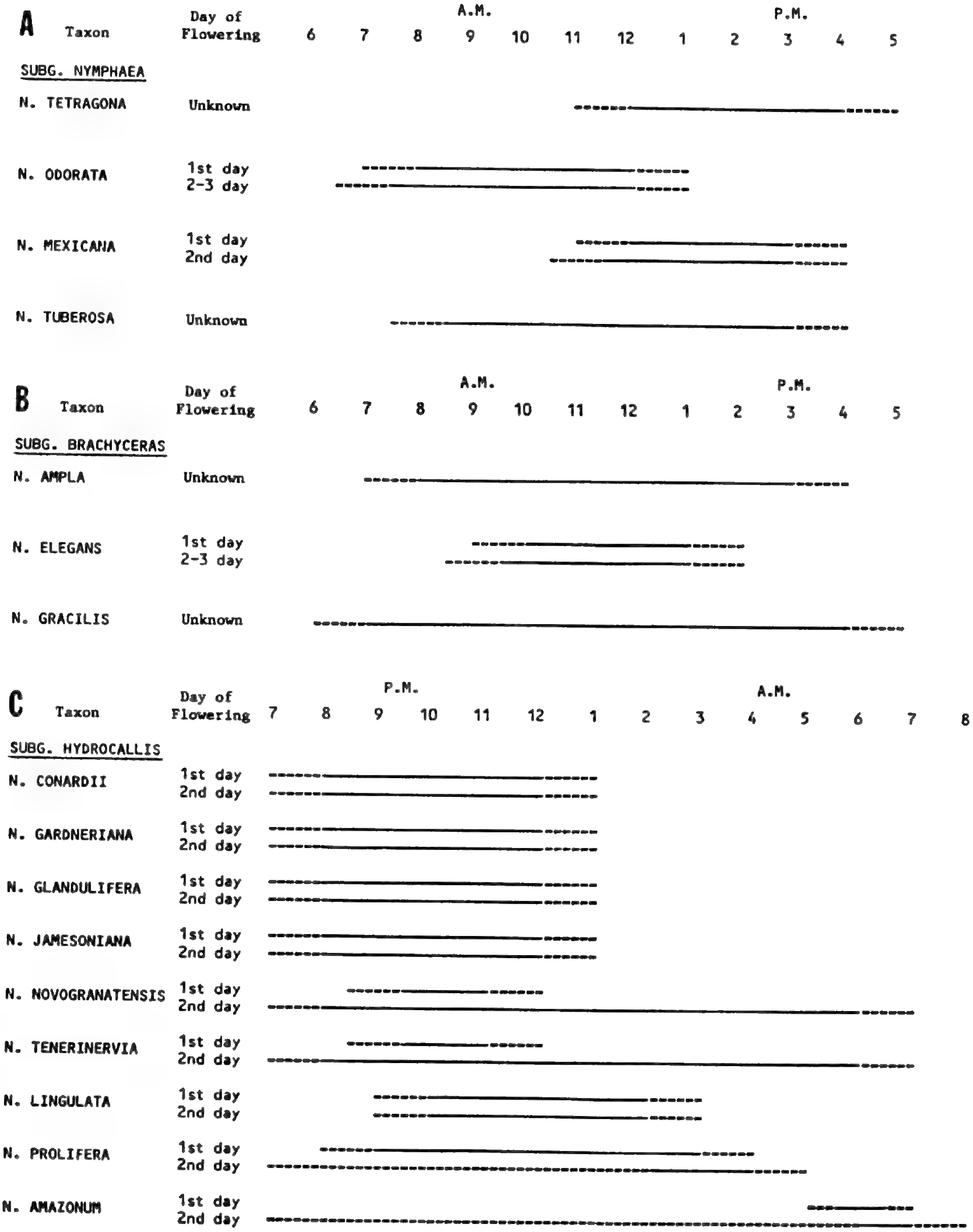

FIGURE 1. *Flower-opening times for selected species of* Nymphaea. *Data sources indicated in text. Dashed lines = partially open flowers, solid lines = fully open flowers.—A. North American species of subg.* Nymphaea.—*B. Neotropical species of subg.* Brachyceras.—*C. Subg.* Hydrocallis.

the night, and close in the early dawn. Their anthers do not dehisce until a few hours before dawn when cross-pollination[3] of first-day flowers is possible. Thus *N. amazonum* is effectively isolated reproductively from other species of subg. *Hydrocallis* even though it may make use of the same pollinators (Cramer et al., 1975).

Floral responses in the night-blooming subg. *Lotos* have received little or no attention. Flowers here reportedly open at dusk and remain open until ca. 11:00 A.M. the following morning (Conard, 1905; Hutchinson & Dalziel, 1966; Wiersema, 1982). First-day (pollen-receptive) flowers of *N. lotus* I observed in cultivation did not open for this lengthy period, but were open for only a few hours around midnight. If these observations are consistent with natural populations, for which scrutinous data are lacking, then cross-pollination in some species of this subgenus could occur only at night, with the diurnal portion of flowering on later days, providing no opportunity for successful cross-pollination.

No evidence suggests that seasonal separation of flowering periods exists in *Nymphaea*. Waterlilies usually commence flowering once sufficient vegetative growth has occurred and continue flowering throughout the growing season. In many populations of *N. prolifera* and *N. lasiophylla* C. Martius & Zucc., however, normal flowers are replaced by tuberiferous flowers (see page 801) during part or all of the growing season. This does not seem to be temporal separation of flowering but rather a shift from sexual to asexual reproduction, the former not being successful in areas where this phenomenon has been observed.

In many species the flowering cycle is extended, with anther dehiscence continuing into a third or fourth day. Species with extended flowering cycles increase the percentage of pollen-releasing (or functionally male) flowers relative to first-day (or functionally female) flowers. Thus the percentage of insect visits involving female flowers would be reduced, but larger pollen loads might be found on insects (Capperino & Schneider, 1985). A longer flowering cycle might also attract more pollinators to a population by displaying a greater number of open flowers.

Other floral modifications. A number of additional morphological or behavioral differences in flowers have been noted among waterlilies. The functional significance of many of these has yet to be determined. Perhaps the foremost among them relates to the carpellary appendages, which are absent in subg. *Anecphya*, triangular to tapering in subgenera *Nymphaea* and *Brachyceras*, and most strongly developed in subgenera *Lotos* and *Hydrocallis*, the only night-blooming subgenera, where they are linear to highly clavate. They attain a length of nearly 3 cm in some flowers of *N. oxypetala* Planchon of subg. *Hydrocallis*. The structural differences in these appendages among species of *Nymphaea* suggest differences in function. Hypotheses concerning the function of the carpellary appendages have suggested that they may serve as a source of food, a source of heat, or a source of volatile odor-producing compounds (Meeuse & Schneider, 1980; Prance, 1980; Schneider, 1982a, b). Similar structures in the related genus *Victoria* Lindley, which exhibits a night-blooming beetle-pollination syndrome, are known to have both thermogenic and nutritive functions (Knoch, 1899; Valla & Cirino, 1972; Prance & Arias, 1975). An additional function of undetermined importance for such appendages in *Nymphaea* may be to control access to the stigmatic disk. In first-day flowers the appendages are erect or spreading, allowing free access to the stigmatic region; however, in second-day and later flowers they are incurved over the stigma. In species such as *N. lotus* of subg. *Lotos* or *N. amazonum* of subg. *Hydrocallis*, they completely cover the stigma. In many species, especially diurnal species with less-developed appendages, the inner stamens form part of this barrier.

It has been suggested that the carpellary appendages may play a role in deepening or broadening the pool of stigmatic fluid and thus improving the ability of flowers to wash pollen from the bodies of insect visitors. However, *N. gigantea* Hook. of subg. *Anecphya*, which lacks carpellary appendages, does not appear to exhibit any reduction in the size of the stigmatic pool (Schneider, 1982b). Comparisons of the quantity of stigmatic fluid among *N. elegans*, *N. odorata*, and *N. mexicana* by Capperino & Schneider (1985) contradict this hypothesis as well, as flowers of *N. elegans*, with the least-developed appendages, produce the greatest amount of fluid.

In the pantropical, diurnally flowering subg. *Brachyceras*, the stamens bear prolonged connective appendages in many species. These appear to form the inner surface of an oil-covered and very

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[3] As some species of *Nymphaea*, including *N. amazonum*, are clonal, cross-pollination as here used may involve either xenogamy or geitonogamy, in contrast to self-pollination involving autogamy.

slippery circular palisade surrounding the central pool of stigmatic fluid in first-day flowers. Insect visitors that enter this region inevitably fall into the stigmatic pool where pollen is washed from them. The same result is achieved in the diurnally flowering subg. *Anecphya* by means of the large number of weakly supported, nodding stamens having narrow filaments, which form an almost insurmountable wall around the stigmatic region (Schmucker, 1932; Meeuse & Schneider, 1980).

Flowers of certain species of *Nymphaea* are characterized by abundant sclereids in some floral parts. In *N. caerulea* Savigny of subg. *Brachyceras*, elongate bipolar or acicular sclereids are found in the stamens (Chifflot, 1902). In several species of subg. *Hydrocallis*, such acicular sclereids are abundant throughout the staminal tissue, and in a few species they are evident in the stigmatic ray tissue as well. In *N. oxypetala* of this subgenus, tiny spherical sclereids are produced in and apparently released from staminal tissue adjacent to the anther sacs (Chifflot, 1902; Wiersema, 1987). Asterosclereids and trichosclereids are also found in the floral tissues of certain species (Malaviya, 1962). All of the sclereids mentioned above are impregnated with calcium oxalate crystals. It has been suggested that the asterosclereids or trichosclereids may provide support (Conard, 1905; Malaviya, 1962) or internal water recovery (Schanderl, 1973). Neither of these explanations is sufficient to explain the spherical sclereids found in stamens of *N. oxypetala* or perhaps the great abundance of acicular sclereids in stamens in other members of subg. *Hydrocallis*. That these structures may help deter beetle predation on floral parts has not been investigated.

Differences in pollen morphology exist within *Nymphaea*. The pollen of night-blooming and presumably beetle-pollinated subgenera is smoother than the highly puckered or ornamented pollen of the three diurnally flowering subgenera, which are apparently pollinated by bees and/or flies (Wiersema, 1987).

Waterlily seeds also vary. Those of temperate members of subg. *Nymphaea* are completely devoid of surface papillae, whereas those of tropical subgenera usually bear numerous surface papillae in various arrangements. A basic difference between the environmental requirements of temperate vs. tropical seeds is that the former must be adapted to endure colder (and perhaps freezing) temperatures, whereas the latter must often withstand periods of drought. Indeed, seeds of most temperate species exhibit little resistance to drought (Conard, 1905), and those of many tropical species do not tolerate freezing. It is hypothesized that the surface papillae may be important in conferring drought resistance to tropical seeds, perhaps by absorbing water. It is interesting to note that *N. mexicana*, a subtropical member of the mostly temperate subgenus *Nymphaea*, has papillose seeds.

A number of waterlily species produce seeds without cross-pollination. In those thus far examined, autogamy rather than agamospermy has been responsible (Wiersema, 1987). Two different methods are employed in producing seeds autogamously. One involves homogamy, the early dehiscence of stamens on the first day of flowering when the stigma is receptive to pollen. I have observed this in *N. jamesoniana* and *N. lingulata* Wiersema of subg. *Hydrocallis* and *N. ampla* (Salisb.) DC. of subg. *Brachyceras*, and it has been reported for *N. alba* of subg. *Nymphaea* (Heslop-Harrison, 1955). The second method involves maintaining the receptivity of the stigma in second-day flowers, such that pollen being released at the normal time can effect self-pollination. This method is apparent in several taxa of subg. *Hydrocallis*, such as *N. amazonum* subsp. *amazonum*, *N. conardii* Wiersema, and *N. rudgeana*. Autogamy has also been reported among other members of subg. *Brachyceras*, such as *N. caerulea* and *N. stellata* Willd. (Conard, 1905). In the latter species and in *N. ampla* (Prance & Anderson, 1976), reports have suggested pollen release in buds.

With the exception of the reports concerning autogamy in the temperate day-flowering *N. alba*, all other reports of autogamy involve tropical diurnally and nocturnally flowering species. No records of autogamy are known for subgenera *Lotos* or *Anecphya*.

ASEXUAL REPRODUCTION

A number of asexual modes of reproduction are employed by waterlily species. The most widespread is stolon formation, as in *N. lotus* of subg. *Lotos*; *N. amazonum*, *N. gardneriana* Planchon, *N. lasiophylla*, *N. lingulata*, and *N. tenerinervia* Caspary of subg. *Hydrocallis*; and *N. mexicana* of subg. *Nymphaea*. In *N. mexicana*, stolons are of greater diameter and develop an unusual terminal perennating structure at the end of the growing season. This structure consists of a compact series of leaf buds from which hang several starch-laden roots reminiscent of a bunch of bananas, hence the common name "banana waterlily."

Several other members of subgenus *Nymphaea*, namely *N. odorata*, *N. tuberosa*, *N. alba*, and *N. candida* J. S. Presl, possess horizontal rhizomes in contrast to the erect rhizomes of all other species. Several shoots may eventually develop from a single horizontal rhizome. On the main rhizome of *N. tuberosa* small tuberous shoots develop which, due to a constricted area at their base, are readily detachable and serve as propagules.

Two other forms of asexual reproduction have been observed, one involving proliferation of floral tissues, the other proliferation of leaf tissues. In the former, all but the outermost appendages of flowers are aborted, and an enlarged tuber is formed centrally which gives rise to whorls of leaves and additional tuberiferous flowers. A few orders of branching may result, leading to the formation of a large number of small tubers. The tubers readily abscise, float briefly, and eventually become rooted and develop into mature plants. This process occurs regularly in the neotropical *N. lasiophylla* and *N. prolifera* of subg. *Hydrocallis* (Wiersema, 1987). Similar abortive flowers have been reported in other syncarpous *Nymphaea* (Bose, 1961; Mohan Ram & Nayyar, 1974; Majeed Kak, 1977; Mitra & Subramanyam, 1982) but only as an unusual occurrence. This is a very effective method of reproduction and dispersal, particularly in *N. prolifera*, which commonly inhabits lowland savannas subject to periodic flooding.

Proliferation of leaf tissue occurs in *N. micrantha* Guillemin & Perrottet of subg. *Brachyceras*. In this species new plants are formed on the upper surface of a leaf opposite the insertion of the petiole. These develop extensively only after the leaf is detached from the parent plant (Conard, 1905; Hutchinson & Dalziel, 1966). The effectiveness of this reproductive process is unknown. *Nymphaea micrantha* is found only in west tropical Africa.

EVALUATION OF REPRODUCTIVE STRATEGIES

Perhaps the best way of evaluating the overall reproductive strategies of waterlilies is to examine distributional ranges of various species as reflections of their colonizing abilities. Reproductive strategy is one of several factors that contribute to distributional success. Table 1 provides a ranking of temperate, subtropical, and tropical species derived from their natural ranges. Such a measure cannot account for differences in population frequency within ranges, hidden instances of artificial dispersal, or problems of questionable taxonomy; however, it is still useful. Table 1 also provides information on the reproductive alternatives employed by each species, insofar as information is available. All of these species are assumed to be capable of normal sexual outcrossing. Several questionable species from the paleotropics have been excluded.

Two elements seem to be important in interpreting the colonizing ability of a given species, its dispersal capability, and its ability to become established and persist in a new location. In cases involving overland dispersal, seeds are the probable dispersal units and waterbirds the likely agents. Although most aspects of seed release appear to be similar among the various species, the number of seeds per fruit and the size of the seeds are two variables that could affect dispersal capability. *Nymphaea tetragona*, which is dispersed solely by seeds, has comparatively large seeds with relatively few per fruit, two traits that could potentially retard dispersal. However, *N. tetragona* has the broadest distribution of any species. Even *N. mexicana*, having the largest seeds (almost twice as large) with the fewest per fruit of any *Nymphaea* species, has been successfully dispersed along the Gulf Coast of North America. The smallest and probably most numerous seeds are found in *N. jamesoniana*, the most widely distributed neotropical species. Thus there appears to be little relationship between these seed variables and dispersal capability, which appears to be adequate for most species.

If dispersal factors do not appear to limit overall distribution, then factors relating to establishment must be considered more important. Ecological factors certainly affect germination, seedling development, and successful maturation of a colonizing species. If these initial barriers can be overcome, establishment and long-term survival in a new environment become heavily dependent on reproductive ability.

Several key observations can now be made with reference to Table 1. All ten of the most widely distributed tropical species utilize at least one reproductive alternative to total reliance on xenogamy or geitonogamy. In seven of the ten this alternative is autogamy. Of the ten most narrowly distributed species, only one is known to be autogamous. As already mentioned, reproductive strategy is one of several factors that affect overall species distributions. However, in terms of distributional success for tropical *Nymphaea* species, autogamy seems to be the most important reproductive alternative.

The importance of autogamy to tropical waterlily species is to provide for seed production in the absence of potential pollinators and to enhance seed production when xenogamy or geitonogamy become inefficient. It also would eliminate the need for a second individual in colonizing situations; however, this obstacle is easily overcome by clonal or

TABLE 1. *Distributional success of* Nymphaea *species in relation to reproductive strategy. All species known or assumed to be capable of xenogamy. Data mostly from Conard (1905), Wiersema (1987), or personal observation.*

Species	Subgenus	Index[1]	Reproductive alternatives[2]	
			Autogamy	Asexual
TEMPERATE				
N. tetragona	*Nymphaea*	310		
N. candida	*Nymphaea*	130		HR
N. alba	*Nymphaea*	110	A	HR
N. odorata	*Nymphaea*	90		HR
N. tuberosa	*Nymphaea*	30		HR
SUBTROPICAL				
N. elegans	*Brachyceras*	40		
N. mexicana	*Nymphaea*	35		S
TROPICAL				
N. lotus	*Lotos*	140		S
N. jamesoniana	*Hydrocallis*	125	A	
N. ampla	*Brachyceras*	115	A	
N. caerulea	*Brachyceras*	115	A	
N. amazonum	*Hydrocallis*	100	A	S
N. rudgeana	*Hydrocallis*	100	A	
N. conardii	*Hydrocallis*	90	A	
N. nouchalii	*Lotos*	90		S?
N. prolifera	*Hydrocallis*	90		FLP
N. stellata	*Brachyceras*	85	A	
N. capensis	*Brachyceras*	70		
N. gardneriana	*Hydrocallis*	70		S
N. oxypetala	*Hydrocallis*	70		
N. glandulifera	*Hydrocallis*	65	A	
N. gigantea	*Anecphya*	60		
N. tenerinervia	*Hydrocallis*	40		S
N. lingulata	*Hydrocallis*	35	A	S
N. lasiophylla	*Hydrocallis*	30		FLP, S
N. micrantha	*Brachyceras*	30		FOP
N. gracilis	*Brachyceras*	20		
N. petersiana	*Brachyceras*	20		
N. potamophila	*Hydrocallis*	20		
N. sulphurea	*Brachyceras*	20		
N. novogranatensis	*Hydrocallis*	15		

[1] Latitudinal range + longitudinal range (in degrees).
[2] HR = horizontal rhizomes; S = stolons; FLP = floral proliferation; FOP = foliar proliferation.

multiple-flowered individuals, as there is no evidence of self-incompatibility in *Nymphaea*. In the neotropics several night-blooming species of subg. *Hydrocallis*, such as *N. prolifera*, *N. gardneriana*, *N. lasiophylla*, and *N. tenerinervia*, rarely produce seeds in natural populations, although they are capable of seed production if cross-pollinated (Wiersema, 1987). Reports on pollinators in this subgenus have implicated only scarab beetles of the genus *Cyclocephala* Latreille (Cramer et al., 1975; Prance & Anderson, 1976; Prance, 1980; Wiersema, 1987). Asexual reproduction has seemingly allowed the four species mentioned to exist in areas where these pollinators are absent. Further overland expansion from such sites is probably more difficult in the absence of seed production. Nonautogamous species without asexual alternatives would be completely restricted by pollinator availability. The narrow distribution of most tropical species in this latter category suggests that pollinator distribution may be an important element in restricting their spread.

The paleotropical and widespread *N. lotus* and *N. nouchalii* Burm. f. of the night-blooming subg.

Lotos have not been observed to be autogamous, however. To account for the distributional success of these taxa either: a) autogamy has gone undetected, b) the pollinators utilized are more widely distributed or a range of pollinators is used, or c) stolons are more effectively employed in dispersal than in other waterlily species. A fourth possibility, that of human dispersal, may account for some of this distribution, as these species are cultivated, and the existence of *N. lotus* in the neotropics has been attributed to artificial introduction (Wiersema, 1982). However, floristic accounts have considered them indigenous throughout most of their paleotropical ranges.

In temperate species, all of subg. *Nymphaea*, autogamy is clearly not as important in conferring distributional success, as it has been observed only in one species. With the exception of the detachable tubers produced by *N. tuberosa*, seeds are the only effective dispersal agent produced in this subgenus. How then are the limits of pollinator availability overcome by wide-ranging temperate species? These diurnally flowering species either employ pollinators that are more widely distributed or utilize a range of pollinators. The latter explanation is probably correct, in view of the variety of insect visitors reported for day-blooming species in temperate regions (Robertson, 1889; Conard, 1905; Meeuse & Schneider, 1980; Schneider & Chaney, 1981; Schneider, 1982a; Capperino & Schneider, 1985), but it needs to be confirmed with comprehensive studies of species–pollinator relationships.

Pollinator relationships of most tropical day-blooming species in subgenera *Anecphya* and *Brachyceras* remain to be assessed; however, in subg. *Brachyceras* autogamy has become an important alternative to total reliance on outcrossing.

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REPRODUCTIVE BIOLOGY OF SELECTED AQUATIC PLANTS

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ABSTRACT

Aquatic weeds are species that inhabit bodies of water in such quantities that they either interfere with man's usage or become a health hazard by serving as a breeding area for insects, especially mosquitoes. These plants are most often introduced species. They increase in numbers mostly by vegetative reproduction, including stem or leaf fragmentation, budding, or turion formation. For dioecious species in which only one sex occurs in an area, vegetative means are the only methods of reproduction. Monoecious species or species with perfect flowers often produce viable seeds, which usually are not important for increasing the population size, as they are deposited in large mats and do not get enough light or other requirements for germination. Some species that reproduce sexually, such as Eichhornia azurea, *are self-sterile, but others, such as* Eichhornia crassipes *or* Ottelia alismoides, *are self-compatible.* Ottelia alismoides, *in fact, almost always is self-pollinated. Before the flowers open, the pollen tubes grow to the stigma from the anther. The flower eventually opens, but fertilization has already occurred. Pollination may be by insects (e.g.,* Hydrocharis morsus-ranae*) or by wind (*Potamogeton nodosus*); or it takes place at the surface of water by contact between stigma and anther (*Lagarosiphon*), by airborne pollen (*Hydrilla verticillata*), or by water-borne pollen (*Elodea canadensis*); or pollination may occur underwater (*Najas minor*).*

Aquatic weeds are species that inhabit bodies of water in such quantities that they either interfere with man's usage or become a health hazard by serving as a breeding area for insects. Such species are often introduced. Cook (1987) discussed 12 species that he considered to be the most notorious aquatic invaders and pointed out that only one, *Trapa natans*, relies on sexual processes for its reproduction and spread. Of the remaining 11, he noted that only *Myriophyllum spicatum*, *Najas minor*, and *Pistia stratiotes* regularly develop seed in their native and adventive ranges. *Salvinia molesta* is a sterile hybrid, and the rest have well-developed self-incompatibility mechanisms.

An understanding of their reproductive biology, both sexually and vegetatively, is important in developing methods of control for aggressive species. Aquatic flowering plants have pollinating systems ranging from those independent of the aquatic environment, such as wind and animal, to varying degrees of adaptation to the aquatic environment, beginning with pollination at the surface of the water, to underwater pollination with the pollen adhering to the surface of air bubbles, to a totally aquatic system in which pollen sinks in the water. The following selected list of aquatic weeds begins with the least adapted to the aquatic environment and terminates with the most adapted.

INSECT POLLINATED

Eichhornia crassipes (C. Mart.) Solms-Laub. (Pontederiaceae). Water-hyacinth.

Water-hyacinth is a free-floating annual or perennial with rosettes, well-developed stolons, and swollen to bulbous petiole bases. It is native to tropical South America but has been introduced ornamentally into warmer parts of all continents for its showy blue flowers (Barrett, 1982; Cook, 1987). *Eichhornia crassipes* spreads vegetatively by daughter rosettes that form rapidly on brittle stolons and separate from floating mats quite easily (Barrett, 1979).

Water-hyacinth is tristylous and self-compatible (Barrett, 1979). Barrett (1980a) studied fertility of nine clones of *Eichhornia crassipes* from different regions of the world. Eight of the nine populations flowered regularly during the study period and the ninth flowered frequently following the study period. Artificial crosses, both selfed and outcrossed, were made with each clone that flowered during the study period, totaling 2,546 crosses. Of these, 94.7% produced capsules, with an average of 143.3 seeds per capsule. All populations exhibited a high degree of self-compatibility, although degree of seed production varied among clones. Percentage of capsule set was significantly higher

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among all of the out-crossed than among all of the selfed plants.

A similar amount of seed production has been found in natural populations (Barrett, 1980b). He studied open-pollinated and artificially pollinated plants from 19 populations, with capsule production ranging from 72.3% to 100% per month for artificial pollinations, whereas it ranged from 8.1 to 68.7% for open-pollinated plants. Seeds per capsule were considerably fewer in open-pollinated ones, ranging from a mean of 3.1 to 40.8 per capsule, compared with artificially pollinated ones of 74.1 to 188.7 per capsule.

According to Barrett (1980b), *Eichhornia crassipes* can begin flowering 10–15 weeks after germination, soon for a perennial. One inflorescence with 20 flowers has the potential of producing 3,000 seeds, and up to four inflorescences can be produced by a single rosette during a 21-day period. Since flowering in subtropical to subtemperate regions may occur over five to nine months, the species can produce astronomical numbers of seeds. Regardless, most individuals in natural populations are probably produced vegetatively.

Seedlings were observed in only three of the 19 populations studied by Barrett (1980b). Apparently, seeds produced in dense floating mats of water-hyacinth either sink to the bottom or accumulate in the mat. Shading from the mats or low light levels coupled with low temperatures in deep water prevent the seeds from germinating.

Eichhornia azurea (Sw.) Kunth (Pontederiaceae). Rooted water-hyacinth.

Rooted water-hyacinth is an attached perennial with distichous, linear submersed leaves and elliptic to obovate floating leaves. The inflorescence is a compact spike of blue flowers, each having erose perianth lobes and a bilobed yellow spot in the center of the upper lobe. Vegetative reproduction is by chance fragmentation of the robustly branched stems (Barrett, 1978). The species is native to the Neotropics (Horn, 1987) and has been introduced to various regions as an ornamental (Barrett, 1978).

Unlike *Eichhornia crassipes, E. azurea* is tristylous and partially self-sterile. Barrett (1978) artificially selfed long-styled forms with the low-level anthers. Only 12% fruit set occurred. In contrast, when mid-level anthers were utilized, 94% fruit set occurred. A semihomostylous race has been observed in Costa Rica. This one has one whorl of anthers about the same level as the stigma. High seed set occurs when pollen from this anther whorl is used for selfing.

Ottelia alismoides (L.) Persoon (Hydrocharitaceae). Duck-lettuce.

Duck-lettuce is an annual or perennial from attached basal rosettes, with long-petiolate orbicular to ovate leaves. The flowers are borne singularly in solitary spathes terminating long scapes. They are perfect or very rarely imperfect (Cook & Urmi-König, 1984b), fragrant, and have staminodia that are important in attracting insect visitors. Cook (1982) indicated that, although no field observations have been published, the species is almost certainly insect pollinated. He also indicated that it is highly self-compatible and occasionally cleistogamous.

The plants are weeds of rice fields in the southern United States (Dike, 1969), Italy, and Southeast Asia (Cook & Urmi-König, 1984b). Increase in population size is apparently by seed, since no specialized means of vegetative propagation occurs (Cook & Urmi-König, 1984b).

Egeria densa Planchon (Hydrocharitaceae). Brazilean-elodea.

Brazilean-elodea is a rooted perennial with cauline leaves that are mostly in whorls of four. The flowers are imperfect and solitary on axillary peduncles that project the flowers to or above the water surface. Staminate and carpellate flowers contain glistening green functional nectaries. The flowers are frequently visited by small Diptera (Cook & Urmi-König, 1984a), but there is no evidence yet as to whether these insects are important in pollen transfer, since seed-set is so rare in nature and in cultivation.

Egeria densa is native to southeastern Brazil, Uruguay, Argentina, and possibly Paraguay. The species has been introduced into North America, Europe, Asia, Africa, and Australia. Only in warm temperate and cool subtropical climatic regions has it developed into an aquatic weed. Outside its native range, only in Chile are carpellate flowers known (Cook & Urmi-König, 1984a). No specialized overwintering structures are produced. Stem fragments root readily and develop into new shoots, so rapidly that the species often quickly overgrows a lake. Spread of *Egeria densa* probably results from its popularity in aquaria.

Hydrocharis morsus-ranae L. (Hydrocharitaceae). European frogbit.

European frogbit is a free-floating, stoloniferous perennial with basal, petiolate leaves. The flowers are borne in spathes and terminate pedicels that project the flower well above the spathe. Cook (1982) indicated that the carpellate flowers possess staminodia modified into nectaries that secrete a nectar attractive to insects. The staminate flowers appear quite similar to the carpellate flowers but lack these nectaries. They apparently offer no reward, but rely on mimicking the nectar-bearing carpellate flowers for insect attraction.

Hydrocharis morsus-ranae first appeared in the Western Hemisphere in 1932 at the Ottawa Botanic Garden, where it was cultivated (Dore, 1968). It was first noticed as an escape in 1939 in the Rideau Canal, from which it spread into the Ottawa and St. Lawrence rivers (Dore, 1968) and into the United States in 1974 (Roberts et al., 1981). This spread may have been by seed and by hibernacula. Cook & Lüönd (1982b) indicated that the species can grow from one hibernaculum to cover an area of one meter in diameter in one season.

Pistia stratiotes L. (Araceae). Water-lettuce.

Pistia is a monotypic genus of rosulate-leaved, free-floating, stoloniferous plants occurring in subtropical and tropical Africa, Asia, and America. The leaves are densely short-pubescent and surround a single terminal spathe that has the spadix adnate to its median line. The plants are monoeceious, with staminate and carpellate flowers on one spadix.

Cook (1987) indicated that the species is probably mostly self-pollinated, possibly by insects. Wilson (1960) stated that in Florida the ovary of water-lettuce tends to enlarge and become inflated, but no seeds are produced. He suggested that this lack of seed-set is probably due to absence of pollinators. His suggestion would tend to support Cook's view of the species being insect pollinated.

Pistia is important because of its vegetative reproductive capabilities. New plants are produced at the ends of the stolons and are separated from the parent plant by fragmentation. The species can reproduce rapidly enough to clog waterways.

WIND POLLINATED

Potamogeton nodosus Poiret (Potamogetonaceae). Floating pondweed.

Potamogeton nodosus is a perennial from elongate rhizomes with long-petiolate, lanceolate submersed and floating leaves with cuneate bases. The inflorescence is a compact spike held above the surface of the water (Haynes, 1978).

The species can cover huge areas of lakes in the southern United States. There are probably only one or a few clones, as *Potamogeton nodosus* increases in number mostly by rhizome growth. Pollination is predominantly anemophilous (Philbrick & Anderson, 1987). As such, the species is adapted for outcrossing.

Myriophyllum spicatum L. (Haloragaceae). Eurasian milfoil.

Eurasian milfoil is a submersed, rooted, stoloniferous perennial with whorled pinnately compound leaves and emergent imperfect flowers. The plants are monoecious and wind pollinated.

Myriophyllum spicatum is native to northern Eurasia (Cook, 1987) and has spread into the Western Hemisphere from Ontario and Quebec south to Florida and west to Wisconsin, Oklahoma, Texas, and Mexico, as well as to British Columbia, Washington, and California (Aiken, 1981). The species has often choked waterways (Coffey & McNabb, 1974), but in some places dramatic decline in the number of plants has occurred (Bayley et al., 1968; Elser, 1969) to the extent that the species no longer poses an environmental problem in these places.

Spread of Eurasian milfoil is mostly by vegetative fragment and seed (Cook, 1987).

POLLINATION AT SURFACE OF WATER

Hydrilla verticillata (L. f.) Royle (Hydrocharitaceae). Hydrilla.

Hydrilla is a perennial, rooted plant with the lower nodes having opposite leaves and the upper nodes having whorls of three to eight leaves. The flowers are imperfect and are produced singly in the leaf axils. Carpellate flowers are sessile with an elongating hypanthium that projects the perianth and stigma to the water's surface. As the hypanthium elongates, the perianth is forced open by a gas bubble (Cook & Lüönd, 1982a). Upon reaching the water surface, the perianth lobes open further, forming a funnel that is underwater below and open to the air above. The stigmas are at the bottom of this funnel. The subsessile staminate flower buds are released from the spathe by pedicel abscission and float on the surface at about a 45° angle. An hour or more after the bud is released, the perianth segments retract slightly, with each anther adhering to the convex part of the perianth. Soon the perianth spreads horizontally on the water surface; shortly after this the stamens suddenly spring from a horizontal to a vertical position; the anthers burst and scatter pollen in the air. As the pollen falls, most grains land on the water and are lost for reproductive purposes, but some fall into the funnel-shaped perianth of a carpellate flower, contacting a stigma. This is apparently a risky method of pollination, but, according to Cook & Lüönd (1982a), seed production is adequate to maintain hydrilla populations in areas that dry out and where hibernacula are not produced, or at least have not been observed.

Most increase in plant density is by hibernacula, which occur in two forms. The first form is from erect stems and is olive green and ovoid-conical with spreading apices that give the structure the appearance of a sandbur. Hibernacula of the second type are brown, subterranean structures that appear as minute potatoes at the tips of long, stringy, white, leafless rhizomes. Cook & Lüönd (1982a) indicated that the first type has food reserves in leaves, whereas the second has food reserves in swollen stem tissue.

Lagarosiphon major (Ridley) Moss (Hydrocharitaceae). African-elodea.

African-elodea is a rooted submerged perennial with alternate leaves. The flowers are from axillary, solitary spathes. The staminate spathes enclose many pedicellate flower buds, whereas the carpellate spathes contain only one sessile flower.

The staminate flower buds are released and rise to the water surface, remaining closed for a short while before eventually opening by the reflexing of perianth parts. The open flower, with three fertile horizontal and three sterile erect stamens, floats on the reflexed perianth. The staminodia function as a sail.

Carpellate flowers are projected to the water surface by an elongate hypanthium (Healy & Edgar, 1980). A meniscus is formed on the water surface by the carpellate flower, which then is slightly below the surface but with the styles protruding above the surface film. As staminate flowers move along the water, propelled by staminodia sails, one flower eventually tips into the meniscus, thereby causing a horizontal fertile stamen to contact an erect stigma.

Lagarosiphon has become an important weed in New Zealand, where it is replacing *Elodea canadensis* that has attained its maximum density and is declining (Healy & Edgar, 1980). Only carpellate plants are known in New Zealand, however, where it spreads by vegetative fragments.

Elodea canadensis Michaux (Hydrocharitaceae). Canadian-pondweed.

Canadian-pondweed is an attached species with cauline leaves in whorls of three. The flowers are axillary, imperfect, and elevated to the water surface by an elongate pedicel on the staminate flower and by an elongate hypanthium on the carpellate flower. The carpellate flower opens by recurving of the sepals and petals, which float on the water surface. The styles spread between the sepals and then recurve, with the tips usually becoming submersed. Upon reaching the surface, the staminate flower opens by the sepals and petals spreading there. The anthers dehisce in an upright position, scattering the pollen onto the surface of the water. Pollen floats on the water surface until it contacts a stigma, initiating germination.

Elodea canadensis is widespread in North America, where it is not known to become weedy. It was introduced into Europe in the early nineteenth century (Cook & Urmi-König, 1985), whereas the first record in Australia is 1931 (Aston, 1973). The European material has almost exclusively been carpellate plants. Vegetative reproduction is mostly from stem fragmentation. Not all nodes, however, are capable of rooting and developing a new plant.

SUBMERSED POLLINATION WITH POLLEN ADHERING TO AIR BUBBLES

Ruppia maritima L. (Potamogetonaceae). Ditch-grass.

Ditch-grass is an annual or perennial of brackish or saline waters with alternate leaves, these having the blades adnate to the stipules for the entire length of the stipules. The flowers are perfect and are produced in a capitate spike that is first enclosed by the sheathing leaf bases. The pollen is four times as long as broad, arcuate, swollen at the ends and at the center on the convex side, and three celled. Its exine is reticulate (Haynes, 1978). The gynoecium is of four or five distinct, stipitate carpels that have the gynophore elongating after anthesis. Pollination is mostly underwater. Following maximum peduncle elongation, the anthers dehisce underwater, releasing pollen that is trapped in air bubbles (Verhoeven, 1979). As the bubbles remain with an inflorescence for several hours, the pollen grains can only contact a stigma of that flower (Verhoeven, 1979), making self-pollination almost certain. Such a system insures ample seed set, which is important for an often annual species.

Out-crossing does occur occasionally in *Ruppia maritima*. Air bubbles, with their trapped pollen grains, break free from the inflorescence occasionally and rise to the water surface. Once on the surface, the bubble breaks, liberating the pollen grains, which float on account of trapped air in the reticulations of the exine. Should they contact a stigma that is at the water surface, cross-pollination occurs. More likely, however, these grains are blown from the *Ruppia* zone.

UNDERWATER POLLINATION

Zannichellia palustris L. (Zannichelliaceae). Horned-pondweed.

Horned-pondweed is an annual rooted plant with alternate, opposite, and occasionally whorled, linear leaves on the same plant. The flowers are imperfect, both staminate and carpellate in the same leaf axil. The carpellate flower is surrounded by a spathelike envelope and consists of four or five separate carpels, each with a funnel-shaped stigma. The staminate flower is outside the envelope, with a filament that projects the anther over the stigmas. Pollen is released in a gelatinous mass (Haynes & Holm-Nielsen, 1987) and falls directly into the funnel-shaped stigma, thus insuring self pollination.

Zannichellia is an annual without any vegetative perennating structure. It therefore depends entirely on seed production for surviving the unfavorable season.

Najas minor All. (Najadaceae). Water nymph.

Najas minor is a rooted, submersed annual with subopposite, serrulate leaves. The plants are monoecious, with flowers solitary in the leaf axils, the staminate flowers mostly above the carpellate ones. Pollination is entirely underwater. The pollen is heavier than water, and, after being released, it slowly descends through the water column, possibly contacting a stigma. Although this is not a system that insures pollination, seed set is very good.

The species occurs in northern Africa, Europe, Asia, and North America (Triest, 1987). In the past 50 years, it has become widespread in eastern North America (Haynes, 1977, 1979; Meriläinen, 1968), where it has become a troublesome weed in some areas. Increase in numbers is mostly from seed. Meriläinen (1968) suggested that the species has been spread by migrating waterfowl.

DISCUSSION

Some species of aquatic vascular plants have become weedy, especially in areas outside their natural ranges. These weedy species have posed environmental problems, either by interfering with recreation, such as by clogging waterways or by lowering the quality of fishing, or by forming breeding areas of noxious insects. Reproduction sufficient to overtake a body of water most often is vegetative, either by stem fragmentation or by production of hibernacula. Almost all species also, at least occasionally, undergo sexual reproduction. Most have very little adaptation for adequate transfer of pollen. Instead, they project the inflorescence above the water for either animal or wind pollination. A few, however, have developed methods of pollen transfer either at the water surface or underwater. Among these few, some, such as *Najas minor*, are annuals and depend entirely on seed production for maintaining the population.

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POLLINATION POSTULATES AND TWO-DIMENSIONAL POLLINATION IN HYDROPHILOUS MONOCOTYLEDONS[1]

Paul Alan Cox[2] *and R. Bruce Knox*[3]

ABSTRACT

A set of pollination postulates are proposed to unify vector identification in pollination biology. These postulates were used to test theoretical predictions concerning two-dimensional pollination systems in Halodule, Halophila, Ruppia, Lepilaena, *and* Amphibolis. *The general syndrome of pollination on the water surface is illustrated by intertidal populations of* Amphibolis antarctica, *whose staminate flowers abscise during low spring tides and float to the surface where they dehisce, expelling a cottony mass of filamentous pollen. The pollen floats and forms search vehicles or pollen assemblages that collide with stigmas on the water surface. The search efficiency of large search vehicles was examined by video analysis of* Ruppia spiralis *pollination. Large search vehicles were found to be more likely to hit stigmas than small ones.*

Although the determination of the vectors responsible for transporting pollen from flower to flower is a central task of pollination biology, no standard criteria for vector determination exist. Historically, methodologies for vector determination range from careful ecological studies to conjecture based upon superficial examination of dried herbarium specimens or worse. As a result, the literature of pollination ecology is uneven in rigor. Perhaps since anthecology originated as a specialization of plant taxonomy, textbooks and reviews tend to favor claims with historical priority. Thus, even incorrect ideas are notoriously difficult to remove from the literature.

An example may be found in the literature concerning the pollination ecology of *Freycinetia arborea* Gaud. (Pandanaceae) in Hawaii. Pollination by rats was suggested by Degener (1930), who made no experiments or observations of pollinator visitation. No consideration was given to how *F. arborea* was pollinated before the introduction of rats to Hawaii by Polynesian colonists in 400 A.D. (Jennings, 1979). However, despite several previous detailed accounts of *Freycinetia* pollination in the Dutch, German, and English literature (see reviews in Cox, 1981, 1984), Degener's rather anecdotal sketch emerged as authoritative. Frequently cited in textbooks, but sometimes attributed to a secondary source (Proctor & Yeo, 1973), the story of rat pollination of *Freycinetia* thus began a life of its own. Each recounting of the story added to both its detail and apparent authenticity. Although the original report did not indicate the time of day that pollination supposedly occurs, this important detail later appeared in a major compendium (Faegri & van der Pijl, 1979). Degener (pers. comm.), however, never witnessed rat visitation but only inferred it from scratches on the floral bracts. Subsequent studies demonstrated such scratches to be caused by the introduced white-eyes that now pollinate *F. arborea.* Electron microscope analysis of bird specimens collected in the nineteenth century indicates that formerly pollination was mediated by now extinct honeycreepers (Cox, 1983a).

Such confusion in vector identification is reminiscent of disputes concerning pathogen determination in medicine in the 1850s. The prevailing theory was that diseases like tuberculosis are caused by a variety of climatic, environmental, and organic factors. However, Robert Koch (1880) proved that tuberculosis is caused by a single bacterium. His

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TABLE 1. *Postulates.*

Koch's Postulates

1. Pathogen must be demonstrated in all cases of the disease.
2. Pathogen must be cultivated in pure culture.
3. Cultured pathogen must cause disease in healthy individuals.
4. Pathogen must be re-isolated from these infected individuals.

Pollinaton Postulates

In the field:

1. Pollen transfer from anther or pollen presentation apparatus to vector must be observed.
2. Pollen transport by vector must be observed.
3. Pollen transfer from vector to stigma must be observed.
4. Pollen deposited by vector on stigma must be demonstrated to effect fertilization.

rigorous methodology has since been encapsulated in a series of postulates named after him (Table 1). Brock (1966) and Harper (1978) have suggested that ecology could benefit from similar rigor.

Using Koch's postulates as a model, we propose a standard set of postulates for vector determination in pollination biology (Table 1). Our postulates require confirmation of each stage of the interaction between anther, vector, and stigma. We submit that unless these postulates have been met, the efficacy of a presumed vector in pollination has yet to be proven. We additionally suggest that all such determinations be made in the natural populations rather than in the laboratory, where unnatural conditions can deceive even the most careful investigators.

We used these pollination postulates to guide our studies of pollination in hydrophilous monocotyledons and to test previous theoretical predictions concerning two-dimensional pollination systems (Cox, 1983b).

THEORETICAL PREDICTIONS OF TWO-DIMENSIONAL POLLINATION SYSTEMS

The probability of a pollen grain reaching the stigma can be modeled for aquatic regimes where wind, currents, and orbital wave motion drive it along an essentially random path. In the simple case of a pollen grain tracing a Brownian path, it can be shown that the pollen grain will eventually hit any coplanar stigma, given enough time (Cox, 1983b; Hersch & Griego, 1969). However, in three dimensions there is a probability that a pollen grain on a random trajectory will not hit any given stigma even given an infinite amount of time. Since such fractal motion is recurrent in two dimensions but not three, it was predicted that selection will favor the evolution of two-dimensional pollination systems where such systems are possible, i.e., in aquatic regimes such as ponds, and intertidal regions (Cox, 1983b).

The theoretical effectiveness of two-dimensional pollination systems can be examined through the use of search theory (Cox, 1983b; Koopman, 1956). Of particular interest are the effects of pollen morphology on stigma encounter rates. The probability P of a pollen grain encountering a fixed stigma, if the pollen grain traces a random path in the same plane, can be shown to be

$$P = 1 - e^{-wL/A}, \tag{1}$$

where w is the width of the path swept by the pollen grain, L is the length of the search path, and A is the search area (Cox, 1983b). Hence at low encounter probabilities, even a small increase in the pollen grain diameter will result in a very large increase in probability of encountering a stigma. Of particular interest is the exponential nature of this function: at low encounter probabilities a doubling of pollen grain diameter will result in a more than two-fold increase in the probability of hitting a stigma.

From these theoretical considerations two general predictions can be made concerning hydrophily (water-pollination): 1) a 2-D pollination system will be more efficient than a 3-D system, and thus favored by natural selection if pollen and stigmas can be dispersed in the same plane; and 2) in a 2-D pollination system, pollen grains or aggregations of large dimension will be much more likely to hit stigmas than small ones. Following the nomenclature of search theory (Koopman, 1956; Cox, 1983b), such aggregations will hereafter be termed "search vehicles."

EMPIRICAL PROPERTIES OF TWO-DIMENSIONAL POLLINATION SYSTEMS

These theoretical predictions concerning two-dimensional pollination were tested in five different genera of marine and freshwater aquatic plants. In accordance with our postulates, we observed in each species the release of the pollen from the anther to the surface, transport of the pollen by the water surface, and deposition of the pollen from the water surface onto the stigma. We are currently studying the efficacy of fertilization under field conditions. Such confirmation is important

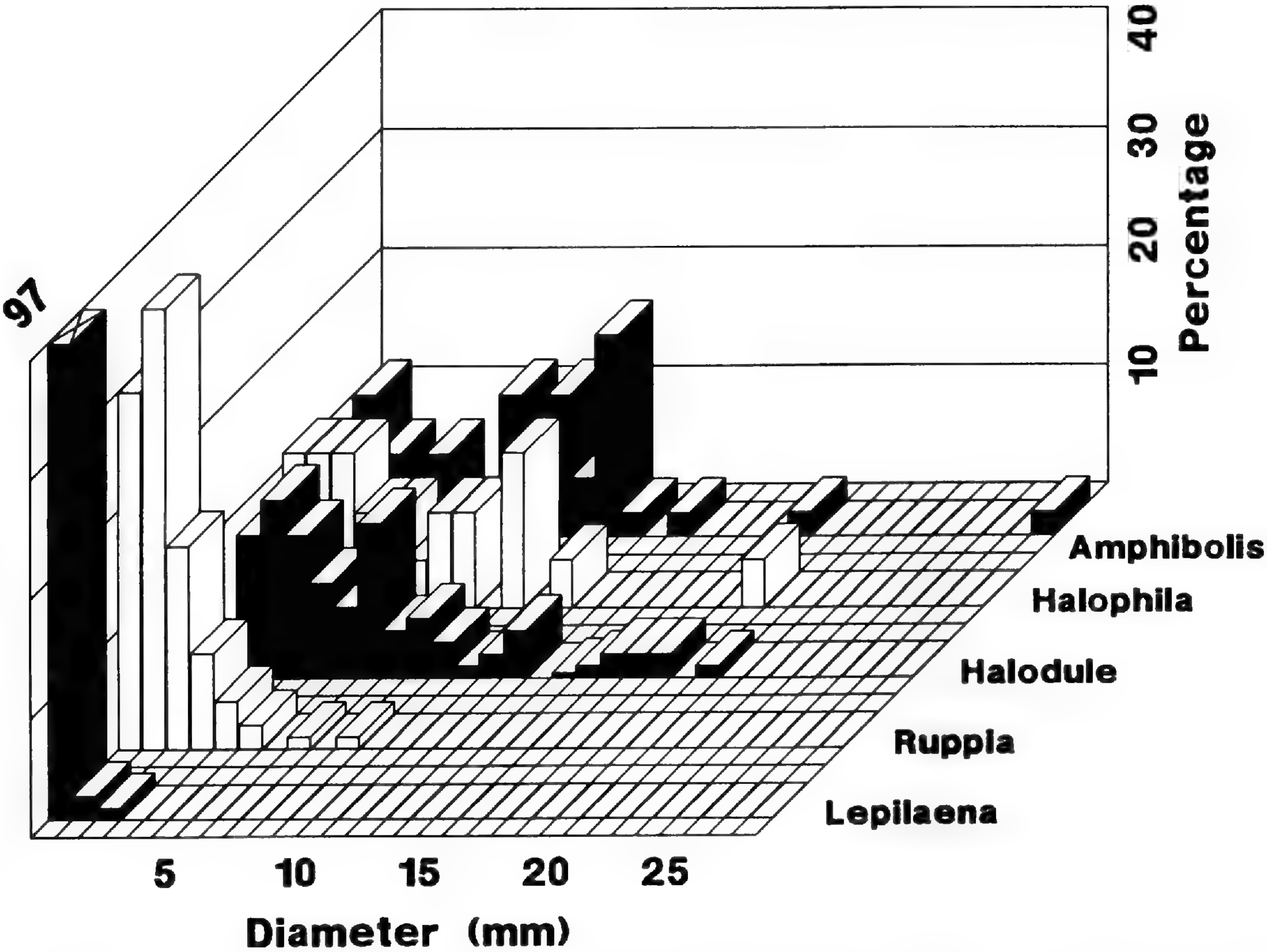

FIGURE 1. *Size distribution of floating search vehicles (pollen aggregations) from five genera of hydrophilous monocotyledons:* Halodule pinifolia *(median = 5,000 μm, N = 114)*, Halophila ovalis *(median = 8,000 μm, N = 17)*, Ruppia spiralis, *Altona, Victoria, population (median = 1,361 μm, N = 300)*, Lepilaena cylindrocarpa *(median = 338 μm, N = 172), and* Amphibolis antarctica *(median = 8,500 μm, N = 40)*.

because of the possibility of apomixis in some dioecious seagrasses, such as *Halophila stipulacea* (Forsk.) Aschers. (Hydrocharitaceae), where seed has been found to develop in pistillate cultures (McMillan, 1980).

Our study focused on genera in which pollen is transported in direct contact with the water. However, plants in which pollination occurs by the collision of floating staminate flowers with buoyant pistillate flowers, such as some genera of the Hydrocharitaceae, e.g., *Vallisneria, Nechamandra, Enhalus, Lagarosiphon,* or *Appertiella,* can also be said to have in effect two-dimensional pollination systems (Cook, 1982; Ernst-Schwarzenbach, 1945; Troll, 1931; Wylie, 1917; Cox, 1988a). Taxa also exist that have submarine two-dimensional pollination systems, such as *Thalassia testudinum* Banks ex Konig (Hydrocharitaceae), where pollen is released at the substrate surface and dispersed in negatively buoyant search vehicles (Cox & Tomlinson, 1988; Cox, in press). Pollination is submarine and essentially occurs along the plane of the substratum.

In the species we studied, e.g., *Halodule pinifolia* (Miki) den Hartog (Cymodoceaceae), *Halophila ovalis* (R. Br.) Hook. f. (Hydrocharitaceae), *Ruppia maritima* L. ex Dumort (Ruppiaceae), *Lepilaena cylindrocarpa* (Koernicke ex Walp.) Benth. (Zannichelliaceae), and *Amphibolis antarctica* (Labill.) Sonder & Aschers. ex Aschers. (Cymodoceaceae), we found pollination to occur on the water surface. In these species the pollen is hydrophobic and forms floating search vehicles that collide with the buoyant stigmas. However, the search vehicles are formed differently and are of different size in each species (Fig. 1). The pollen grains of *Halodule pinifolia*, for example, are filiform and link together in search vehicles that resemble snowflakes, while the pollen grains of *Lepilaena cylindrocarpa* are small, spherical, and dispersed in a floating mat of mucilaginous slime. The pollen grains of *Halophila ovalis* are oval and of medium size, but are dispersed in long floating mucilaginous tubes of thecal origin (Cox & Knox, 1986; Pettitt, 1980, 1981). These tubes link together to form featherlike search vehicles. *Ruppia spiralis* pollen grains have a boomerang shape, forming search vehicles by lining up side-to-side (Cox & Knox, 1986; Gamerro, 1968; Verhoeven, 1979; Van Vierssen et al., 1982). Similar evolutionary convergences can also be found in stigma morphologies: the marine genera have filamentous, smooth stigmas while the freshwater genera have small indusiate stigmas that create small depressions on the water surface. It therefore appears that there has been convergent evolution towards a surface pollination syndrome.

TWO-DIMENSIONAL POLLINATION IN *AMPHIBOLIS ANTARCTICA*

The pollination ecologies of *Halodule pinifolia, Halophila ovalis, Ruppia spiralis,* and *Lepilaena cylindrocarpa* will be reported in detail elsewhere (Cox & Knox, in press). However, many of the essential features of surface-pollinated taxa are illustrated by the pollination ecology of *Amphibolis antarctica,* a dioecious seagrass found in the waters of Western Australia, Southern Australia, Victoria, and Tasmania (Ducker et al., 1977; Aston, 1973).

Amphibolis antarctica plants produce solitary floral units (for discussions of floral terminology see McConchie et al., 1982; Tomlinson, 1982) at the ends of short lateral leafy branches with distichous phyllotaxis. The staminate floral units are bipartite, with two fused stamens borne on a short pedicel. The pistillate floral units consist of two free carpels, each with a sessile ovary bearing three slender styles (McConchie et al., 1982; Tomlinson, 1982). A few days prior to dehiscence, the pedicel bearing the staminate floral units elongates, pushing the fused anthers up from between the bracts. However, the floral units (Fig. 2A) are still hidden by the leafy shoots until they abscise and float to the surface. Within the anthers, the mature tricellular pollen grains are filamentous and 3,000–5,000 μm long, with forked tails (Ducker et al., 1978). The mature pollen "noodles" lack a developed exine (Pettitt et al., 1983). Details of pollen–stigma interactions and pollen tube growth have been investigated by Pettitt et al. (1980, 1983). In pistillate plants the mature styles protrude from the shoots in a plane orthogonal to the plane of phyllotaxis.

Pollination in *Amphibolis antarctica* has been described as submarine, i.e., occurring beneath the surface of the water (Ducker et al., 1978; Pettitt et al., 1980, 1981, 1983). However, the possibility of variation is indicated by previous observations that the male flowers may be shed, releasing their pollen on the surface of the sea, with the floating pollen forming large aggregates (Ducker et al., 1978).

We studied the pollination ecology of *Amphibolis antarctica* in an intertidal population at Point Lonsdale, Victoria, Australia, attempting to verify each of the previously discussed pollination postulates. At 3:04 P.M. on December 13, 1986, during a low (0.3 m) tide, numerous staminate and pistillate plants in the population were examined and found to have mature flowers. At low tide, the tops of the plants were observed floating on the surface, with the plane of the distichous phyllotaxis coplanar with water surface. As a result, one set of stigmas from each pistillate floral unit penetrated the water surface. A few abscised staminate flowers that had already released their pollen were found along the beach, but no pollination events were observed.

Between 4:40 P.M. and 5:20 P.M. on December 15, 1986, during an even lower tide (0.2 m), several thousand staminate floral units were observed to abscise (Fig. 3A) and float to the surface (Fig. 3B). Once on the surface, the anthers dehisced longitudinally and extruded flocculent masses of floating pollen (Figs. 2A, 3C). The pollen mass from each male floral unit rapidly expanded on the water surface into large floating search vehicles (median diameter = 8,500 μm, N = 40) of fractal geometry (Fig. 3D). The tops of nearly all of the mature pistillate plants in the population were exposed during this extremely low tide so that one set of stigmas in each floral unit penetrated the water surface (Fig. 3E). Pollination was observed to occur on the water surface through the collision of the floating search vehicles with the stigmas (Figs. 2B, 3E). As the tide came back in, thousands of empty staminate floral units were washed up along the beach. Field experiments with mature and slightly immature pollen showed mature pollen to float, while slightly immature pollen proved to be neutrally buoyant.

By observing actual pollination events at the water surface, we can with confidence ascribe a two-dimensional surface pollination syndrome to *Amphibolis antarctica.* Two-dimensional surface pollination is probably characteristic of *A. amphibolis* in the intertidal zones where the stigmas have the potential to be exposed during low tides. The species can grow and flower at greater depths, however, where pollination, if it occurs at all, must of necessity be submarine. Although we believe *Amphibolis antarctica* to be primarily surface-pollinated, submarine pollination cannot be ex-

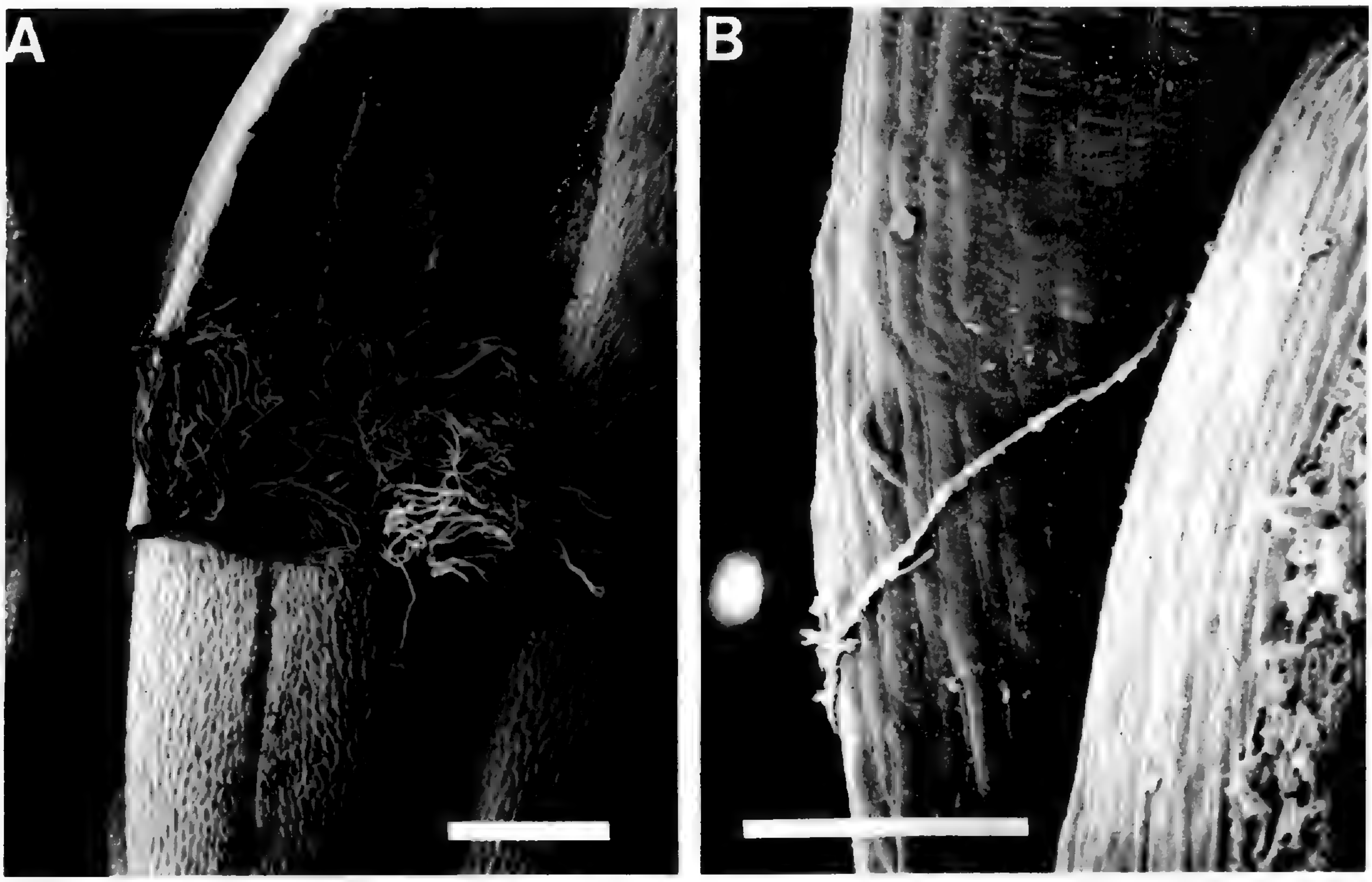

FIGURE 2. *Reproductive structures of* Amphibolis antarctica.—*A. Staminate floral unit prior to dehiscence, with the filiform pollen exposed (scale = 1 mm).*—*B. Filiform pollen grain on an* Amphibolis *stigma from a natural pollination event in the Point Lonsdale, Victoria, population (scale = 100 μm).*

cluded on the basis of our current observations and may also occur in the species.

The floral morphology of *A. antarctica* permits only one of the two sets of stigmas in each pistillate floral unit to encounter the water surface and hence be pollinated. This may relate to the fact that only one of the two ovaries develops, while the other one aborts (Tomlinson, 1982). This condition is analogous to the situation in *Ruppia*, where the inflorescence frequently floats on the surface in such a way that only one of the sets of stigmas is exposed to floating pollen while the other is submerged. Germination in *A. antarctica* is viviparous (Fig. 3F) (Black, 1913), with the mature seedling being released together with an unvascularized "grappling apparatus" (Fig. 3G) that develops as an outgrowth of the female floral unit (McConchie et al., 1982). This grappling apparatus presumably assists in attaching the seedling to a substrate.

SEARCH VEHICLE SIZE AND SUCCESS in *RUPPIA SPIRALIS*

Although two-dimensional search theory predicts that large search vehicles are much more likely to encounter stigmas than small search vehicles (Cox, 1983b), there has yet to be an empirical test of this prediction. We therefore studied pollen/stigma encounters in a *Ruppia maritima* population growing in a brackish pond near Queenscliff, Victoria. Using an immersible camera stand, we filmed natural pollination events with a video camera equipped with a macro lens. The video tape was then analyzed frame by frame with a high-resolution freeze-frame video deck attached to a Zeiss Videoplan digital imaging system. Dimensions of all search vehicles were calculated by digitizing their images on the video screen. The size distributions (largest diameters) of 1,000 such search vehicles chosen at random from the video footage were calculated and recorded. Then the video tape was analyzed again to determine the sizes of search vehicles that actually collided with stigmas. This was accomplished by finding a frame in which a search vehicle could be seen to hit the stigma, and then reversing the tape several frames so that the dimensions of the search vehicle prior to collision could be determined. This procedure was repeated for 100 such search vehicles.

The respective size distributions of successful search vehicles together with the size distributions of all search vehicles are shown in Figure 4. The median size of all search vehicles was found to be 812 μm (N = 1,000), while the median size of successful search vehicles was much larger (1,388 μm; N = 100). A *U*-test for the difference between the medians was significant at the 0.05 level. This

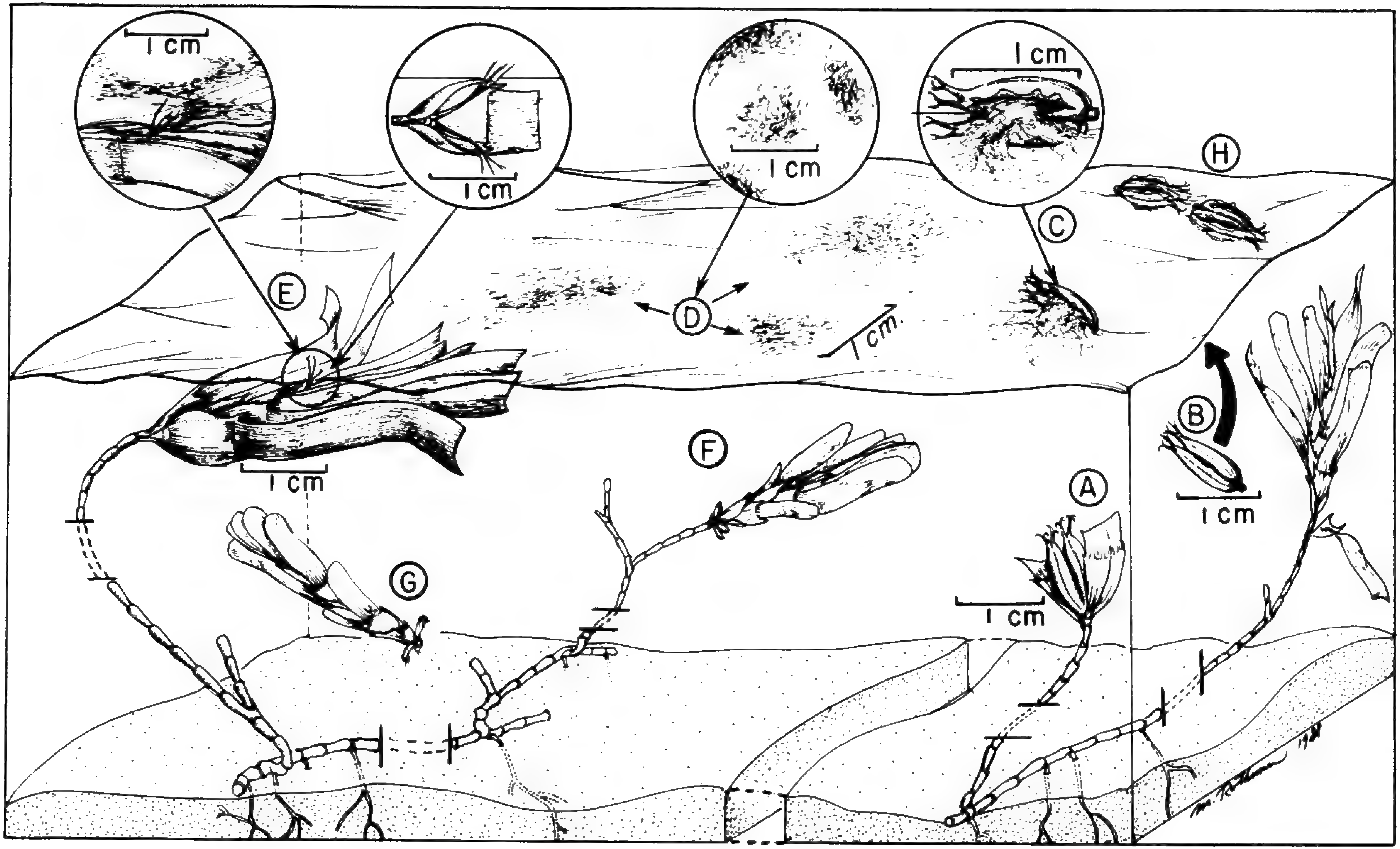

FIGURE 3. *Pollination of* Amphibolis antarctica *in an intertidal population at Point Lonsdale, Victoria, Australia.—A. Staminate plant with staminate floral unit prior to abscission.—B. Abscised staminate floral unit floating to surface.—C. Abscised staminate floral unit at dehiscence, releasing cottony mass of pollen.—D. Fractallike search vehicles of* A. antarctica *pollen floating on surface of sea.—E. Top of pistillate plant floating on water surface with plane of distichous phyllotaxy coplanar with water surface. Note styles protruding from water surface. Upper left insert illustrates contact of search vehicle with stigmas.—F. Vivparous seedling growing on maternal parent.—G. Dispersal of abscised seedling.*

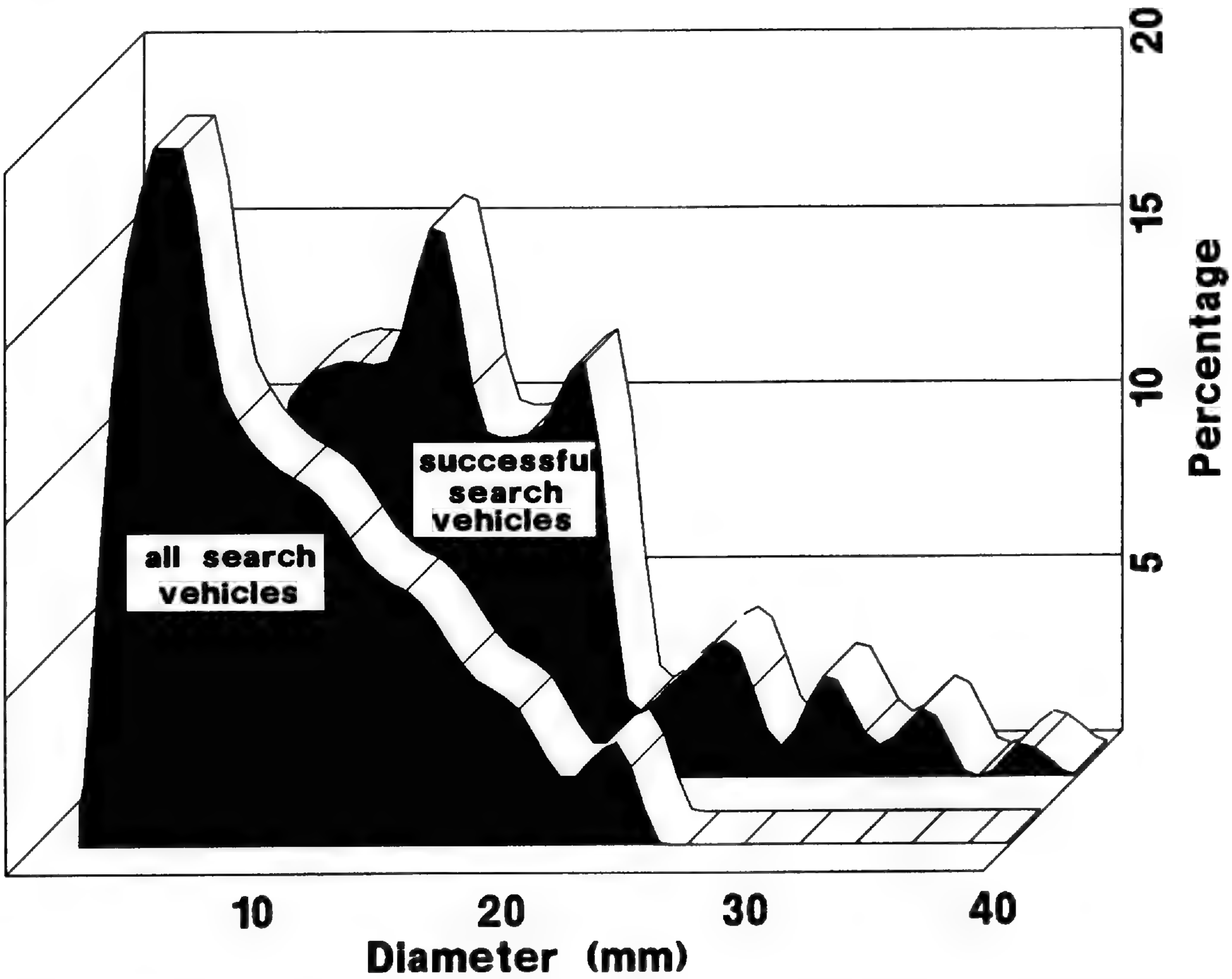

FIGURE 4. *Size distributions of* Ruppia spiralis *search vehicles filmed near Queenscliff, Victoria. The distribution labeled "all search vehicles" represents the size distribution of 1,000 search vehicles chosen at random, while the distribution labeled "successful search vehicles" represents the size distribution of 100 search vehicles that collided with stigmas.*

suggests that larger search vehicles do, in accordance with theoretical predictions, have a much greater chance of successfully encountering a stigma than small search vehicles.

Many questions, however, remain concerning two-dimensional pollination. What is the role of stigma morphology on search vehicle encounter rates? Computer simulations (P. A. Cox & J. Sethian, unpubl. data) indicate filamentous stigmas to be far more efficient in pollen capture, but the relative importance of stigmatic texture is unknown. The stigmas of the five surface-pollinated genera we studied are smooth, while the stigmas of the two-dimensional submarine-pollinated species *Thalassia testudinum* are densely papillate (Cox & Tomlinson, 1988). Major questions also remain concerning mixed modes of pollination. Is it possible that some seagrasses have both surface and submarine modes of pollination as has been suggested by Hartog (1970) for *Phyllospadix* and *Zostera* (Cock, 1980)? If so, what are the relative importances of these different modes? Another important question concerns the effect of two-dimensional pollination systems on breeding systems. If the pollen shadows are far smaller than the average clone size of the species, will there be strong selection for obligate outbreeding systems (Cox, 1988) such as dioecism? It is of interest in this regard that 75% of the seagrass genera are dioecious. Gene flow between populations mediated by pollen exchange must be exceedingly rare in seagrasses (Cox, 1983b) and even rarer in freshwater hydrophilous plants, since the pollen cannot move from one pond to another (Cook, 1987). The evolutionary ecology of such genetically isolated populations merits further investigation. Finally, convincing evolutionary explanations have yet to be made of lack of a developed exine in the pollen of many hydrophilous plants (Ducker et al., 1978). We believe that more light will be shed on these questions as further ecological studies are made of two-dimensional pollination systems.

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BREEDING SYSTEMS, POPULATION STRUCTURE, AND EVOLUTION IN HYDROPHILOUS ANGIOSPERMS[1]

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ABSTRACT

True hydrophily occurs in 18 submersed angiosperm genera. Of these, 17 are monocots, 12 are marine, and 5 contain annuals. Three genera include hermaphroditic species, 8 have monoecious species, and 13 have dioecious species. The prevalence of dicliny in hydrophiles has led to assumptions of outcrossing and high levels of genetic variability in these plants. Many water-pollinated species, however, may often fail to meet all conditions necessary for outcrossing. In hydrophiles, decreased seed output associated with dicliny increases the probability of dispersal by vegetative propagules. The predominant role of asexual reproduction and clonal growth in many hydrophile populations may restrict outcrossing despite the high potential for xenogamy in some species. This inference is substantiated by preliminary genetic analyses which indicate very low levels of variability and high homozygosity in hydrophile populations. A shift to asexual reproduction is offered as one explanation for the slow evolutionary rates associated with this biological group of species. Exceptions to these conclusions are noted in annual species, which must reproduce sexually to survive. Annual hydrophile genera have higher species diversity and possibly greater genetic variability within and between populations.

Aquatic plants are notorious for their anatomical, morphological, and physiological peculiarities. A question relating to their unusual biological features is whether the course of evolution in aquatic plants differs fundamentally from that of terrestrial plants. This question is difficult to address because water plants are not a monophyletic group; therefore, the assessment of "peculiarities" would necessarily involve interpreting patterns of convergent evolution. Certainly, there is no reason to suspect that hydrophytes do not follow evolutionary paths dictated by the same basic factors that have influenced terrestrial plant evolution. On the other hand, there are evolutionary patterns associated with the "biological group" of submersed hydrophilous angiosperms that warrant consideration. A particularly striking feature of these species is their slow rate of evolutionary diversification, a conclusion revealed by several lines of evidence.

Data tabulated for 31 principally aquatic families (from Cook et al., 1974) furnish an average of about eight species per genus. The number of extant species in most hydrophilous angiosperm genera, however, is fewer than eight (Table 1). In comparison, some genera of nonhydrophilous submersed aquatic plants (e.g., *Potamogeton, Myriophyllum, Ranunculus*) may contain 35–100 or more species. Not all hydrophilous genera, however, have few species; *Najas* contains 35–50 species, the largest number among hydrophilous genera (Table 1). Furthermore, the fossil record indicates that at least several hydrophilous angiosperms have undergone a prolonged period of morphological "stasis." In an evolutionary study of the genus *Ceratophyllum*, Les (1986a: 32) observed: "One interesting aspect of the fossil record is that most of the extinct taxa can be associated with the extant genus *Ceratophyllum*, and often with extant species . . . ." Similar statements were made by Hartog (1970) with respect to the hydrophilous seagrasses, e.g. (p. 15): "It is noteworthy that these Tertiary [seagrass] fossils all belong to still existing genera and that at least two of them can be identified with still existing species." And (p. 30): ". . . evidence for the great age of recent species . . . is supported by the fact that fossil remains of *Cymodocea* from the European Eocene can be identified with still existing species." Hartog (1970)

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TABLE 1. *Synopsis of angiosperm genera with submersed hydrophilous species. H = hyphydrophilous; E = ephydrophilous; Mo = monoecious; D = dioecious; Hm = hermaphroditic; P = perennial; A = annual; M = marine; B = brackish; F = fresh (compiled from Aston, 1973; Cook, 1982; Cook et al., 1974; Cox, 1983; Edwards, 1976; Hartog, 1970; Haynes, 1977; Haynes & Holm-Nielsen, 1987; Hutchinson, 1975; Les, 1986a; Sculthorpe, 1967).*

	Number of Species	Sexual Reproduction	Sexual Condition	Life Form	Habitat	Pollen
DICOTYLEDONS						
Ceratophyllaceae						
Ceratophyllum (H)	6	rare to common	Mo	P	B, F	precocious
MONOCOTYLEDONS						
Hydrocharitaceae						
Elodea (E)	5	rare	D, Mo	P	F	globose
Halophila (H)	8	rare to common	D, Mo	P	M	chains & precocious
Thalassia (H)	2	rare to common	D	P	M	chains & precocious
Najadaceae						
Najas (H)	35–50	prolific	Mo, D	A, P	B, F	precocious
Posidoniaceae						
Posidonia (H)	3	rare to common	Hm	P	M	filiform
Ruppiaceae						
Ruppia (E)	1–7	common	Hm	A, P	M, B, F	chains
Zosteraceae						
Heterozostera (H)	1	common	Mo	P	M	filiform
Phyllospadix (H)	5	common	D	P	M	filiform
Zostera (H)	12	rare to common	Mo	A, P	M	filiform
Zannichelliaceae						
Althenia (H)	2	common	D	P	B, F	globose
Amphibolis (H)	2	common	D	P	M	filiform
Cymodocea (H)	4	rare	D	P	M	filiform
Halodule (H)	6	rare	D	P	M	filiform
Lepilaena (E, H)	4	common	Mo, D	A, P	B, F	globose
Syringodium (H)	2	common	D	P	M	filiform
Thalassodendron (H)	2	infrequent	D	P	M	filiform
Zannichellia (H)	1–5	common	Mo, D, Hm	A, P	B, F	globose & precocious

attributed the slow rate of evolution in seagrasses to the relative uniformity of the marine environment, and Les (1986a) related stasis in *Ceratophyllum* to interactions of hydrophily and aspects of the breeding system.

Are the slow evolutionary rates that apparently characterize various unrelated hydrophile species a consequence of their unique pollination system? This question has prompted the present study to review not only the pollination system but the overall reproductive biology of hydrophilous angiosperms. Specifically, the intent of this paper is to hypothesize possible evolutionary implications associated with peculiarities of hydrophile reproductive biology. Establishment of a theoretical basis will provide a means for testing hypotheses empirically. Although this symposium focuses on freshwater angiosperms, consideration must also be given here to marine angiosperms, which dominate this biological group.

SALIENT FEATURES OF HYDROPHILY

True hydrophily includes hyphydrophily where pollen is transported exclusively under water, and ephydrophily where pollination occurs at the surface (Faegri & van der Pijl, 1979). Various mechanisms by which pollen is transported above the water surface (e.g., *Enhalus*, *Vallisneria*) mimic hydrophily but are not considered here.

Hydrophily is viewed as a derived condition in angiosperms and probably developed from both anemophily and entomophily (Faegri & van der Pijl, 1979); however, the immediate precursor to hydrophily in most instances appears to have been anemophily (Les, 1988b). Hydrophily is unique to submersed aquatic angiosperms and occurs only within 18 genera which represent seven families and which constitute a heterogeneous group phylogenetically. The taxonomic distribution and selected features of these genera are summarized in Table 1, from which several associations are apparent. Except for *Najas*, there are 1–12 species in hydrophilous genera. The frequency of sexual reproduction ranges from common to rare. Nearly all genera are principally perennial, and all (even annuals) possess mechanisms for vegetative reproduction. An overwhelming consistency is the diclinous sexual condition (monoecy or dioecy), with hermaphroditic flowers occurring in only three genera. Most hydrophilous genera are marine; seven genera occur in freshwater.

Like anemophily, hydrophily is an abiotic pollen-transfer mechanism and therefore inherently "wasteful" (i.e., much of the pollen produced does not contact a receptive stigma) because of nondirectionality (Faegri & van der Pijl, 1979; Cox, 1983). The three-dimensionality of hyphydrophily leads to high pollen wastage, although higher efficiency may be attained in shallow water where pollen loads may concentrate. Ephydrophily reduces pollen wastage by confining the dispersal of grains to the two-dimensional water surface (Faegri & van der Pijl, 1979). Because of the stochastic nature of hydrophily, the highest level of efficiency is probably achieved with autogamous pollinations, where the shortest transport distance is involved, and presumably decreases with the greater distances involved in geitonogamous (involving different flowers on one individual) or xenogamous (involving flowers on different individuals) pollinations. Underwater pollination in some species is enhanced by the reduction of water currents over plant beds (which assists pollen deposition) and the relatively large area of pollen influence around female flowers (Ackerman, 1983, 1986).

Hydrophile pollen exhibits structural modifications that apparently maximize transport efficiency. The surface area of most hydrophile pollen is increased variously (Table 1). In some species, globular pollen grains form filiform chains, or the grain itself is highly elongate (Pettitt & Jermy, 1975; Cox, 1983). In other species, precocious germination of the pollen tube (Fig. 1A) may increase surface area to maximize capture by the stigma (Sculthorpe, 1967; Faegri & van der Pijl, 1979; Cox, 1983; Les, 1986a). In *Ceratophyllum*, the surface area is increased further by the occasional branching of pollen tubes (Fig. 1B), and grains with precocious pollen tubes have been observed to mass together (Sehgal & Ram, 1970), thereby mimicking pollinia. Typically, the exine of hydrophilous pollen is highly reduced (Pettitt & Jermy, 1975).

Hydrophily and anemophily are the major abiotic pollination systems in plants. Understandably, the two systems share certain similarities in their floral syndromes, such as frequent dicliny, reduced perianths, high pollen/ovule ratios, reduced pollen exines, and enlarged receptive surfaces (Faegri & van der Pijl, 1979; Les, 1986a; Sculthorpe, 1967; Whitehead, 1969). Both systems lack the specificity and constancy associated with biotic pollination systems. There are, however, various differences between the two abiotic systems. Anemophily relies on the availability of wind, whereas availability of water is seldom a liability to submersed plants. Pollen dispersal distances of anemophiles are limited only by the longevity of grains and their ability to be carried aloft. Dispersal distances in hydrophiles are restricted entirely to the dimensions of the body of water they inhabit. For freshwater species, this distance may be quite small, e.g., a pond, pool, or small lake. A further consideration is that hydrophiles are generally confined to shallow depths, and pollen transported to deeper water has little chance of encountering plants. With respect to ephydrophily, Cook & Urmi-König (1985: 118) stated: "Pollen transfer on the surface of the water may well be efficient over distances best measured in centimeters, but for distances measured in meters or kilometers it will become inefficient or even ineffective."

Hydrophile pollen is not subject to desiccation, but studies are needed to determine the duration of its viability. In *Zostera*, pollen retains viability for over 48 hours (De Cock, 1980). Although pollen of hyphydrophiles frequently contains starch to promote sinking (Sculthorpe, 1967; Les, 1986a), it is conceivable that water currents may facilitate resuspension of grains (particularly in very shallow water), which may increase opportunities for contact with submerged receptive stigmas.

A Hypothesis of Outcrossing in Hydrophiles

Most angiosperms are hermaphroditic (Bawa & Beach, 1981), with dioecy (depending on the region) occurring in only 2–28% of species (Bawa, 1980) and monoecy equally rare (Grant, 1975).

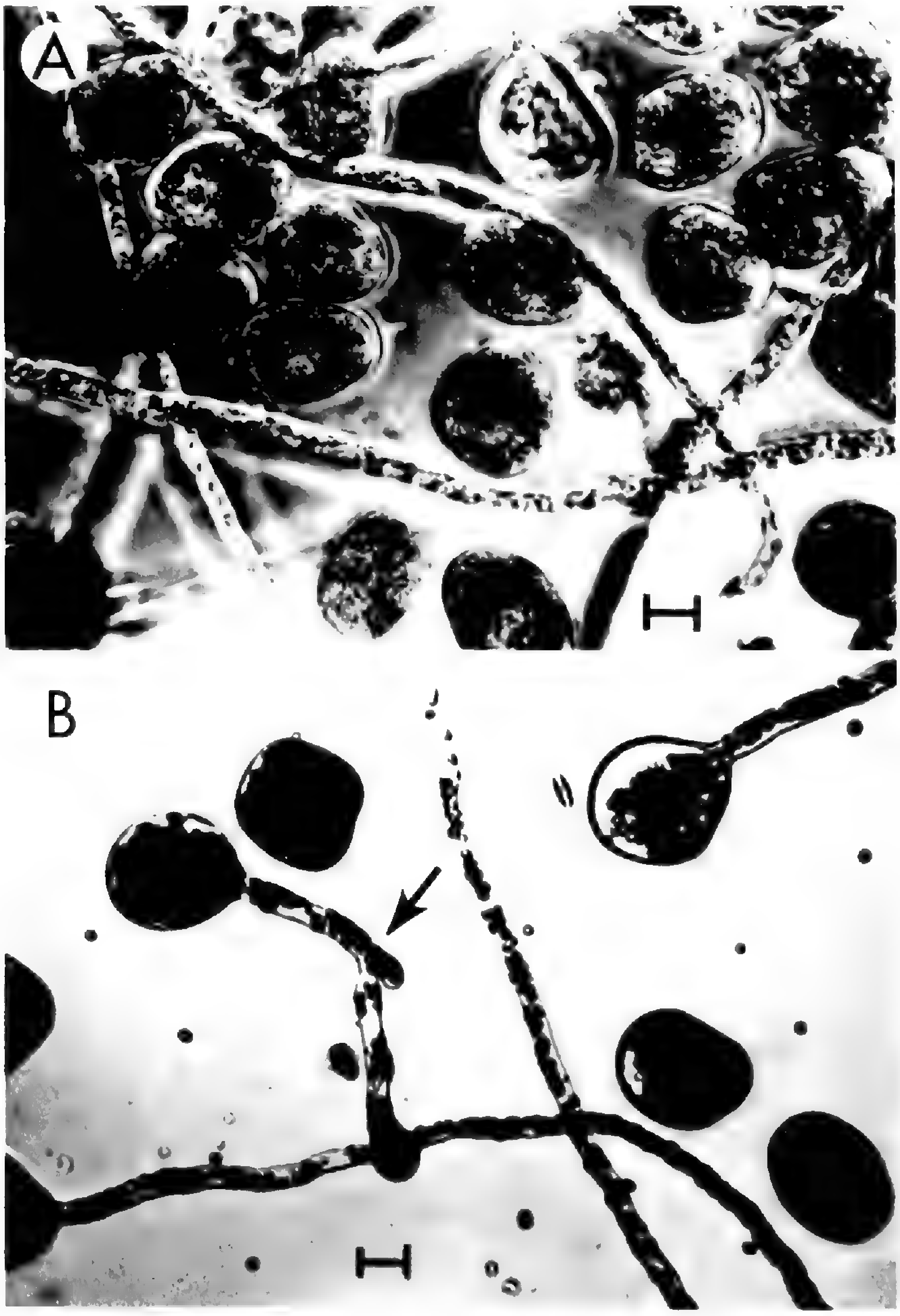

FIGURE 1. *Pollen tube modifications in* Ceratophyllum demersum.—*A. Precocious germination of grains showing elongated pollen tubes.—B. Branching of pollen tubes (at arrow). Scale bars = 5 μm.*

In contrast, 13 of the 18 genera (72%) of hydrophilous angiosperms have dioecious species; 8 genera (44%) have monoecious representatives; and only about 8.7% of hydrophile species are hermaphroditic (Table 1). The association between dioecy and hydrophily was noted by Sculthorpe (1967), who did not provide an evolutionary explanation for the co-occurrence of these traits.

Others, however, have viewed the predominance of dicliny in hydrophiles as evidence of an inevitable association with outcrossing and production of genetically variant progeny (Hartog, 1970; Pettitt et al., 1981). Although dioecy is associated with reduced prolificity because of the presence of males (Lloyd, 1980), it has been postulated (in seagrasses) that ". . . gains in survival attributable to continuous out-breeding outweigh the disadvantages of diminished seed production" (Pettitt et al., 1981: 137). These conclusions can be interpreted as a hypothesis that embraces three components: 1) hydrophiles are characterized by outcrossing, which leads to the production of genetically variable offspring; 2) the selective advantage of outcrossing in hydrophiles offsets the evolutionary costs associated with transitions to dicliny; and 3) dicliny has evolved in hydrophiles as a mechanism for promoting outcrossing. The appealing rationality of such a hypothesis belies the fact that it rests entirely on circumstantial evidence associated with sexual conditions and is not substantiated by more empirical evidence. Furthermore, it is difficult to rationalize the slow evolutionary diversification of this group with a supposed history of outcrossing and prolific genetic variability. It is possible that few species have made the transition to hydrophily in recent time, and therefore the hydrophile genera have simply not had sufficient time to diversify. This interpretation, however, is incongruent with fossil evidence that indicates a great age of many hydrophile genera. Obviously, it is necessary to consider other sources of data that may be more pertinent in assessing the extent of outcrossing in hydrophiles.

TESTING THE "OUTCROSSING HYPOTHESIS"

In hydrophiles, the possibility of outcrossing (natural crossing as defined by Grant, 1975) exists only when several conditions are satisfied. One requirement is for sexual reproduction. A second requirement is for xenogamy, which assures that sperm of one individual reach the eggs of different individuals. Thirdly, the parents contributing gametes must differ genetically and their offspring must survive. By evaluating the ability of hydrophiles to satisfy these conditions, it may be possible to assess better the role of outcrossing in these species. To interpret fully the significance of outcrossing in hydrophiles, it is also necessary to understand the relative level of inbreeding that may occur in outcrossing species.

THE EXTENT OF SEXUAL REPRODUCTION IN HYDROPHILES

There has been much discussion regarding the costs and benefits of sexuality in organisms. Using a group selection model, Lloyd (1980) argued that dioecious populations experience a cost of sex, whereas hermaphroditic populations do not. Furthermore, he pointed out that asexual reproduction results in greater prolificity than dioecy, raises the potential rate of increase, and may aid in the long-term persistence of asexual populations and species. He concluded, however, that asexuality does not appear to have been significant in group selection against dioecy because of the relatively lower evolutionary success of asexual lines. Nevertheless, hydrophyte reproduction occurs both sexually and asexually, most species have well-developed means of vegetative reproduction, and most reproduction in perennial hydrophytes is estimated to be asexual (Hutchinson, 1975).

Approximately half of hydrophile genera are characterized by rare sexual reproduction (Table 1). A quote from Hartog (1970: 34) illustrates this point: ". . . inflorescences, flowers, fruits and seeds . . . are not often found in most seagrasses, and in some species they are not known at all or only incompletely." The rarity of fruiting in the freshwater genera *Elodea* and *Ceratophyllum* is also widely recognized (Cook & Urmi-König, 1985; Les, 1986a).

One facet of sterility in dioecious hydrophiles is the low percentage of flowering in several species. The seagrasses *Halophila stipulacea, Halodule beaudettei, H. bermudensis, H. ciliata, Cymodocea rotundata, C. serrulata, C. angustata,* and some *Posidonia* species are rare-flowering according to Hartog (1970). McMillan (1976, 1979, 1980) noted that environmental conditions have wide effects on the reproductive biology of many seagrasses. Even when flowering, dioecious hydrophiles may exhibit another facet of sterility. In *Thalassia testudinum,* fewer than 1% of plants may flower simultaneously in "beds," and beds are often unisexual (Hartog, 1970; Durako & Moffler, 1987). Such conditions may result in frequent sterility of the species, such as that reported by Edwards (1976). Similarly, plants of *Thalassodendron ciliatum* and *Elodea* species typically exist in unisexual colonies with plants of both sexes rarely coexisting (Hartog, 1970; Cook & Urmi-König, 1985). Such circumstances surely contribute to low fruit production in these species. Cook & Urmi-König (1985) attributed the unisexuality of *Elodea* populations to differential competition for habitat by the sexes. Alternate explanations, however, include the possibility that unisexual populations are derived clonally, or that sex expression is affected by environmental rather than by strictly genetic factors.

A further restraint of sexuality is the rarity of seedling production in some plants with high seed output, e.g., *Zostera noltii* (Hartog, 1970).

Agamospermy is possibly mistaken at times for sexual reproduction in some hydrophiles. In *Halophila stipulacea,* cultured plants induced to flower produced no males, yet the females produced seed (McMillan, 1980), a good reason to suspect agamospermy. In *H. hawaiiana,* male and female plants are not known to coexist (Herbert, 1986). Although agamospermous reproduction is genetically equivalent to vegetative propagation, one obvious difference is production of fruits allowing for "normal" dispersal. It would be an important contribution to test experimentally for agamospermy among other hydrophilous species.

Although gene recombination via sexual reproduction is viewed as important for response to changing or heterogeneous environmental conditions, genetic uniformity enforced by vegetative reproduction may be more advantageous for a species already adapted to uniform habitat conditions (Grant, 1981; Lloyd, 1980). Therefore, the relative uniformity of freshwater and marine environments (Hartog, 1970; Tiffney, 1981) provides one explanation for the ubiquity of efficient vegetative reproduction in hydrophytes.

Demands on parental energy for reproductive effort have been implicated in compromises between sexual and asexual avenues in some plants. In many instances, the relationship is inverse, i.e., high fruit production with low vegetative propagation and vice versa (Salisbury, 1942; Harper, 1977). In hydrophiles, free-fruiting species often exhibit less vegetative development than rare-fruiting species. Of the freshwater hydrophiles, poor vegetative development occurs in the genera *Althenia, Lepilaena, Ruppia, Najas,* and *Zannichellia,* which are all typically free-fruiting (Table 1). Of these genera, *Najas, Zannichellia,* and *Lepilaena* are mainly annual. In *Ruppia,* little biomass is allocated to reproductive structures in perennial species, whereas allocation to reproductive structures in annuals is always much higher (Brock, 1982). The freshwater genus *Elodea* has coarse vegetative growth and low seed output. All species of *Ceratophyllum* are perennial, yet much higher seed output occurs in species with fine foliage than in the coarse-leaved species *C. demersum* (Les, 1986a). Sometimes in *Zannichellia* relatively robust plants have been associated with lower flower and fruit production and behave like perennials, whereas slender plants have higher flower and fruit production (Uotila et al., 1983). Similar associations are not as evident in marine hydrophiles, possibly because a well-developed vegetative system for anchoring plants against forces of tidal currents and wave action is essential for marine existence (Hartog, 1970). In the marine genus *Zostera,* however, a relationship exists between fruiting and shoot development. Arber (1920: 127) observed: "In *Zostera marina* . . . the fertile and sterile plants are readily distinguishable from one another, since in the fertile plant the stem is slender, erect, and much branched, while that of the sterile individual is thick, creeping, more luxuriantly leafy, and anchored to the soil by adventitious roots . . . ." Furthermore, annual individuals of *Zostera marina* can be distinguished readily from perennial individuals by the former's lack of vegetative shoots and rhizomes (Keddy & Patriquin, 1978). Although most species within the principally annual genus *Najas* have relatively fine foliage, the perennial species *N. marina* is characterized by very coarse leaves and has the ability to form vegetative turions (Agami et al., 1986).

Differential resource allocation to reproduction has been studied in terrestrial plants in some detail (Silvertown, 1982) and provides a convenient explanation for the association of high vegetative development with low sexual reproduction in some hydrophytes. It is possible that the development of effective perennating mechanisms in hydrophytes was accompanied by a sacrifice of sexual reproduction. It could be argued that vegetative growth and reduced reproductive effort in perennials vs. high sexuality and reproductive effort in annuals are merely adaptive life history traits. On the other hand, the shoot dimorphism described above between both fertile/sterile and annual/perennial individuals of *Zostera marina* indicates that tradeoffs in reproductive allocation do occur. In *Zostera marina,* the different reproductive strategies (annual, perennial, sexual, asexual) are employed depending upon environmental circumstances (Phillips et al., 1983). Although other factors may be involved, it is possible that the relationship between low sexual reproduction and high vegetative development noted in hydrophiles and other hydrophytes is due in part to constraints related to resource allocation.

From the above discussion, it is evident that sexual reproduction in water-pollinated plants is not commonplace. This conclusion is important because, despite any other factor, outcrossing cannot occur in hydrophile populations that reproduce only asexually.

THE EXTENT OF XENOGAMY IN HYDROPHILES

Hermaphroditic, monoecious, and dioecious sexual conditions in hydrophiles allow for three possible means of gametic exchange: autogamy, geitonogamy, and xenogamy. Although outcrossing can occur only when gametic exchange is xenogamous, xenogamy is possible with all three sexual conditions.

Autogamy in many hermaphroditic terrestrial plants is prevented or restricted by mechanisms such as dichogamy, herkogamy, heteromorphy, and self-incompatibility (Faegri & van der Pijl, 1979; Lewis, 1979). Heteromorphy is associated with biotic pollinators (Lewis, 1979) and is unknown in hydrophiles. Incompatibility mechanisms have not been reported in hydrophiles, presumably because of constraints imposed by the water-liability of recognition substances and by reduction of the exine in hydrophilous pollen (Pettitt & Jermy, 1975). Herkogamy, the spatial separation of sexes, is not characteristic of hermaphroditic hydrophiles. This leaves only the possibility of dichogamy, the temporal separation of sexes, as a means of preventing autogamy in hermaphroditic hydrophiles.

Autogamy is possible only in three genera (*Posidonia, Ruppia, Zannichellia*) which have members with hermaphroditic flowers. Sexual reproduction in these genera is common (Table 1). Aston

(1973) described fruit production as "prolific" for *Posidonia*, and the numerous fruits of *Ruppia* and *Zannichellia* taken from waterfowl stomachs (up to 4,000 and 10,000 per stomach, respectively) indicate high fruit production in these genera (McAtee, 1939). A single plant of *Zannichellia* is capable of producing more than two million seeds in six months (Yeo, 1966). Discounting apomixis, the prolific fruit production in these genera reflects their successful adaptation to hydrophily. Much of this prolificity, however, probably results from autogamy.

In hermaphroditic *Zannichellia* (Aston, 1973), autogamy is possible due to the enclosure of stamen and carpels within the cuplike perianth, although the flowers may be dichogamous. Most species of *Zannichellia*, however, are monoecious and even some dioecy has been reported (Muhlberg, 1982). In monoecious *Zannichellia*, the arrangement of flowers results in functional bisexuality. Male and female flowers are typically adjacent and appear ". . . to rise as a group in a leaf axil" (Sculthorpe, 1967: 298). Although the anther of the male flower is raised above the carpels, pollen grains have a higher specific gravity than water and ". . . sink on to the peltate or tongue-shaped stigmas . . ." (Sculthorpe, 1967: 299). Arber (1920: 71) reported a similar scenario for *Zannichellia*. She noted that, "The anther dehisces and the pollen grains fall into the open mouths of the cornucopia-shaped stigma . . . ." These accounts suggest that dichogamy does not occur in *Zannichellia* and that selfing would be commonplace. Hutchinson (1975: 232), however, presumed that local turbulence would displace the descending pollen of *Zannichellia*, ". . . so that occasional cross-pollination can occur even when . . . the male and female flowers [are] very close together." The description of pollination in *Zannichellia* by Haynes & Holm-Nielsen (1987: 264) renders Hutchinson's presumption untenable: ". . . the anther of the staminate flower arches over the funnel-shaped stigmas of the carpellate flower. Pollen transfer is entirely underwater: it is released from the anther in a gelatinous mass and falls directly into the stigma." Although monoecious *Zannichellia* cannot be categorized as autogamous, these descriptions of pollination in the genus indicate predominant geitonogamy (virtually the genetic equivalent of autogamy). Even the effects of turbulence that Hutchinson proposed would probably result in geitonogamy rather than xenogamy, as the gelatinous pollen masses would be more likely to settle than to be transported laterally. Furthermore, the floral morphology of *Zannichellia* does not appear to be adapted for xenogamy. Pollen/ovule ratios are not known specifically in *Zannichellia*; however, they are probably relatively low, with only a single stamen for every cluster of four one-ovuled female flowers. The sculptured exine of *Zannichellia* pollen is atypical of hydrophilous angiosperms (Pettitt & Jermy, 1975). The pollen shape is globular and the grains do not form chains (Table 1), an indication that it is not as well-adapted for transport over distances as that of other hydrophiles. For *Zannichellia*, the high percentage of fruiting is likely a result of autogamy in hermaphroditic plants or of geitonogamy in monoecious plants, rather than of xenogamy.

Exceptions may occur with *Zannichellia contorta* and *Z. peltata*, in which the anther filaments are much longer than those of other species, and their pistillate and staminate flowers arise at different nodes (Talavera et al., 1986; Van Vierssen & Van Wijk, 1982). With the greater spatial separation of anthers and pistillate flowers in these species, the opportunity for xenogamy is enhanced. Haynes & Holm-Nielsen (1987) concluded that generally the pollination system in *Zannichellia* limits outcrossing but is valuable for the annual habit because pollination is essentially assured.

The pollination system of *Ruppia* has been described in some detail. In *Ruppia cirrhosa*, the hermaphroditic-flowered inflorescence reaches the surface of the water but remains submersed; the anthers dehisce, are carried to the surface by air bubbles, and release pollen explosively when contacting the atmosphere. Cohering pollen grains cover the surface in chainlike strings and eventually reach the carpels, which are raised to the surface by bending of the inflorescence. In *R. maritima*, the discoid, peltate stigmas form a canopy above the anthers and trap the ascending pollen chains; the grains drift around the stigma to its surface, where some adhere and germinate. (For details see Arber, 1920; Gamerro, 1968; McCann, 1945; Sculthorpe, 1967.)

In *Ruppia* it is difficult to ascertain the extent of autogamy. Frequent fruit production can be explained either by autogamy (such as described for *R. maritima* above) or by xenogamy. The observance of spreading surface pollen masses of *Ruppia* (Faegri & van der Pijl, 1979) demonstrates the potential for xenogamy. The two-dimensional nature of the ephydrophilous mechanism "concentrates" the pollen, thereby increasing the chances for pollen capture. In aquarium studies, however, pollen of *R. megacarpa* remained mostly near the stigmas of the flower from which it was released (Van Vierssen et al., 1982), an indication that selfing may occur frequently in the species. In any case, sexual reproduction in *Ruppia* plays a large role in its propagation (Edwards, 1976).

Information on the reproductive biology of the marine *Posidonia* is too general to infer much of its breeding system. The flowers consist of three or four sessile anthers surrounding the simple carpel, which terminates in a feathery, lacerate stigma (Sculthorpe, 1967). When the anthers dehisce, clouds of filamentous pollen are released into the water (Pettitt et al., 1981). Because the carpel is surrounded by anthers, the potential for autogamy might be quite high. Without direct observations and knowledge of possible dichogamy, however, this conclusion can only be implied.

In monoecious plants, autogamy is prevented but geitonogamy is not. Hartog (1970), however, attributed cross-fertilization to all monoecious seagrasses (*Zostera, Heterozostera, Halophila decipiens*) due to their protogyny.

In the monoecious *Zostera marina*, the potential for xenogamy is indeed increased by protogyny (Arber, 1920). Pollen is shed in cloudy masses, with pollen tubes already beginning to protrude (Arber, 1920). Pollen is released either slowly under water or quickly in floating masses, which readily adhere to any object coming in contact with the grains (De Cock, 1980). Despite widespread protogyny in *Zostera* (Sculthorpe, 1967), the proximity of male and female flowers within a spathe (Aston, 1973) suggests the possibility of occasional geitonogamy among flowers within the spathe. In fact, De Cock (1980) observed that self-pollination in *Zostera* will occur in the absence of cross-pollination and takes place widely in plants cultured in aquariums. The extent of geitonogamy in natural populations of *Zostera* is not clearly known.

A similar situation exists in the related genus *Heterozostera*. Although male and female flowers occur within the same spathe, the flowers are protogynous, with the stigmas falling off prior to the opening of anthers within the same spadix (Aston, 1973; Hartog, 1970). *Halophila decipiens*, the sole monoecious species of the principally dioecious genus, is likewise protogynous, with male and female flowers occurring within the same spathe (Hartog, 1970).

In the monoecious *Ceratophyllum demersum*, xenogamy is probably infrequent. The rarity of flowering and the aggressive vegetative growth of this species greatly limit sexual reproduction (Les, 1985). When sexual reproduction occurs, the self-compatibility of the species allows for geitonogamy (Les, 1980, 1985). Although xenogamy is possible, transport of pollen tends to be within large clones (Les, 1986b).

Flowers of the monoecious *Lepilaena australis* are similar to those of *Zannichellia* but appear to be more conducive to xenogamy. Female flowers are borne on the upper parts of the plant and occur at the ends of peduncles up to 14 cm long. The male flowers are very short-stalked and occur on the lower portions of the plant (Aston, 1973). In this arrangement, geitonogamy would require the upward transport of pollen, and lateral movement of pollen would be more likely to facilitate xenogamy. In monoecious *Lepilaena preissii*, however, the male and female flowers are clustered together (Aston, 1973) and here geitonogamy is more likely. Pollination in the monoecious *Lepilaena cylindrocarpa* is ephydrophilous. Stigmas create depressions in the water surface into which floating pollen grains released from submersed anthers were drawn (Van Vierssen et al., 1982). This arrangement would facilitate geitonogamy (as pollen from the same plant would be in closest proximity to the stigmas), although xenogamy may occur as well.

The freshwater genus *Najas* is predominantly monoecious (with only one dioecious species) and annual (Haynes, 1977). The pollination biology of *Najas* is not known in detail, but several aspects have been described. Sculthorpe (1967) observed that pollen tube germination is precocious, often as the microspores are released from the floral envelope. He reasoned that the dense growth of plants would place male and female flowers together, and that liberated pollen would be (p. 301) ". . . caught haphazardly on the elongated stigmas." Aston (1973) observed that pollen is discharged apically through an opening in the floral envelope and is transported through the water to the stigmas. There is no indication that *Najas* possesses any mechanisms to prevent geitonogamy.

Dioecy is the only sexual condition that ensures xenogamy, and all dioecious hydrophiles must be regarded as possessing a high outcrossing potential. Dioecy does not guarantee outcrossing, however, which will occur only when all conditions have been satisfied.

THE EXTENT OF GENETIC VARIATION IN HYDROPHILE POPULATIONS

The genetic structure of a hydrophile population ultimately determines the extent of outcrossing. In sexual and xenogamous populations, outcrossing will occur whenever sexual reproduction is consummated between genetically different individuals. How different genetically are individuals in

TABLE 2. *Flowering frequency and short-shoot sex ratios for five populations of* Thalassia testudinum. *M = male; F = female (adapted from Durako & Moffler, 1985a).*

Sites	Flowering Frequency	Sex Ratio M:F
Cockroach Bay	38%	1:1
Egmont Key	26%	1.7:1
Big Coppit Key	25%	1:3.1
Lassing Park	22%	1.4:1
No Name Key	3%	2.0:1

TABLE 3. *Flowering frequency and plant sex ratios in three species of dioecious* Elodea; *F = female, M = male (computed from data in Catling & Wojtas, 1986 (A); Cook & Urmi-König, 1985 (B)).*

Species	% in Flower	Sex Ratio F:M
A. *Elodia bifoliata*	53	1.8:1
B. *E. bifoliata*	87	1.2:1
A. *Elodea nutallii*	32	1.6:1
B. *E. nutallii*	—	1.2:1
A. *Elodea canadensis*	32	1.4:1
B. *E. canadensis*	—	1.2:1

hydrophile populations? Few published studies have addressed this essential question.

Dioecy and outcrossing are typically equated despite unresolved questions whether heterosexual individuals of dioecious plant species always differ genetically. Although sex in the majority of dimorphic plant species is believed to be determined solely by genetic factors (Lloyd & Bawa, 1984), diphasic responses have been reported in many dioecious plants, including species reported to have sex chromosomes (Freeman et al., 1980). If diphasic sex changes can occur in hydrophiles that reproduce extensively by vegetative growth, then there would be at least the potential for clonally derived individuals to express different sexes. Unfortunately, there is little available evidence to provide a satisfactory resolution to the question of whether such changes occur in dioecious hydrophiles or not.

In addition to direct observation of population sexuality over several seasons, Lloyd & Bawa (1984) regarded consistent sex production in widely spaced ramets or branches and sex ratios of unity as circumstantial evidence of phase stability in dioecious plants. Few studies of dioecious hydrophiles have provided direct observation of phase stability or change. Grey & Moffler (1978) reported an overall female-biased sex ratio of 3:1 for *Thalassia testudinum*, although they observed a range of ratios from 21:0 to 1:1. Durako & Moffler (1985a) determined that three out of four populations of *T. testudinum* were characterized by male-biased ratios (Table 2). Further studies of *Thalassia* demonstrated that male-biased ratios occurred only in one of three years of observation and correlated with highest seed output (Durako & Moffler, 1985b). There was no apparent relation of the ratios to flowering frequency; male bias occurred at flowering frequencies from 3–38% (Table 2). In *Thalassia testudinum*, the variation of sex ratios among populations and their deviation from unity may indicate that sex expression in this species is affected by environmental conditions. Durako & Moffler (1985a, b), however, attributed the yearly differences in the sex ratios not to sex change but to annual variation in the density of males; the female densities remained fairly constant temporally.

Biased sex ratios also occur in other dioecious hydrophile species. Estimates of flowering frequency and sex ratios computed from data published by Cook & Urmi-König (1985) and Catling & Wojtas (1986) for three dioecious and ephydrophilous species of *Elodea* indicate female-biased ratios of 1.2–1.8:1 (Table 3). In *Elodea*, the highest female bias was found in *E. bifoliata*, the most frequently flowering species (Table 3). Greater female-biased sex ratios occur in dioecious marine hydrophiles, epitomized by *Phyllospadix*, with an approximately 12:1 ratio of female to male plants (Dawson, 1966). Using specimen lists cited in Hartog (1970), flowering frequencies and sex ratios were computed for seven dioecious species of hydrophilous seagrasses (Table 4). There are some indications of stability in the sex ratios of these species. The 11:1 ratio calculated for *Phyllospadix* approximates the 12:1 ratio reported independently by Dawson (1966); both the frequency of flowering and the sex ratio are nearly equal for two species of *Syringodium*. Although sex ratios of three species of *Elodea* are similar, Cook & Urmi-König (1985) have discussed various aspects of sex instability in the genus. Sex ratios of unity were noted only in *Thalassia testudinum*, *Halodule uninervis*, and *Thalassodendron ciliatum*; most other ratios were female-biased (Tables 3, 4). An interesting trend in the data is a possible relationship between sex ratios and flowering frequency. A decrease in the frequency of flowering is associated with a lower female bias in the sex ratios; lower floral frequencies appear to be asso-

TABLE 4. *Flowering frequency and plant sex ratios in seven dioecious marine hydrophiles; F = female, M = male (computed from data in Hartog, 1970).*

Species	% in Flower (seasonal)	Sex Ratio F:M
Phyllospadix scouleri	83	11:1
Phyllospadix torreyi	78	4.2:1
Syringodium filiforme	39	1.4:1
Syringodium isoetifolium	38	1.3:1
Halodule uninervis	18	1:1
Thalassodendron ciliatum	12	1:1
Cymodocea nodosa	12	1:3

TABLE 5. *Sex ratios in a population of* Ceratophyllum demersum *from Okauchee Lake, Wisconsin, U.S.A. M = male; F = female; * = female-biased.*

Plant Number	Number of Male Flowers	Number of Female Flowers ( ) = fruits	Plant Sex Ratio (M:F)	Average Combined Sex Ratio (M:F)
1	22	3	7.3:1	7.3:1
2	0	2	0:2*	4.4:1
3	0	1 (1)	0:2*	3.1:1
4	15	2	7.5:1	4.1:1
5	12	5	2.4:1	3.5:1
6	51	6	8.5:1	5.0:1
7	7	9	0.8:1*	3.7:1
8	39	10	3.9:1	3.7:1
9	14	9	1.6:1	3.3:1
10	1	2	0.5:1*	3.2:1
11	1	0	1:0	3.2:1
12	15	7	2.1:1	3.1:1
13	7	3	2.3:1	3.1:1
14	3	8 (3)	0.3:1*	2.6:1
15	1	0	1:0	2.7:1
16	1	2	0.5:1*	2.6:1
17	10	1	10.0:1	2.7:1
18	5	3	1.7:1	2.7:1
19	0	6	0:6*	2.5:1
20	0	5	0:5*	2.3:1
21	2	5	0.4:1*	2.2:1
22	6	1	6.0:1	2.3:1
23	10	5	2.0:1	2.2:1
24	28	38	0.7:1*	1.8:1
25	24	12	2.0:1	1.8:1
26	6	7	0.9:1*	1.8:1
27	16	5	3.2:1	1.8:1
28	26	10	2.6:1	1.9:1
29	12	6	2.0:1	1.9:1
30	12	7	1.7:1	1.9:1
Total	346	184	—	1.9:1

ciated with equal or male-biased ratios (Table 4). This trend is also apparent in *Elodea*, but to a much lesser degree (Table 3). Sex ratios of the dioecious *Thalassodendron ciliatum* indicate a male bias at low flowering frequencies of 15–19% (Kay, 1971). *Syringodium* flowers commonly, and produces mostly female flowers (Kay, 1971). An exception to this trend occurs in the infrequently flowering genus *Cymodocea*, which has been observed to produce only female flowers (Kay, 1971). The absence of male flowers, however, was possibly due to the sampling of a single clonal population (Kay, 1971). In other populations of *Cymodocea*, however, sexes co-occur but are partitioned spatially into unisexual zones (Caye & Meinesz, 1985). It is possible that the relationship of reduced female-bias and low flowering frequency may result in part from sampling error.

Sex-ratio data must be interpreted cautiously. The different methods of assessment (e.g., plant ratios, short-shoot ratios, single population ratios, multiple population ratios) and wide variability in sample size are only two shortcomings. Furthermore, there have been no real efforts to distinguish between genets and ramets in populations where studies have been conducted. Because of the effective system of vegetative reproduction in hydrophiles, sex-ratio data may be misleading. Apomixis and other factors that can influence sex ratios have been summarized elsewhere (e.g., Opler & Bawa, 1978). Ultimately, a precise knowledge of sex expression in dioecious hydrophiles will be required before any reliable conclusions can be drawn from sex-ratio data.

Less is understood of sex ratios in monoecious hydrophiles. In *Ceratophyllum demersum*, plants fruit rarely, but fertile specimens are typically male-biased (Les, unpubl.). Sex ratios computed for a fertile population of *C. demersum* from Wisconsin, U.S.A., provide some insights into its sex ratios. The ratios were calculated by counting all flowers on 30 dissected plants. The range of sex-ratio variation in this population is extensive. Most plants are male-biased (up to 10:1); however, nearly a third of the sample is female-biased (Table 5). Although the species is monoecious, unisexual plants were observed for both sexes. The overall sex ratio was male-biased at 1.9:1. Fruiting was low (2%), and fruits were found only on plants with female-biased ratios. In species of *Ceratophyllum* where fruiting is more common, sex ratios appear to be less male-biased (Les, unpubl.). Reasons for the wide amplitude of sex distribution on *Ceratophyllum* plants are not clear, but it is apparent that sex ratios are not rigidly fixed genetically. The potential for environmental influence of sex expression in *Ceratophyllum* was demonstrated by the sole production of male flowers on plants of *C. demersum* and *C. echinatum* grown under continuous illumination (Les, 1980). Plants from the same population observed in the field were normally monoecious.

In *Zostera marina*, a consistent sex ratio of one pistil to one anther was observed from a population in France, despite wide variability in the flower number per spathe (Jacobs & Pierson, 1981). In monoecious *Zannichellia*, the close association of male and female flowers indicates a probable 1 : 1 ratio. Such consistent values may indicate tighter genetic regulation of sex expression in these species. Sex ratios of other monoecious hydrophiles have not been studied in any detail.

Although hydrophily is often equated with outcrossing, a critical point is made by Faegri & van der Pijl (1979: 41): ". . . hydrophilous mechanisms give no guarantee against autogamy. However, the gregarious habit of the plants in question will generally cause allogamy and counteract auto- and geitonogamy unless *the whole meadow represents a single clone*" [emphasis mine]. The extent of clonal growth in hydrophiles is surely an important determinant of their population structure.

Hutchinson (1975) recognized that most reproduction in hydrophytes is asexual, and as a result (p. 238) ". . . large clonal populations are likely to be very common in lacustrine angiosperms." He also observed that for perennial species (p. 233), ". . . any given specimen is much more likely to have arisen by asexual than by sexual processes."

An important difference between asexual reproduction in terrestrial plants and aquatic plants is that vegetative buds, fragments, turions, etc. in the latter can facilitate dispersal without the planting requirement necessary for fragments of most terrestrial species (Hutchinson, 1975). This feature is evidently one of the most important mechanisms for dispersal in aquatic plants, particularly those that produce small quantities of seeds. The efficiency of vegetative dispersal in hydrophilous species is exemplified by the spread of *Elodea canadensis* across Europe, which occurred within 50 years following its introduction from an uncertain North American source. This feat was accomplished entirely by vegetative means, as the species is dioecious and (with one exception) only female plants were introduced (Cook & Urmi-König, 1985; Grant, 1981). Cook & Urmi-König (1985: 118) remarked that the ". . . aggressive vegetative growth [of *Elodea*] leads to . . . the consequence that one habitat becomes fully occupied by one genotype."

Similar conclusions have been drawn for other hydrophiles. In *Cymodocea serrulata*, the "only" means of medium- or long-range dispersal is by vegetative fragments, and clonal growth patterns are typical due to the vigorous vegetative growth (Kay, 1971). In *C. nodosa*, seeds are not disseminated, and sexually derived offspring must be spatially and temporally restricted (Caye & Meinesz, 1985). Likewise, vegetative reproduction is more prevalent than sexual reproduction in the maintenance and spread of *Thalassia* (Kay, 1971; Grey & Moffler, 1978). In *Halophila*, *Thalassia*, *Cymdocea*, and *Halodule*, sexual reproduction is rare and reproduction is mostly vegetative (Edwards, 1976; Jacobs & Dicks, 1985). For *Halophila hawaiiana*, Herbert (1986: 101) stated that ". . . it is possible that the monospecific meadows of *Halophila* in the Hawaiian islands are made up of plant material from a single genetic individual." According to Obermeyer (1966), propagation of *Halophila ovalis* is mainly vegetative and may lead to the formation of "homogeneous colonies." *Zostera marina* reportedly flowers infrequently and maintains stable population sizes by vegetative reproduction (Harrison, 1979). Both *Zostera* and *Heterozostera* reproduce asexually by unusual vegetative propagules (Cambridge et al., 1983). *Ceratophyllum demersum* is rare-flowering and highly clonal (Les, 1986b). Haynes & Holm-Nielsen (1987) stated that all Zannichelliaceae "grow clonally."

Widespread vegetative growth in hydrophilous species may lead to the formation of large, genetically uniform populations in which outcrossing would be thwarted even among sexual, xenogamous individuals. Hutchinson (1975), however, noted that the few aquatic annuals such as *Najas* are exceptions to the generalization that most hydrophytes reproduce asexually. Development of an annual habit in hydrophiles, where consistently high levels of seed production are essential for survival, may have provided an escape from constraints on outcrossing imposed by dense clonal growth. Although vicinism may also occur in diclinous annuals such as *Najas*, there is at least a much higher potential for dispersal of sexually derived propagules to other sites, which betters the chances that future generations will breed with genetically different individuals.

The foregoing discussion cites only circumstan-

TABLE 6. *Summary of enzyme variability in species from 13 hydrophilous angiosperm genera. * = enzyme displaying intra- or interpopulational variability at one or more loci; all other enzymes monomorphic (compiled from A: McMillan et al., 1981; B: Les, 1986b; C: McMillan, 1981; D: McMillan & Williams, 1980; E: McMillan, 1982; F: Triest et al., 1986; G: McMillan & Phillips, 1981; H: Gagnon et al., 1980).*

Species	Enzymes Surveyed
Amphibolis antarctica (A)	APH, EST, G-6-PD, GOT, MDH, PER, PGI, PGM
A. griffithii (A)	APH, EST, G-6-PD, GOT, MDH, PER, PGI, PGM
Ceratophyllum demersum (B)	APH, ADH, EST, GOT, G-6-PGD, GDH, IDH, LAP, MDH, PGI, PGM
Cymodocea rotundata (C)	APH, EST, G-6-PD, GOT, MDH, PER, PGI, PGM
C. serrulata (C)	APH, EST, G-6-PD, GOT, MDH, PER, PGI, PGM
Halodule pinifolia (A)	APH, EST, G-6-PD, GOT, MDH, PER, PGI, PGM
H. uninervis (A)	APH, EST*, G-6-PD, GOT, MDH, PER, PGI, PGM
H. wrightii (A)	APH, EST, G-6-PD, GOT, MDH, PER, PGI, PGM
Halophila decipiens (D)	APH, GDH, GOT, MDH, PER, PGI, PGM
H. hawaiiana (D)	APH, GDH, GOT, MDH, PER, PGI, PGM
H. johnsonii (D)	APH, GDH, GOT, MDH, PER, PGI, PGM
H. minor (D)	APH, GDH, GOT, MDH, PER, PGI, PGM
H. ovalis (A)	APH, EST, GDH, GOT, MDH, PER, PGI, PGM
H. stipulacea (D)	APH, GDH, GOT, MDH, PER, PGI, PGM
H. sp. (A)	APH, EST, GDH, GOT, MDH, PER, PGI, PGM
Heterozostera tasmanica (E)	APH, G-6-PD, GOT, MDH, PER, PGI, PGM
Najas marina (F)	ADH*, ME*, SkDH, XDH
Posidonia australis (A)	APH, EST, GDH, GOT, MDH, PER, PGI, PGM
P. sinuosa (A)	APH, EST, GDH, GOT, MDH, PER, PGI, PGM
Phyllospadix scouleri (G)	ADH*, APH, EST, G-6-PD, GDH, GOT, MDH, PER, PGI, PGM
P. serrulatus (G)	ADH, APH, EST, G-6-PD, GDH, GOT, MDH, PER, PGI, PGM
P. torreyi (G)	ADH, APH, EST, G-6-PD, GDH, GOT, MDH, PER, PGI, PGM
Syringodium filiforme (E)	APH, G-6-PD, GOT, MDH, PER, PGI, PGM
S. isoetifolium (E)	APH, G-6-PD, GOT, MDH, PER, PGI, PGM
Thalassia hemprichii (E)	APH, G-6-PD, GOT, MDH, PER, PGI, PGM
T. testudinum (E)	APH, G-6-PD, GOT, MDH, PER, PGI, PGM
Thalassodendron ciliatum (E)	APH, EST, G-6-PD, GOT, MDH, PER, PGI, PGM
Zostera capensis (E)	ADH, APH, GOT, MDH, PER, PGI, PGM
Z. capricorni (E)	APH, ADH, GOT, MDH, PER, PGI, PGM
Z. marina (H)	ADH, CAT, DIA, G-6-PD, G-6-PGD, GDH, GTR, GOT*, HK, IDH, MDH, PGI*, PGM, PMI, SDH, SOD
Z. marina (E)	APH, GOT, MDH*, PER, PGI, PGM*
Z. muelleri (E)	APH, ADH, GOT, MDH, PER, PGI, PGM
Z. novazelandica (E)	ADH, APH, GOT, MDH, PER, PGI, PGM

tial evidence for assessing the degree of genetic variation in hydrophile populations; however, there is some empirical evidence that can be brought to bear on this issue. The use of enzyme gel electrophoresis has allowed for the direct estimation of genetic variation in plant populations (Gottlieb, 1981; Brown, 1979; Hamrick et al., 1979). Fortuitously, most electrophoretic studies on aquatic plants have been carried out with seagrasses (Wain et al., 1985), all of which are hydrophilous.

Approximately 30 species representing 12 genera of seagrasses have been studied electrophoretically (Wain et al., 1985). These analyses consistently report genetic uniformity and provide little evidence of electrophoretically detectable genetic variation in hydrophile populations (Table 6). According to Wain et al. (1985: 43), "In most species [of seagrasses] there exists no intraspecific variation in banding patterns, even across large geographic distances." Furthermore, the level of heterozygosity in seagrasses is apparently extremely low (Wain et al., 1985; McMillan, 1982). Of the 32 hydrophile species studied, enzyme variability has been reported only in *Zostera marina*, *Halodule uninervis*, *Phyllospadix scouleri*, and *Najas marina* (Table 6). As Crawford (1983) discussed, enzyme uniformity of this sort is more characteristic of self-pollinating plants than of outcrossers.

Preliminary studies of *Ceratophyllum* have given similar results. Populations of the rare-flowering *C. demersum* are relatively uniform both morphologically and genetically, and are probably clonal (Les, 1988b). Populations of the more sexual species *C. echinatum* are more variable morphologically and display patterns of intrapopulational variability that are quite representative of the species as a whole (Les, 1988a). An electrophoretic study of populations of both species is under way in hopes of providing further insight into the genetic structure of populations of the predominantly sexual vs. asexual species of *Ceratophyllum*.

Enzyme polymorphisms have been reported in electrophoretic studies of the annual species *Najas marina* (Triest et al., 1986), a possible indication of greater genetic diversity in this genus. Further electrophoretic surveys are necessary to determine the extent of intrapopulational genetic variation in other *Najas* species and annual hydrophiles in general. An informative study would be to compare populations of *Najas* and *Zannichellia* electrophoretically. Although both genera are annual, *Zannichellia* has few species compared with *Najas*, a possible outcome of the predominantly geitonogamous/autogamous breeding system of *Zannichellia*.

Despite the large number of electrophoretic studies carried out on hydrophiles, an adequate understanding of population structure in this group is far from being reached. A major difficulty has been that most studies have reported genetic data qualitatively rather than quantitatively (Table 6). Because data have not been presented in allelic form, it is not possible to compute appropriate quantitative measurements of population structure such as fixation indices, average heterozygosity, proportion of loci polymorphic, number of alleles/locus, and gene diversities (Nei, 1987). Furthermore, no study has measured outcrossing rates quantitatively in any hydrophilous species. Because models for estimating outcrossing rates should be evaluated in terms of the pollination system of a species (Shea, 1987), it may first be necessary to develop a specific model for hydrophilous plants. Electrophoretic approaches provide a powerful means of estimating population structure and outcrossing rates. The scarce amount of genetic variation detected in hydrophiles thus far is an impetus for continuing investigations in this area.

A satisfactory resolution to the question of population structure in hydrophiles will not come until rigorous genetic analyses have been carried out. On the other hand, it is important to emphasize that the widely held assumption of extensive genetic variability in hydrophile populations is not supported by available data. The high degree of clonal growth attributed to hydrophiles may result in genetically uniform populations. Even in instances where sex expression of dioecious hydrophiles may be under strict genetic control, clonal growth allows for the possibility of the establishment of extensive unisexual populations. Because of these factors, clonal growth may thwart outcrossing in many hydrophiles. In support of this conclusion are preliminary electrophoretic data which indicate little detectable genetic variation in hydrophile populations.

Assumptions that hydrophiles are outcrossing and produce genetically variable offspring should not be taken for granted. The inefficiency of hydrophily, reduced sexuality, of autogamy and geitonogamy, and widespread clonal growth have the potential to restrict outcrossing greatly in this group. Because no studies have characterized genetically the actual level of inbreeding vs. outcrossing in any particular hydrophyte species, however, it is premature to argue too strongly either for or against the first component of the outcrossing hypothesis.

COSTS VS. BENEFITS OF DICLINY IN HYDROPHILES

The second component of the outcrossing hypothesis, that outcrossing in hydrophiles offsets evolutionary costs associated with transitions to dicliny, is even more difficult to assess. One difficulty with pursuing this possibility is that it remains to be proven conclusively that hydrophiles are highly outcrossing.

Plant breeding systems involve three general mechanisms: inbreeding, outcrossing, and apomixis (Briggs & Walters, 1984). Historically, outcrossing has been associated with enhanced genetic variability and heterozygosity, whereas inbreeding and obligate apomixis are related to low genetic variability (Faegri & van der Pijl, 1979; Briggs & Walters, 1984). With adapted gene complexes preserved by well-developed asexual reproduction systems, it is reasonable to assume that it would be advantageous for sexual reproduction in hydrophiles to provide a means of outcrossing that could respond facultatively to changing environmental conditions. Because dicliny may promote or enforce xenogamy, the prevalence of the unisexual condition in hydrophiles has been linked to outcrossing and widespread genetic variability. Presumably, a rich gene pool would facilitate adaptation and response to environmental changes. Therefore, enhanced genetic variation is interpreted as a major possible benefit of dicliny.

Grant (1975) pointed out the liability of inefficient sexual reproduction in diclinous plants, a cost related to reduced seed output in populations. If sex ratios are equal, half of the flowers would not bear seeds in either monoecious or dioecious species. This outcome could have serious consequences in hydrophiles in which seed output is suppressed by other factors such as infrequent sexual reproduction and extensive vegetative growth. Female-biased or equal sex ratios, however, may maximize seed production in dioecious species (Grant, 1975; Opler & Bawa, 1978). As discussed above, female-biased sex ratios have been noted in *Elodea*, *Phyllospadix*, *Syringodium*, and *Thalassia*, and ratios of unity have been found in *Halodule* and *Thalassodendron*. It is important to emphasize that female-biased sex ratios do not always alleviate problems of low seed production. A surplus of females in a population (in favor of reduced males) may also result in low seed output because of inadequate pollination (Grant, 1975). This limitation may have been responsible for a 28% loss in seed set observed in a population of the monoecious *Zostera marina* (Churchill & Riner, 1978). A compromise between seed output and adequate pollination may be reflected in male-biased sex ratios reported in *Ceratophyllum*, *Cymodocea*, and *Thalassia*.

Low seed output in hydrophiles may be specially implicated in their dispersal mode. Dispersal has been described as the physical basis of gene flow and in most plants occurs via transport of pollen or fruits (Grant, 1981). In aquatic plants, dispersal of vegetative propagules is also of great importance. In hydrophiles, reduced seed output may result in a greater dependence on the transport of pollen and vegetative propagules as avenues of dispersal and gene flow. This relationship may be quite significant for freshwater hydrophiles where pollen gene flow is restricted to the single body of water in which the population occurs. In such instances, interpopulational gene flow may be entirely by transport of vegetative propagules. In contrast to perennial species, seed output of diclinous annual hydrophiles is extremely high, reaching levels of 100 seeds/m^2 in *Lepilaena* (Vollebergh & Congdon, 1986). Evidently, adaptation to the annual habit has overcome seed limit costs of dicliny. In some diclinous annuals, such as monoecious *Zannichellia*, however, seed set is ensured by geitonogamy (Haynes & Holm-Nielsen, 1987), thereby negating any possible advantages of outcrossing associated with monoecy.

These circumstantial data provide no satisfying resolution to the question of whether or not the costs of dicliny are outweighed by its selective advantages. Better insight into this matter may be gained by studying the relative fitness of closely related species in genera such as *Zannichellia* that possess monoecious, dioecious, and hermaphroditic sexual conditions.

EXPLANATIONS FOR THE EVOLUTION OF DICLINY IN HYDROPHILES

The third component of the outcrossing hypothesis is that dicliny evolved in hydrophiles principally as a mechanism of promoting outcrossing. This element of the hypothesis can be challenged outright because dicliny does not always guarantee outcrossing. Lewis (1979: 4) emphasized that ". . . separation of sexes . . . offers no protection against sib-mating, because pollen from a male plant is equally effective on a female whether it be a sib or non-sib," and that ". . . separation of sexes has a limited value as an outbreeding device in static plants." It is also important to realize that inbreeding is not restricted to hermaphroditic species but can also result in diclinous species as a result of geitonogamy, and possibly even from xenogamy due to vicinism (Grant, 1981). Furthermore, anomalies such as geitonogamy in monoecious *Zannichellia* make it difficult to accept outcrossing as the compelling force in the evolution of dicliny.

Some consideration has been given to other factors influencing sexual conditions in plants such as relative resource allocation to maternal and paternal function, and constraints imposed by the dynamics of the pollination system (Bawa & Beach, 1981). Unfortunately, these discussions have not considered water-pollinated plants.

If outcrossing has been important in the evolution of hydrophiles, then why are so many species characterized by infrequent sexual reproduction? On the other hand, if outcrossing has not been evolutionarily important in this group, then why has dicliny been conserved? This dilemma may be resolved by taking into account the early evolution of hydrophilous plants. Kimura & Ohta (1971) observed that the extent of genetic variability derived from sexual recombination could be attained by mutation alone given sufficient time, and they emphasized that gene recombinations are broken up by sexual recombination as quickly as they are made. They believed that the greatest advantage of sexual reproduction is to enhance the rate of evolution.

Although the process of adaptation accompanying the transition to hydrophily may have occurred slowly by mutation alone, the combination of sexual recombination and an outcrossing breeding system would have facilitated the process by generating pools of genetic variability more rapidly. In this way, the ancestors of modern hydrophiles may have benefited greatly from sexuality and the outcrossing potential conferred by dicliny, especially if their progenitors lacked other mechanisms to prevent autogamy. In species where hydrophily was derived mainly from lines of self-compatible anemophilous plants, dicliny may have preceded hydrophily.

Once species had become well adapted to hydrophily and a submersed existence, greater fitness may have resulted from maintaining genetically uniform rather than highly variable offspring. Because aquatic environments are relatively constant, vegetative growth would maintain adaptive gene complexes and prevent their breakup by sexual reproduction. The phasing out of sexual reproduction may have been accompanied by greater resource allocation to vegetative growth. A shift to asexual reproduction would likely result in slow evolutionary rates and low species diversity in the group, precisely the pattern that we see in the fossil record of several modern species. By this scenario, dicliny in extant hydrophiles is essentially a relictual condition of uncertain consequence to their present reproductive biology. There are additional appealing aspects of this interpretation. Because dispersal in rare-flowering perennial hydrophiles is likely to be predominantly by vegetative propagules, many populations would be expected to be clonal and genetically uniform. The available data show that these patterns commonly occur in water-pollinated plants. The maintenance of sexuality in extant annual hydrophiles may account for their higher species diversity, the result of accelerated evolutionary rates associated with sexual recombination and outcrossing.

SUMMARY

Because of the prevalence of dicliny in hydrophiles, it is widely believed that water pollination in aquatic plants is linked to an outcrossing breeding system. Actually, there is little evidence that three necessary conditions for outcrossing (sexuality, xenogamy, genetically variable populations) are met by many extant species. Interrelationships of inefficient pollen transfer, reduced sexuality, widespread clonal growth, and diminished seed production in hydrophiles may reflect a major adaptive shift towards asexuality as a means of preserving adaptive gene complexes in stable aquatic environments. This hypothesis explains the apparent slow evolutionary rates and low species diversity of some hydrophilous species noted in the fossil record, as well as the greater species diversity observed in sexual, annual, potentially outcrossing species. If this interpretation is correct, then dicliny persists in modern perennial hydrophiles as a relictual condition associated with their early evolution.

Although the course of evolution in water-pollinated plants does not appear to differ fundamentally from that of other plants, the complex interactions of hydrophily and other aspects of their reproductive biology are likely to have profoundly influenced the patterns of their present diversity. As we improve our methods of evaluating the breeding systems and population structure of hydrophilous species, so will our understanding of evolution in this unusual group of plants be expanded.

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EVOLUTION OF UNDERWATER OUTCROSSING FROM AERIAL POLLINATION SYSTEMS: A HYPOTHESIS[1]

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ABSTRACT

It is evident that underwater outcrossing (hypohydrophily) arose from aerial pollination systems. However, no mechanism to explain this transition has been proposed. Herein I suggest a system involving bubble pollination, similar to hydroautogamy in Potamogeton, *as an intermediate in the transition from aerial to submerged pollination systems. Such an intermediate would provide the opportunity for the gradual evolution of characters that are needed for underwater outcrossing without sacrificing seed production during the transition.*

There is general agreement that water pollination (hydrophily) is derived from aerial pollination, for the aquatic habit itself is derived in angiosperms (Arber, 1920; Daumann, 1963; Sculthorpe, 1967). Although we have some understanding of the mechanisms of pollen transfer in hydrophiles, there has been little published to explain the origin and subsequent radiation of hydrophilous systems. Hydrophily has been most widely investigated in marine angiosperms (e.g., Ducker & Knox, 1976; Ducker et al., 1978; Cock, 1980; Pettitt, 1984; Pettitt et al., 1980, 1981). Our understanding of the floral biology of freshwater hydrophiles is narrower than in marine groups, even though the unusual mechanisms of pollen transfer in some, e.g., the Hydrocharitaceae, have received considerable attention (e.g., Cook, 1982; McConchie, 1982; Wylie, 1917).

Arber (1920) and Sculthorpe (1967) proposed that marine angiosperms arose from freshwater stock (Hartog, 1970, presents a contrasting view), hence hydrophily likely arose in freshwater systems. Thus, study of hydrophily in freshwater groups could be central to understanding the origin of and selective pressures behind hydrophily, matters that remain to be adequately addressed. Herein I propose a mechanism by which underwater outcrossing evolved from aerial pollination systems. This hypothesis could serve to reorient investigations of the evolution of hydrophily and its role in diversification of aquatic angiosperms.

BACKGROUND

Over 90% of aquatic angiosperms bear aerial flowers and have the same manner of pollination as their terrestrial ancestors (Arber, 1920; Sculthorpe, 1967). Far fewer exhibit a system whereby water is the vector for pollen transfer, i.e., hydrophily. Currently two classes of hydrophily are recognized: 1) epihydrophily; pollination at the water surface, i.e., in two dimensions, and 2) hypohydrophily; pollination below the water surface, i.e., in three dimensions. However, it is evident that epihydrophily embraces at least two rather dissimilar subtypes. In one, the flowers undergo anthesis above the water surface and the reproductive structures (e.g., stigmata, pollen) remain dry: dry-epihydrophily. *Vallisneria* represents the best-known example of dry-epihydrophily (Cook, 1982, and references therein). In contrast, many seagrasses exhibit wet-epihydrophily, where the reproductive structures are wet at anthesis but in close association with the water surface, e.g., the pollen floats just below the water surface but not upon it. Hypohydrophily is more similar to wet- than dry-

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epihydrophily. In fact, wet-epihydrophily may be but an evolutionary "refinement" of the more general hypohydrophily.

It is clear that wet-epihydrophily and hypohydrophily require greater modification and adaptation of reproductive structures than does dry-epihydrophily. Many of these modifications no doubt reflect specialization to facilitate pollen release and capture in water, a medium that in addition to being wet is significantly more viscous than air. Features that are associated with wet-epihydrophily and hypohydrophily are summarized in Table 1.

Hypohydrophily occurs in relatively few angiosperm families (Arber, 1920; Cox, 1983; Daumann, 1963; McConchie, 1982; Sculthorpe, 1967); most are monocotyledons. The Ceratophyllaceae are the only dicotyledonous exception. From its taxonomic distribution it is evident that hypohydrophily is polyphyletic, with convergence toward a similar overall morphology.

The Najadales (sensu Cronquist, 1981) exhibit a complete range of pollination systems (aerial, epihydrophily, hypohydrophily) and thus are an ideal group in which to search for clues to the evolution of hypohydrophily. This order comprises 10 families and nearly 200 species (Cronquist, 1981). Phylogenetic relationships in this and related orders are largely unclear, but the families are believed to be closely related (Cronquist, 1981; Dahlgren & Clifford, 1982; Tomlinson, 1982). Eight of the 10 families are made up of freshwater or marine aquatic taxa. The species in the remaining two families grow as emergents in marshy habitats. Aerial pollination characterizes most species of Potamogetonaceae, Aponogetonaceae, Scheuchzeriaceae, and Juncaginaceae. Dry-epihydrophily is found in *Ruppia* (Ruppiaceae) (Verhoeven, 1979) and *Lepilaena* (Zannichelliaceae) (Vierssen et al., 1982). Wet-epihydrophily occurs in a number of seagrasses. Hypohydrophily is found in the largely freshwater *Najas* (Najadaceae) (Sculthorpe, 1967) and *Zannichellia* (Zannichelliaceae) (Vierssen et al., 1982) in addition to some seagrasses. Given our limited understanding of the distinctions between wet-epihydrophily and hypohydrophily, no attempt will be made to distinguish them. For brevity, the term hypohydrophily will be used in the following discussions to include both wet-epihydrophily and hypohydrophily.

It is generally believed that floral biology has played an important part in the evolution of angiosperms (Baker, 1963; Crepet, 1983, 1984; Grant, 1949, 1963; Grant & Grant, 1965; Stebbins, 1970; and others). Therefore, it is not unreasonable to propose that diversification of hypohydrophilous systems has played an integral role in speciation, e.g., *Najas* (ca. 40 species) (Haynes, 1977).

Mechanisms that ensure pollination during evolutionary transitions in floral structure have been proposed as being primary in the evolution of pollination systems (Baker, 1963; Stebbins, 1970, 1974). Given the almost universal occurrence of aerial flowers among angiosperms, adaptations for an aerial floral biology are undoubtedly well fixed in the angiosperm genome. An impediment to the formulation of hypotheses regarding the evolution of hypohydrophily has been a lack of obvious intermediate pollination systems. Hypohydrophily requires the abandonment or modification of a suite of characters that are intimately tied to the dry, aerial flowering condition. The mechanical and biochemical ramifications entailed in adapting to un-

TABLE 1. *Features often associated with hypohydrophily and wet-epihydrophily.*

Feature	References[1]
General	
Similarities with anemophily	3, 6, 14
Specialized pollen–stigma recognition system	10, 11, 12
Reduction in flower size	9
Reduced perianth	9, 11, 15
Single ovule/ovary (usually)	3, 14, 15
Unisexual flowers	3, 5, 9, 11, 14, 15
Lack of scent and nectar; colorless	9
Reduction in stamen number/flower	15
Reduced anther wall	6, 14, 15
Pollen	
High pollen/ovule ratio	3, 6, 13, 14
Reduced exine	3, 4, 7, 10, 11, 14, 15, 16
Elongate (by various means)	1, 2, 5, 8, 9, 11, 14, 15
Precocious pollen tube production	7, 8, 14, 15
Wettable	3, 4, 10
Stigma/Style	
Large, rigid, and simple (linear)	3, 5, 14
Wettable	3, 10, 11

[1] 1—Arber, 1920. 2—Cox, 1983. 3—Daumann, 1963. 4—Faegri & van der Pijl, 1979. 5—Hartog, 1970. 6—Jaeger, 1961. 7—Mahabale, 1968. 8—McConchie, 1982. 9—Percival, 1965. 10—Pettitt, 1984. 11—Pettitt et al., 1981. 12—Pettitt et al., 1980. 13—Philbrick & Anderson, 1987. 14—Proctor & Yeo, 1972. 15—Sculthorpe, 1967. 16—Wodehouse, 1935.

FIGURE 1. *Scanning electron micrograph of a flower of* Potamogeton pusillus *that illustrates the overall morphology of the flower and the orientation of the stigmata (S), anthers (A), and perianth segments (PS). Scale bar = 1 mm.*

derwater release, transport, and capture of pollen raise significant adaptive obstacles.

The fact that flowers of hypohydrophiles are wet when anthesis occurs makes them unique. The rapid decrease in viability of pollen when wetted (Daumann, 1963; Jones, 1967) illustrates the sensitivity of aerial flowers to the influence of water. Means by which selection for wettability could act upon an aerial flower and yield a "half-wet" intermediate while retaining seed production and sexuality are not evident.

Strong selective pressure to retain aerial flowers, or at least perhaps to avoid flowering under water, is evidenced by the retention of aerial flowers in a clear majority of aquatic angiosperms. This phenomenon is particularly well illustrated in species that exhibit pronounced modification of submerged vegetative structure yet exhibit aerial flower production, e.g., *Utricularia* and *Myriophyllum* (Arber, 1920; Sculthorpe, 1967). Nonetheless, some aquatics have essentially abandoned aerial flowers. These can be organized into two general groups: 1) those that produce submerged, aerial-type flowers that self-pollinate, and 2) those that have apparently dispensed with flower production or with sexual reproduction altogether, and reproduce by a variety of asexual means. Of course many species combine asexual and sexual reproduction. The abundance of species in these two classes underscores the evolutionary importance of alternatives to aerial flower production. The occurrence of hypohydrophilous groups in the extant flora reveals an additional evolutionary pathway, where modification has taken place to allow the employment of the aquatic medium as a pollen vector.

Given that hypohydrophily evolved from aerial-flowered systems, there can be little argument that its evolution would require the submergence of aerial flowers. When typical aerial flowers become submerged, closing of the perianth usually serves to trap and maintain a small bubble of air around the reproductive structures. Therefore, pollination within such flowers is equivalent to selfing in a functionally dry flower (Arber, 1920; Hutchinson, 1975; Sculthorpe, 1967). Thus, little selection for wettability would occur, for during anthesis there is no contact between the reproductive structures and the water. It appears that the evolutionary submergence of flowers *per se* would not necessarily provide the circumstances under which selection leading to hypohydrophily would proceed. The flowers of a progenitor of hypohydrophily would have to have been somehow predisposed such that selection could act on flowers that are open underwater, while the ability to produce seed is retained. That is, an intermediate pollination system ("bridging" of Baker, 1961, 1963) was likely important during the transition.

HYDROAUTOGAMY IN *POTAMOGETON*

I propose that a reproductive system similar to hydroautogamy in *Potamogeton* occupied a key intermediate stage between aerial systems and hypohydrophily. Numerous species of *Potamogeton* exhibit underwater flowering and seed production,

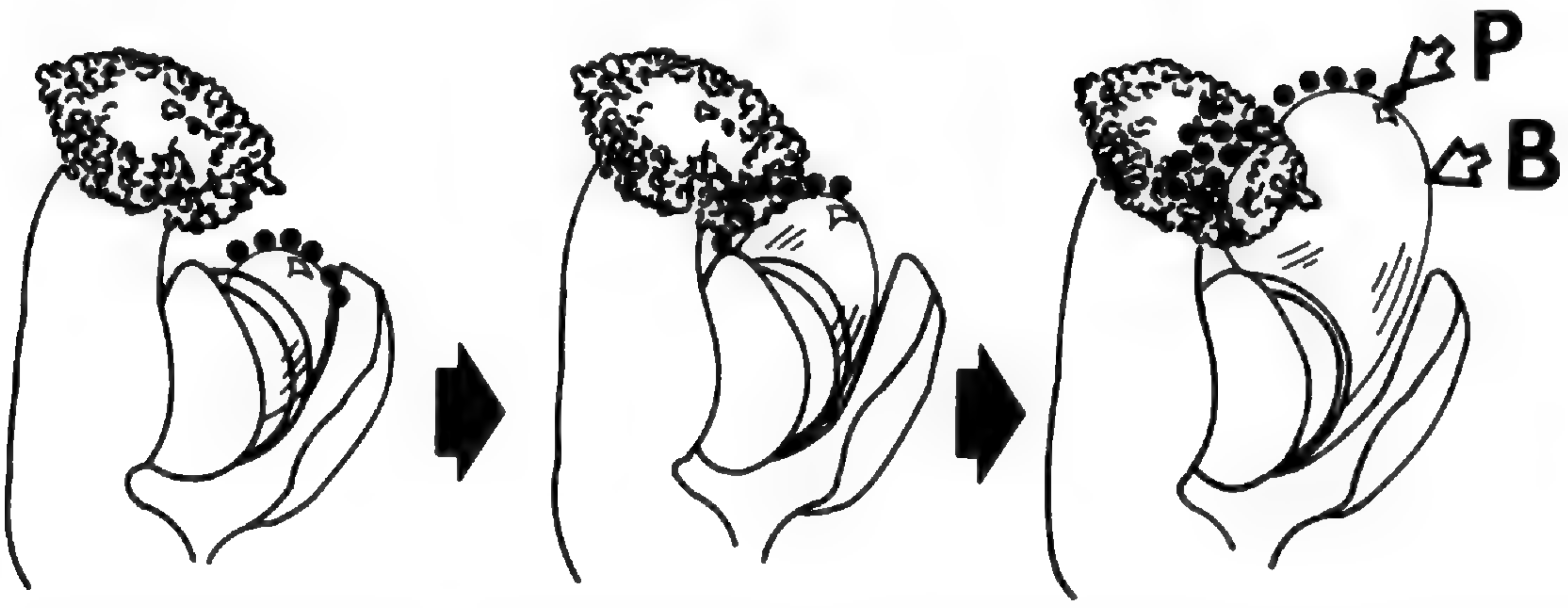

FIGURE 2. *Idealized diagrams of a portion of a* Potamogeton pusillus *flower that illustrate the progressive enlargement of a bubble (B) during anthesis and the deposition of pollen (P) onto the stigma from the bubble surface.*

a derived condition in the genus (Philbrick & Anderson, 1987, and references therein). Flowers of *Potamogeton* open while submerged; thus pollen and stigmata are exposed to water during anthesis. Self-pollination via hydroautogamy (the movement of bubble-borne pollen from anther to stigma within an open flower) rather than hypohydrophily seems to be the principal mechanism of pollination in submerged flowers (Philbrick & Anderson, 1987). During anthesis, bubbles are produced as gas is released from the dehiscing anthers (Figs. 1, 2). Preliminary study with T. Taigen suggests the gas is carbon dioxide. Pollen travels from the anther onto the outer surface of the bubble (Fig. 2). The bubble increases in size until it extends from the anther to the stigma. Pollen is then deposited onto the stigma from the bubble surface (Fig. 2) and self-pollination and subsequent fertilization results. The bubble continues to enlarge until it breaks free from the flower and rises to the surface. Additional bubbles are formed as each anther opens. An important consequence of this system of self-pollination is that the pollen and stigmata are wet during anthesis. In addition, close inspection reveals that individual pollen grains often drift off the bubble surfaces.

In systems where transition is occurring within a pollination-vector category, e.g., one insect species to another, relatively minor changes in floral structure that accommodate a new vector would be more probable than when the shift is from one broad category of pollen vector to another. The hypothesis of "fortunate accidents" formulated by Baker (1963), which suggests a chance preadaptation to an available vector, is more likely to hold when the gross structure of the flower remains unchanged. In contrast, floral modification that allows a change from one type of pollination vector to another, e.g., wind (dry) to water (wet), is less likely to be sudden because of the numerous modifications involved (Table 1). A hydroautogamous system would provide an opportunity for the operation of selective pressures leading to the gradual accumulation of hypohydrophilous features while maintaining seed production.

Lacunae systems such as those in the plant body of *Potamogeton* may have played an important role in the acquisition of hypohydrophily. Lacunae are common in submerged hydrophytes and allow movement of gases within the plant body (Arber, 1920; Hutchinson, 1975; Sculthorpe, 1967). Lacunae are also evident in the inflorescence and floral structures of *Potamogeton* (U. Posluszny, pers. comm.). Gases that are transported via the lacunae build up within the anther and seem to play a role in its dehiscence.

It is reasonable to propose that early in the acquisition of a hydroautogamous-like system the contents of the anther were dry at dehiscence. In such a case, the pollen would be shed dry and presumably remain on the inside surface of the bubble. This is little different from the behavior of airborne pollen when it becomes trapped upon the surface film of water. The water/atmosphere interface is similar in both instances. Similarly, the stigmata remain within the bubble during pollination. However, the surface of the bubble is important because it provides an opportunity for selection to operate. Although the pollen is virtually dry when inside the bubble, humidity levels there would be high, favoring pollen that could withstand the effects of increased humidity, i.e., increased wetting. Similarly, stigmata that could withstand wetting would be favored. Thus, the gradual selection of two major characters that distinguish hypohydrophily from aerial systems would result: wettable pollen and wettable stigmata. The bubble system provides a setting wherein major obstacles in the evolution of hypohydrophily could be surmounted.

Stebbins (1970, 1974) discussed the importance of character syndromes, i.e., correlations between characters, in the evolution of pollination systems. Selective modification of one feature is often manifested in a change in related features. Thus, selection for wetting might have affected pollen and stigmata simultaneously. Selection for wettability would result in the pollen no longer being limited to the inside of the bubble. The pollen could then move to the outside surface of the bubble, as in the extant species. Pollen on the outside of the bubble would be subject to continued selection, as well as "loss" by drifting away; the stage would then be set for the initiation of outcrossing.

Unisexual flowers characterize all of the documented cases of hypohydrophily. Arguments for the evolution of unisexual flowers in terrestrial plants (e.g., Anderson & Stebbins, 1984; Bawa, 1984; Charnov, 1982; Lloyd, 1982) would be equally applicable to hypohydrophilous aquatics. I propose that unisexuality was acquired not before, but after the initial submergence of a bisexual flower and initial selection toward hypohydrophily was on a bisexual flower. Evolution of hypohydrophilous characters from aerial, unisexual flowers seems less likely due to the requirement for simultaneous and somewhat independent acquisition of hypohydrophilous features in both staminate and pistillate flowers (Table 1). Further, seed production via sexual means would be more difficult to maintain.

High pollen production (pollen/ovule ratios) characterizes abiotic pollination systems (e.g., Cruden, 1977; Philbrick & Anderson, 1987; Whitehead, 1969). Lower pollen/ovule ratios are a general feature of predominantly self-pollination systems (Cruden, 1977). Aerial-flowered species of *Potamogeton* exhibit high pollen production and are believed to be anemophilous (Philbrick & Anderson, 1987). Hydroautogamous potamogetons exhibit lower pollen production than aerial taxa but not as low as would be expected for selfers (Philbrick & Anderson, 1987). The maintenance of relatively high pollen production in largely autogamous lineages may be due either to genetic constraints, the relatively recent acquisition of selfing, or the fact that hydroautogamy itself is a somewhat stochastic system. The propensity for continued high pollen production in hydroautogamous taxa may have been instrumental as a preadaptation in subsequent selection for hypohydrophily, a stochastic system that relies, as does anemophily, on high pollen/ovule ratios.

CONCLUSION

There is general agreement that hydrophily evolved from aerial pollination systems. In contrast with some previous ideas, I consider hypohydrophily to be significantly different from dry-epihydrophily, where pollination is effectively aerial. Hypohydrophilous taxa exhibit many more specializations to the aquatic medium in reproductive features.

A major obstacle to the evolution of hypohydrophily is the accumulation of characters that allow for seed set with wetted pollen and stigmata. I suggest that such characters were acquired gradually, and offer a hypothesis where a system that utilizes bubble pollination, similar to hydroautogamy in *Potamogeton*, could serve as an intermediate between aerial pollination systems and hypohydrophily. Hydroautogamy could provide an opportunity for the gradual selection of hypohydrophilous characters without sacrificing seed production.

This hypothesis is the first to address explicitly the issue of the evolution of hypohydrophily from aerial systems. Corollaries of this hypothesis are testable via studies of hydroautogamy in *Potamogeton* (e.g., viability of pollen that is released from the bubble, ability of submerged stigmata to capture water-borne pollen). Further investigation of the mechanisms of hypohydrophily and phylogenetic relationships among hydrophilous and nonhydrophilous taxa will provide information that can be used to evaluate this hypothesis.

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INSECT FORAGERS ON *SOLANUM* FLOWERS IN AUSTRALIA[1]

Gregory J. Anderson[2] *and David Symon*[3]

ABSTRACT

Eighteen native insect species were found on flowers of 18 Solanum *species in a field study in Australia. All of the* Solanum *species studied are endemic to Australia, and about one-half of them are andromonoecious or dioecious. Fifteen of the insect species and 93% of total floral visitors were bees. New records of activity on* Solanum *flowers in Australia are reported for* Braunsapis *and* Xylocopa *(Anthophoridae)*, Leioproctus *(Colletidae)*, *and* Trigona *(Apidae). Two species each of the pollen-collecting bees* Amegilla *(Anthophoridae)*, Nomia *(Halictidae), and* Trigona *are considered the most significant floral visitors. This conclusion is based on the distribution, abundance, and behavior of the bees, and on the high percentage of* Solanum *pollen in pollen loads.* Amegilla *and* Nomia *extract pollen by "buzzing" it out of the anthers;* Trigona *species do not. Species of* Amegilla *are hypothesized to effect interpopulation outcrosses.* Trigona *species are considered important primarily in self-pollination, and species of* Nomia *transmit pollen both within and between plants. This pollinator assemblage is postulated to have been associated with the evolution of dioecy in Australian* Solanum.

Solanum flowers are of the "dish-bowl" type of Faegri & van der Pijl (1979) and as a consequence do not physically exclude floral visitors. However, these wide-open flowers do not represent the cornucopia to bees and other floral visitors that some other dish-bowl species do (e.g., *Tilia*, Anderson, 1976) because floral rewards are limited and there are specialized requirements for pollen extraction. Although extrafloral nectaries have been described in *Solanum*, floral nectar is absent (Anderson & Symon, 1985); and pollen, the only reward offered, is not easily accessible to all floral visitors. *Solanum* is the exemplar of the more than 540 genera whose anthers open by terminal pores rather than by longitudinal slits (Vogel, 1978; Buchmann, 1983). *Solanum* pollen is typical for species with poricidal flowers (Buchmann, 1983) in that it is relatively dry (not sticky) and has a smooth, granulate tectate exine (Anderson & Gensel, 1976). To remove pollen, floral visitors can either "milk" the anthers by stroking them from base to apex with their mandibles (e.g., Thorp & Estes, 1975), dig it out of the terminal pores, steal pollen by biting holes in the sides of the anthers (Buchmann, 1983), or buzz the pollen out of the terminal pores. Thorp & Estes (1975) described buzz or vibratile pollination succinctly as "shivering the indirect flight muscles of the thorax while the wings [are] in repose." Buchmann (1983) estimated that about 60% of angiosperm species with poricidal anthers, including *Solanum*, are buzz pollinated.

The general syndrome of *Solanum* pollination, as described above, is well known. However, there is little known about specific pollinators and pollination. This is particularly true for Australia, where even some of the floral visitors are unknown (see below). Michener's (1965) major study of the bees of Australia reported collections of only three species from three genera on a single species of *Solanum* in southern Queensland. Symon's (1979) review of *Solanum* pollinators includes reports of seven taxa of bees. Armstrong's (1979) thorough overview of biotic pollination in Australia includes only one citation beyond Michener's and Symon's studies. Thus, we present information that expands the data base on *Solanum* pollinators. Also included is an analysis of insect pollen loads and relative abundance of insects on flowers to address the question of their importance as effective pollinators of *Solanum*. Finally, we speculate on the role of pollinators

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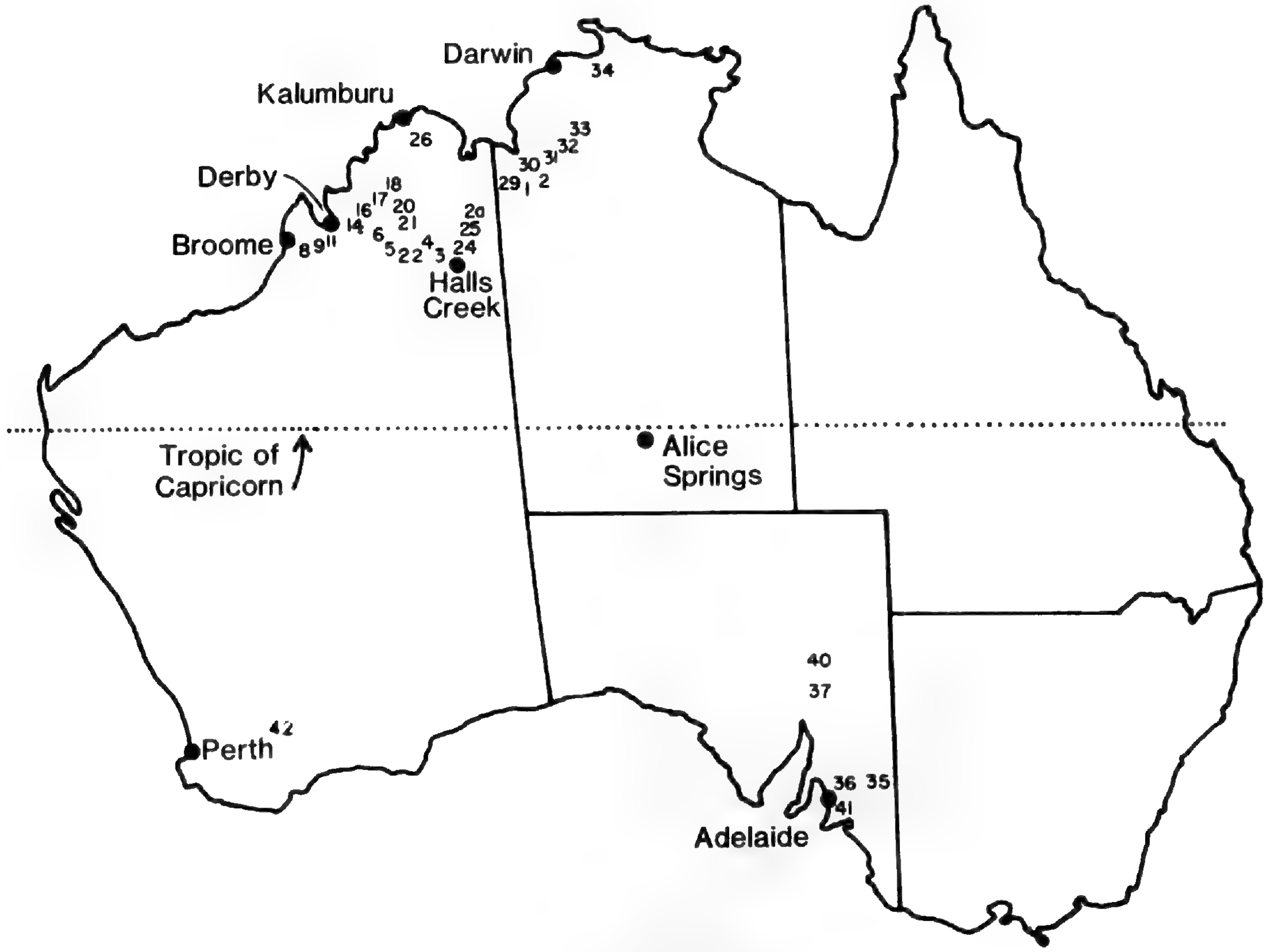

FIGURE 1. *Field collections. Numbers correspond to the study areas cited in Appendix I.*

in the evolution of nonhermaphroditic breeding systems.

METHODS

Insects were collected only from open *Solanum* flowers (i.e., not from the extrafloral nectaries) primarily from natural populations in 1979–1980. The study was centered on andromonoecious or dioecious solanums, the distribution and biology of which are given by Symon (1981). The species studied are as follows. The five-letter abbreviations are those used in Appendix I; the single letters indicate whether the species bears only hermaphroditic flowers (H), or whether it is andromonoecious (A) or dioecious (D): *Solanum asymmetriphyllum* Specht (asymm) (D), *S. beaugleholei* Symon (beaug) (A), *S. cinereum* R. Br. (ciner) (A), *S. cunninghamii* Bentham (cunni) (D), *S. dioicum* W. Fitzg. (dioic) (D), *S. diversiflorum* F. Muell. (diver) (A), *S. eburneum* Symon (eburn) (A), *S. ellipticum* R. Br. (ellip) (H), *S. esuriale* Lindley (esuri) (H), *S. hoplopetalum* Bitter & Summerh. (hoplo) (H), *S. leopoldense* Symon (leopo) (D), *S. lucani* F. Muell. (lucan) (H), *S. parvifolium* R. Br. (parvi) (H), *S. petrophilum* F. Muell. (petro) (H), *S. quadriloculatum* F. Muell. (quadr) (H), *S. sturtianum* F. Muell. (sturt) (H), *S. tudununggae* (tudun) (D).

Because these *Solanum* species occur primarily in northern Western Australia and the Northern Territory, fieldwork was concentrated there. The study in this region ranged over some 5,000 km. Collections were also made in South Australia, including a small sample taken from garden-grown native plants in Adelaide, and from Western Australia (by R. Thorp). Flowers were open, and collections and observations were made throughout the daylight hours. Thousands of individuals were observed, but not all floral visitors were taken. After vouchers were taken within a given area, only observations of behavior were recorded. Specimens netted from flowers were stored with cotton in separate vials to prevent contamination of pollen loads. The plant species, time of day, and notes on insect behavior were recorded at each site. Pollen loads removed from insects were mounted on slides in aniline blue in lactophenol and analyzed for the percentage of *Solanum* pollen and the num-

TABLE 1. *Summary by genus of insect visitors to* Solanum *flowers. See Appendix I for detailed information.* * = *see Discussion; others have reported vibratile activity.*

	Number of Species	Number of *Solanum* Species Visited	Number of Localities	% of Total Sample (individuals)	Vibratile Pollen Removal	Seconds on Each Flower (range)	% Activity after Noon	% *Solanum* Pollen in Pollen Load	Number of Other Pollenomorphs
Infrequent floral visitors									
Diptera		2	3	5	no				
Braunsapis	1	2	2	< 1	no				
Hylaeus	2	1	1	< 1	no				
Lasioglossum	1	1	1	< 1	no*				
Leioproctus	1	1	1	< 1	no				
Xylocopa	1	1	1	< 1	yes				
Abundant floral visitors									
Amegilla	3	7	11	15	yes	1–3	5	79	1.1
Nomia	4	11	20	34	yes	1–10	9	79	1.1
Trigona	2	7	17	44	no	1–90	16	99	0.2

ber of other pollenomorphs. The fidelity to *Solanum* flowers was estimated from these calculations. Plant vouchers are in AD and insect vouchers in the collections of the Western Australian Museum in Perth.

RESULTS

INSECT DIVERSITY AND DISTRIBUTION

Specific data on time and place of collection and on pollen loads carried are presented in Appendix I, and the locations of the collection sites given there are plotted in Figure 1. The data from the Appendix are summarized in Table 1.

More that 150 insects, 93% of which were bees, were collected, representing at least 18 species in two orders (Appendix I). All of the bees were females except one *Amegilla pulchra* taken from *S. ellipticum* in South Australia. In addition to collections from Western Australia and the Northern Territory, a few individuals of *Nomia* and *Amegilla* were taken in South Australia. The following four bee genera are reported here for the first time from *Solanum* flowers in Australia: *Braunsapis*, *Leioproctus*, *Trigona*, and *Xylocopa*. The emphasis in the following analyses centers on the three most frequently collected genera: *Amegilla*, *Nomia*, and *Trigona*.

The collection sites (Fig. 1) of the three primary bee genera correspond to the general range of the solanums in the study area (Symon, 1981). As Table 1 shows, individuals of *Nomia* and *Trigona* were found at nearly twice as many sites as *Amegilla*, and individuals of *Amegilla* were less abundant than either *Nomia* or *Trigona*. The two species of *Amegilla* were equally abundant and widespread; one species was more widely distributed and was locally abundant in *Nomia* (*N. flavoviridis*) and in *Trigona* (undescribed species "B"). While these data accurately reflect the rank-order of occurrence of the genera as we observed them in the field, the frequency figures are biased against *Nomia* and *Trigona*, which were much more abundant than reflected in the collections. *Trigona* was particularly abundant, with sometimes tens of individuals foraging over the flowers of a single plant.

FORAGING BEHAVIOR

As indicated in Table 1, *Amegilla*, *Nomia*, and *Xylocopa* were observed to vibrate or "buzz" the pollen out of the flowers; the remaining five bee genera were not. *Lasioglossum*, however, has been observed to buzz flowers in other studies (e.g., Bernhardt, 1986; Buchmann, 1983). Of the five genera not observed to utilize vibratile extraction, only *Trigona* was found on more than three occasions (Table 1); thus, the other four are not considered primary pollinators. Individuals of *Trigona* collect pollen from the anthers by digging it out of the terminal pores and by scavenging for it on floral parts such as the corolla and stigma (Fig. 2). No obvious differences in behavior were noted for insect visitors to hermaphroditic flowers, to staminate flowers of the andromonoecious species, or to the staminate or pistillate flowers of the dioecious species.

FIGURE 2. *A* Trigona *(within circle) foraging on the stigma of a hermaphroditic flower of the andromonoecious* Solanum beaugleholei. *The flower is about 30 mm in diameter.*

The length of time individual bees stay on flowers is correlated with their size and capability to buzz flowers. The bees that vibrate pollen out of the flowers are generally larger (*Amegilla*—about 13 mm; *Nomia*—8–10 mm) and stay for only a short time (one to a few seconds) on each flower (Table 1). On the other hand, individuals of *Trigona* (smallest of the three species, about 5 mm) spent up to one minute on each flower. Individuals of *Trigona* frequently visited several flowers in the same inflorescence. This is in contrast with *Amegilla*, where an individual usually visits only a single flower per plant and then flies some distance, often away from the population under study. Individuals of *Nomia* most often foraged within and/or among inflorescences of the same population.

Most *Amegilla* visits take place before 10 A.M. (Table 1; Appendix I, column 5). The majority of visits by *Nomia* and *Trigona* also occur during this period, but significant proportions of the individuals of these two genera are also active after noon.

INSECT FIDELITY

The average fidelity for all six major insect visitors (two species each from *Amegilla*, *Nomia*, and *Trigona*) is high (Table 1; Appendix I, column 3). For the genera overall, however, the fidelity estimate for *Trigona* is 20% higher than for either *Nomia* or *Amegilla*. These figures are, as one would expect, paralleled by the estimates of the number of other species visited (Table 1; Appendix I, column 4): *Nomia* and *Amegilla* pollen loads include about seven times as many other species as found in pollen loads of *Trigona*.

The pollen loads from the scopae or corbiculae respectively of the *Nomia* and *Trigona* were somewhat more sticky than those carried by *Amegilla*.

Amegilla scopae are covered with long hairs, among which the drier pollen loads were packed.

DISCUSSION

Solanum flowers present a relatively rich pollen resource for the bees that can exploit them. Although they lack nectar and restrict access to pollen (having only terminal anther pores), they are heavily visited by at least a few species. This is likely a tribute to their local abundance and the relatively large quantity of pollen available per flower (more than one million grains in some species, Anderson & Symon, in press). Although a range of insects was observed to visit the flowers, not all were considered significant pollinators (Table 1). Based on distribution and abundance over the range of the solanums, five of the bee genera and other insect groups are considered relatively insignificant pollinators, but these cannot be ruled out as occasional pollinators (see below). Two species each in *Amegilla*, *Nomia*, and *Trigona* are the primary floral visitors, and, as a consequence of this and their behavior, we propose that they are the major pollinators of the *Solanum* species studied.

Michener (1965) suggested that a large percentage of the Australian bees are oligolectic on the Myrtaceae but proposed that this is due largely to the overwhelming abundance of species in this family. In addition, he listed several genera, including *Nomia*, *Trigona*, and *Amegilla*, as examples of bees visiting a wide variety of species. In fact, some of the same genera of pollen-collecting bees (*Nomia*, *Trigona*, *Braunsapis*, *Xylocopa*) are reported as pollinators of another species from nearby Indonesia that is dioecious and offers only pollen as a reward, *Decaspermum parviflorum* (Myrtaceae) (Kevan & Lack, 1985). Although Michener (1965) did not treat the bee species we studied, this generalist behavior also likely applies to them. On the other hand, the proportion of *Solanum* pollen in pollen loads (79–99%) implies fidelity high enough to consider these polylectic genera to be important pollinators and to be temporally and spatially specialized on *Solanum*. This supports the contention by Thorp (1979) and Armstrong (1979) that most pollen-collecting bees show a high degree of diurnal or temporal constancy. Prance (1985) made a similar suggestion for polylectic bees from the Amazon rain forest.

Although the sticky pollen masses carried by individuals of *Nomia* and *Trigona* might indicate collection of nectar from other species (Thorp, 1979; Buchmann, 1983), the nearly monotypic nature of the loads (especially of the *Trigona*) suggests that some other substance could be involved (perhaps stigmatic exudate, see below). Alternatively, the *Trigona* species could be moistening pollen loads with honey carried in their crops. Obviously nectar or honey from some source other than the *Solanum* flowers provides the carbohydrate resource to subsidize the pollen-collecting activities of the bees.

Nomia and *Amegilla* are ground-nesting, solitary, larger bees and are well represented in Australia (85 and 69 species, respectively; T. Houston, pers. comm.). These genera also share the ability to vibrate pollen out of the anthers. Michener (1965) indicated that the highly social, tree-nesting *Trigona*, although not as diverse in Australia (only about 14 species, T. Houston, pers. comm.), visits a wide range of monocots and dicots. However, this mostly tropical genus (Bernhardt, 1987) does not vibrate pollen out of the anthers and is too small to simultaneously contact stigmata while working anthers of a few of the large-flowered diclinous solanums.

Are species of *Trigona* then simply pollen thieves removing the reward without effecting pollination? In this instance, that conclusion does not seem warranted. We never observed them biting holes in anther bases to steal pollen, and anthers of dried voucher specimens do not have holes. Some individuals of *Trigona* opportunistically collect pollen spread over the flower, taking advantage of the activities of the vibratile pollinators. However, others are active on flowers not visited previously; we regularly observed them digging pollen out of the terminal pores of anthers. Members of *Trigona* were also observed foraging on stigmatic surfaces (Fig. 2). They may have been gathering pollen, but it is also possible that they were collecting stigmatic fluid to cement pollen grains together, as Baker et al. (1973) reported for other angiosperms. In either case, with such behavior they could effectively transmit pollen from anthers to stigmata in even the large-flowered species. Given this, and that *Trigona* species were omnipresent diurnally, were more abundant on *Solanum* flowers than all the other species combined, and showed 99% fidelity, we propose that these little bees are significant pollinators.

In view of the fact that representatives of *Trigona* tended to visit flowers in the same inflorescence, those on the same plant, or those within a population, we suggest that most often they effect self-pollination. This is reinforced by the colony behavior of social bees like *Trigona*, where individuals in various parts of a colony tend not to sample widely but continue to visit one area or population repeatedly (T. Seeley, pers. comm.). Two features of the plants are relevant to this hypothesis as well. First, it is possible to self because most species of *Solanum* that have been studied (outside of the tuberous solanums and their relatives), including those from Australia, are self-compatible (Anderson & Symon, in press; Whalen & Anderson, 1981). Secondly, we observed that populations of most of the *Solanum* species studied are small in size and are widely separated from each other. These populations are even smaller (genetically) when one takes into account that most of the species reproduce vegetatively and form large clones, thus most of what appear to be genets in an area are actually ramets (Symon, 1981; Anderson & Stebbins, 1984; Anderson & Symon, in press). As a result, even many foraging visits between "plants" simply constitute visits to different ramets.

The largest but least abundant bees (*Amegilla*) visit flowers for only a very short time, supporting Buchmann's (1983) suggestion that the length of buzzing time is inversely correlated with bee size. These bees behave like "trap liners" (e.g., Janzen, 1971); that is, most visited only a single flower in an area and then flew off and out of sight, presumably to another *Solanum* flower (based on the nearly 80% purity of pollen loads). Such behavior supports the contention that *Amegilla* species are outcrossing agents transmitting pollen among genets. The bees in the first section of Table 1 were not abundant within any population at any site studied. Thus, if they are significant pollinators, they are also likely to effect outcrossing.

The *Nomia* species are intermediate between the small *Trigona* and large *Amegilla* in temporal pattern, abundance, size, visitation times, and behavior (Table 1). Individuals of *Nomia* visited more than one flower per plant and often visited other plants within the population before flying out of sight. As a consequence, we predict that these species generally effect inbreeding.

It seems that most flowers are visited, and observations of fruit set from the previous season showed a high seed set. Thus, we conclude that seed set is likely not pollen limited. Snow (1986) implied this is often the case for insect-pollinated species.

The nectarless flowers of *Solanum* may promote interplant or interpopulation foraging as suggested by Bernhardt (1987) for Australian *Acacia* (which also has no floral nectar). Bees collecting pollen have to find other species as nectar sources; this interruption raises the possibility of returning to a different plant or population of *Solanum*, thereby increasing the chance of effecting outcrossing. On the other hand, given the population structure of the solanums and the pattern of visitation (especially that of *Trigona*), it is likely that more than three-fourths of interfloral visits result in self crosses. This strong likelihood lends strength to the arguments (Anderson & Stebbins, 1984; Anderson & Symon, in press) that dioecy, which promotes genetically wider crossing, may have been selected in response to several features of the hermaphroditic-flowered progenitors of the andromonoecious and dioecious species. These features include self-compatibility, vegetative reproduction, scattered population distribution, and the behavior of the pollinator assemblage as described herein.

This exclusive pollen-collecting behavior of insects on *Solanum* flowers has been accommodated in the Australian diclinous species. In both andromonoecious and dioecious species, all flowers are morphologically hermaphroditic (Anderson & Symon, in press). In staminate flowers of the andromonoecious and dioecious species the gynoecia are present but reduced. This reduction is presumably of little consequence to the pollen-collecting foragers. Of more importance is the fact that in the dioecious species the pistillate flowers bear anthers with pollen. This pollen reward differs from the usual tricolporate pollen of *Solanum* in that it is inaperturate (Anderson & Gensel, 1976). The inaperturate pollen is fully viable but incapable of germination (Levine & Anderson, 1986). Thus, the Australian dioecious species have a reward system that maintains pollinator visitation, but one that also disallows the self-pollination promoted by the plant biology and pollinator behavior.

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APPENDIX I. *Insects on* Solanum *flowers. See Methods for full names and authorities for the* Solanum *species. sp. = species not identified,* s.n. *= without number,* * *= plant cultivated.*

Insects	*Solanum* Species	Insect Voucher Number	% Fidelity	Number of Other Species Visited	Time of Day Captured	Study Site (see Fig. 1)
		Bees				
Anthophoridae						
Amegilla (Amegilla) aeruginosa (Smith)	cunni	341			7:00	8
		348			7:00	8
	dioic	369	100	0	7:30	18
	eburn	300	72	1	9:30	1, 2
		301	69	1	9:30	1, 2
		304			8:30	30
		305			8:30	30
		435	100	0	8:30	30
		436			8:30	30
		437			8:30	30
		438	87	1	8:30	30
			$\bar{X} = 85$	$\bar{X} = 0.8$		
A. (Amegilla) pulchra (Smith)	diver	306	37	3	15:00	2a
		313	37	2	9:30	3
		398		3	7:30	2a
	ellip	460	100	0	15:00	37
		416	100	0	15:00	37
		472	100	0		40
	esuri	457				41
	hoplo	*s.n.*				42
	sturt	*s.n.*				37
	sp. ?*	474				41
			$\bar{X} = 73$	$\bar{X} = 1.33$		
A. sp.?	dioic	363			9:00	16
		364			9:00	16
Genus (*Amegilla*)			$\bar{X} = 79$	$\bar{X} = 1.09$		11 sites
Braunsapis sp. ?	dioic	351	100	0	8:00	14
	eburn	450			10:30	31
Xylocopa (Koptortosoma) aruana Ritsema	eburn	444	99	1	10:30	31
Apidae						
Trigona (Plebeia) sp. A	cunni	344			7:00	8
		345			7:00	8
		346			7:00	8
		347			7:00	8
	dioic	383	100	0	11:00	21
		384	100	0	11:00	21
	diver	393	100	0	7:30	2a
		396	100	0	7:30	2a
	lucan	408			9:00	24
		409			9:00	24
		410			9:00	24
		411			9:00	24
		412			9:00	24
		413			9:00	24
		414			9:00	29
		415	100	0	9:00	24
		416	100	0	9:00	24
		417	100	0	9:00	24

Appendix I. *Continued.*

Insects	*Solanum* Species	Insect Voucher Number	% Fidelity	Number of Other Species Visited	Time of Day Captured	Study Site (see Fig. 1)
	quadr	418			11:00	25
		419			11:00	25
			$\bar{X} = 100$	$\bar{X} = 0$		
Trigona (*Plebeia*) sp. B	beaug	370			9:00	20
		371			9:00	20
		372			9:00	20
		373			9:00	20
		374			9:00	20
		375			9:00	20
		376	99	1	9:00	20
	dioic	326	100	0	15:00	6
		327	100	0	15:00	6
		328			15:00	6
		329			15:00	6
		330			15:00	6
		352	100	0	9:00	16
		353	100	0	9:00	16
		354			9:00	16
		355			9:00	16
		368			12:00	17
		382			11:00	21
		385	100	0	11:00	21
		386	100	0	11:00	21
	diver	307				
		308	100	0	9:30	3
		309	96	1	9:30	3
		310			9:30	3
		311			9:30	3
		312			9:30	3
		324	100	0	10:00	5
		325	100	0	10:00	5
		394	100	0	7:30	2a
		395	100	0	7:30	2a
		397	90	1	7:30	2a
		400			7:30	2a
		401			7:30	2a
	eburn	303	99	1	10:00	2
		429			15:30	29
		430	100	0	15:30	29
		439	100	0	8:30	30
	lucan	337			15:00	9
		451	100	0	11:30	32
		452			12:30	33
		453			12:30	33
		454	100	0	12:30	33
			$\bar{X} = 99$	$\bar{X} = 0.22$		
Genus (*Trigona*)			$\bar{X} = 99$	$\bar{X} = 0.16$		17 sites
Colletidae						
Hylaeus (*Prosopisteron*) sp. 1	cunni	334			12:00	8
		335			12:00	8
H. (*Rhodohylaeus*) sp. 2	cunni	336	95	1	12:00	8
Leioproctus (*Leioproctus*) sp.	hoplo	*s.n.*				42

APPENDIX I. *Continued.*

Insects	*Solanum* Species	Insect Voucher Number	% Fidelity	Number of Other Species Visited	Time of Day Captured	Study Site (see Fig. 1)
Halictidae						
Lasioglossum sp.	leopo*	459	79	2	10:00	36
	parvi*	*s.n.*				36
Nomia (*Austronomia*) *dimissa* (?) Cockerell	beaug	380	93	1	9:00	20
N. (*Austronomia*) *flavoviridis* Cockerell	beaug	379	83	1	9:00	20
		381	100	0	9:00	20
	ciner*	*s.n.*				36
	dioic	315	75	2	11:00	4
		331	100	0	10:00	6
		332	99	1	10:00	6
		358	100	0	9:00	16
		359	100	0	9:00	16
		360	100	0	9:00	16
		361	65	1	9:00	16
		362	50	2	9:00	16
	diver	317	95	2	10:00	5
		318	98	2	10:00	5
		319	54	2	10:00	5
		320			10:00	5
		321			10:00	5
		322			10:00	5
	eburn	431	100	0	15:30	29
		432	83	1	15:30	29
		433	39	2	15:30	29
		434	84	1	15:30	29
		446	65	1	10:30	31
		447	9	1	10:30	31
		448	10	1	10:30	31
		449	13	3	10:30	31
	ellip	*s.n.*				37
	esuri	458			14:00	35
	lucan	407	100	0	9:00	24
		455	34	3	12:30	33
	petro	*s.n.*				37
	quadr	420			11:00	25
		421	99	1	11:00	25
		422	100	0	11:00	25
	sturt	473	100	0		40
	tudun	428	100	0	11:00	26
			$\bar{X} = 78$	$\bar{X} = 1.0$		
N. (*Hoplonomia*) *rubroviridis* Cockerell	cunni	342	33	1	7:00	8
		343	46	3	7:00	8
		349	98	1	12:30	11
	eburn	302	73	2	10:00	2
	lucan	402	97	2	9:00	24
		403	99	1	9:00	24
		404	100	1	9:00	24
			$\bar{X} = 80$	$\bar{X} = 1.6$		
N. sp. ?	dioic	387	99	1	10:00	22
		388			10:00	22
		389			10:00	22

APPENDIX I. *Continued.*

Insects	*Solanum* Species	Insect Voucher Number	% Fidelity	Number of Other Species Visited	Time of Day Captured	Study Site (see Fig. 1)
		390			10:00	22
	diver	314	37	2	9:30	3
Genus (*Nomia*)			$\bar{X} = 79$	$\bar{X} = 1.14$		20 sites
	Floral Visitors Other than Bees					
Eumenidae (Hymenoptera)	asymm	456	94	0		34
Ants	dioic	333			15:00	6
Diptera	quadr	423–427			10:00	25
	cunni	338			7:00	8
		339			7:00	8

TWO NEW SPECIES OF *CALYPTROCARYA* (CYPERACEAE: SCLERIEAE) FROM VENEZUELA AND OBSERVATIONS ON THE INFLORESCENCE MORPHOLOGY OF THE GENUS[1]

Gerrit Davidse[2] *and Robert Kral*[3]

ABSTRACT

Two new species, C. montesii *and* C. delascioi, *are described from Guárico, Venezuela. Both species have multiple, sessile, headlike inflorescences.* Calyptrocarya delascioi *is the first species in the genus with elongated rhizomes.* Calyptrocarya montesii *is the second species in the genus with three stigmas. A detailed discussion of inflorescence morphology is presented, demonstrating that compound male and female spikelets are borne in separate inflorescence units in all species of the genus.*

A recent review of specimens of *Calyptrocarya* for a treatment in the *Flora of the Venezuelan Guayana* has brought to light two distinctive gatherings of *Calyptrocarya* from a region just north of the flora area.

This tropical American genus has been revised by Koyama (1967, 1969b), who recognized six species. The presence of two undescribed endemic taxa from a small region in the state of Guárico may seem suspicious, yet seems to be justified by their distinctive morphologies. The low mesas of Parque Nacional Aguaro-Guariquito that rise out of the llanos harbor a number of distinctive endemic elements. One of these is *Rhynchospora papillosa* W. Thomas (1984), a species recently described from Montaña de Guardahumo, in Parque Nacional Aguaro-Guariquito. Ironically, the type of *C. montesii* was collected as a mixture in the type gathering (*Delascio, Montes & Davidse 11342*) of *R. papillosa.*

DESCRIPTION OF NEW SPECIES

Calyptrocarya montesii Davidse & Kral, sp. nov. TYPE: Venezuela. Guárico: Distrito Miranda, Parque Nacional Aguaro-Guariquito, Montaña de Guardahumo, ca. 8°88′–8°92′N, 67°44′W, 40–60 m, Dec. 1981, *F. Delascio, R. Montes & G. Davidse 11342A* (holotype, MO). Figure 1.

Species affinis *C. delascioi* a qua habitu caespitoso, culmis capitulis 2, bracteis capitulis longioribus et stigmatibus 3 differt.

Cespitose annual with lax culms and leaves. Roots fibrous, slender. Lowermost leaves mostly sheaths, short, keeled, multinerved, dull brown, friable and soon lost; principal leaves well overtopping the inflorescence, the largest lowest and more approximate with short, dull brown sheaths; blades 10–30 cm long, 3–5 mm wide, linear, thin, flat, glabrous, 3-costate, the midrib projected on the lower surface, the lateral costae projected on the upper surface, the apex abruptly acute, the margins scabro-ciliate only distally, otherwise smooth; upper leaves gradually reduced and more distant, with all but the uppermost blades elongate and overtopping the inflorescence. Culms 6–16 cm long, ca. 0.5 mm wide, all fertile, centrally borne, trigonous; nodes usually 3, the upper 2 usually bearing inflorescences; internodes glabrous with scaberulous culm angles. Inflorescence a congested head

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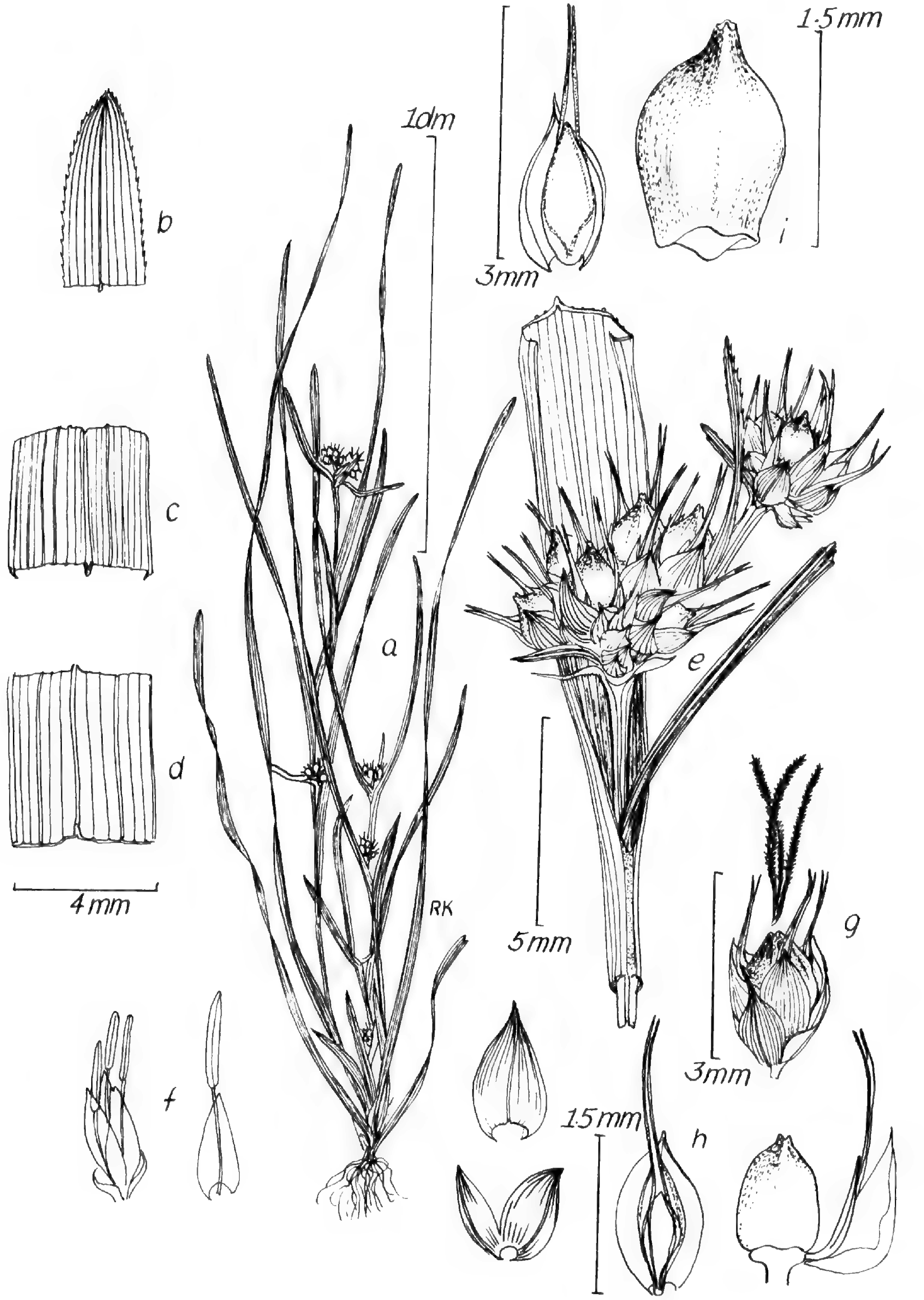


FIGURE 1. Calyptrocarya montesii *Davidse & Kral (from holotype).—a. Habit sketch.—b. Upper surface of leaf blade tip.—c. Upper surface of mid blade.—d. Lower surface of mid blade.—e. Portion of inflorescence showing two heads composed of globose clusters of compound spikelets.—f. Staminate spikelet.—g. Young female compound spikelet.—h. Dissection of female compound spikelet, from left: lowest female spikelet bract; intermediate bract (prophyll); adaxial view of upper bract and sterile spikelet; young fruit with attached upper bract and its sterile spikelet.—i. Left, upper bract complex; right, mature fruit.*

5–8 mm long and wide, composed of smaller globose clusters of compound spikelets; globose clusters sessile or nearly so; involucral bracts 1–3, leaflike, 0.5–8 cm long; lower 1–3 compound spikelets in a globose cluster male, the upper 4–8 compound spikelets female. Male compound spikelets 1.3–2.2 mm long, usually unbranched; lowest bract 1.8–2.2(–8) mm long, membranous or in the lowest spikelet of the head sometimes herbaceous and leaflike, several-nerved; prophyll 1.3–1.6 mm long, 2-keeled, membranous, truncate, inconspicuously many-nerved; bracts subtending the solitary stamens 5–7, the uppermost usually reduced and rudimentary and not subtending a stamen; male flowers solitary stamens, the filaments as long as or slightly longer than the subtending bracts at anthesis, the anthers 0.7–1.2 mm long, linear. Female compound spikelets 3.1–4.2 mm long, composed of 5 primary bracts; lowest bract 1.8–4.2 mm long, ovate, 9–15-nerved, acute or awned to 1 mm; prophyll 1–1.1 mm long, often split into 2 parts, 2-keeled, many-nerved; upper bracts 3, 1.6–2 mm long, 1.4–1.7 mm wide, herbaceous, broadly ovate, 15–19-nerved, prominently apiculate, each subtending 1 sterile, axillary spikelet and surrounding a central, terminal female spikelet; sterile spikelets 2.9–4 mm long including the pedicel, much exceeding the achene, long attenuate, the lowest bract 1.4–2.1 mm long, 2-keeled and clasping at the base, membranous, inconspicuously many-nerved, the upper bract 2.4–3 mm long, 0.4–0.5 mm wide at the base, lanceolate-linear, strongly 2-keeled, the tip of the keels free as awn points 0.1–0.3 mm long, the lateral nerves 2–4; female spikelet a solitary female flower; achenes 1.5–1.6 mm long, ellipsoid; utricle with the base triangular in outline, somewhat thickened and forming a low 3-lobed annulus, the upper part a hyaline, pale brown, smooth to minutely puberulent sac closely appressed to the achene; beak ca. 0.2 mm long; stigmas 3, ca. 1 mm long.

Calyptrocarya montesii is known only from the type collection. It is named in honor of Dr. Rubén A. Montes, a co-collector of this new species.

This species is most clearly characterized by its lax foliage, sessile, multiple inflorescences, and three stigmas. The species appears to be annual, which would be unique in the genus. However, the available specimens are too few to be certain of this interpretation.

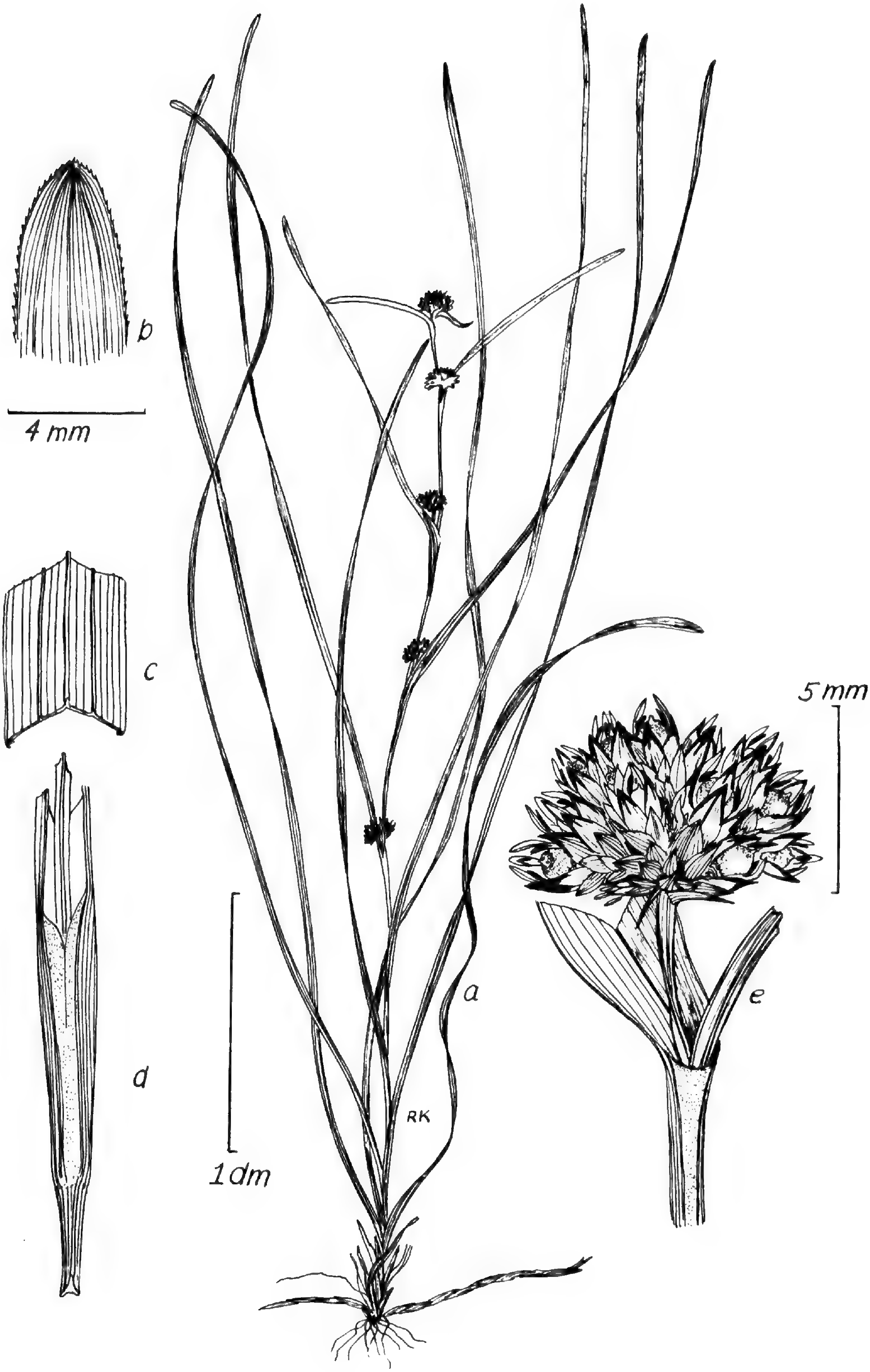
The only other species in the genus with three stigmas is *C. luzuliformis* T. Koyama, from which *C. montesii* differs by having relatively broader, laxer leaves, sessile heads, and minutely puberulent rather than pubescent utricles.

Two other species have sessile headlike inflorescences, *C. monocephala* Hochst. ex Steud. and *C. delascioi*. *Calyptrocarya montesii* differs from *C. monocephala* in its multiple rather than solitary inflorescences, broader and laxer leaves, and three versus two stigmas. *Calyptrocarya montesii* differs from *C. delascioi* in the lack of rhizomes, less numerous inflorescences per culm, much longer involucral bracts, smaller achenes, and three rather than two stigmas.

Calyptrocarya delascioi Davidse & Kral, sp. nov. TYPE: Venezuela. Guárico: Distrito Miranda, Parque Nacional Aguaro-Guariquito, Montaña de Guardahumo, ca. 8°88′–8°92′N, 67°44′W, 40–60 m, Dec. 1981, *F. Delascio, R. Montes & G. Davidse 11336* (holotype, MO; isotype, VEN). Figures 2, 3.

Species rhizomatibus productis gracilibus a congeneribus diversa; folia laxa, culmi capitulis 3–8 sessilibus; stigmata 2.

Rhizomatous perennial with lax culms and leaves; aerial shoots up to 7 clumped together, all fertile; roots fibrous, slender. Rhizomes 1–10 cm long, ca. 1.5 mm thick, scaly, slender; scales 6–10 mm long, purple, multinerved, slightly dilated and open distally at the acute, sometimes bifid apex, usually slightly overlapping, passing into scalelike basal leaves. Principal leaves longest and most crowded toward the culm base, there with short, red to purple loose sheaths to 3 cm long, these ventrally scarious, brownish, nearly open, passing at the orifice into strongly folded dull-green blades; blades 30–60 cm long, 3.5–7 mm wide, well overtopping the inflorescence, linear, very lax, thin, flat, glabrous, 3-costate, the midrib projecting on the lower surface, the lateral costae projecting on both surfaces, the tip obtuse, the margin scabro-ciliate distally, otherwise a smooth nerve; upper leaves gradually shortening, but even the upper ones overtopping the inflorescences. Culms to 35 cm long, ca. 1 mm wide, lax, centrally borne, glabrous, trigonous, each angle with a strong costa, each concave face with several low ribs, nodes 3–9 (–10), all usually bearing inflorescences. Inflorescence a congested head 3.5–7 mm long, 3.5–9 mm wide, composed of globose clusters of compound spikelets; globose clusters sessile or with rays to 5 mm long; involucral bracts inconspicuous, 1–3 mm long, linear-lanceolate; lowest 2–3 compound spikelets in a globose cluster male, the upper 5–8 compound spikelets female, larger and firmer than the male compound spikelets. Male compound spikelets 1.5–2.1 mm long, usually unbranched; lowest bract 1.9–2.1 mm long, 7–11-nerved, lan-


b
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c
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ceolate, acute; prophyll 1.1–1.3 mm long, membranous, 2-keeled, 5–7-nerved; bracts subtending the solitary stamens 6–8, 1–1.6 mm long, lanceolate to linear-lanceolate, membranous, especially the inner, the uppermost 2–3 reduced or rudimentary and not subtending a stamen; male flowers solitary stamens, the filaments flattened, slightly longer than the subtending bracts at anthesis, the anthers 0.5–0.8 mm long, oblong-linear. Female compound spikelets 2.5–4 mm long, composed of 5 or rarely 6 primary bracts, the tips and/or upper margins conspicuously purple, otherwise pale green; lowest bract 1.9–2.3 mm long, ovate, herbaceous, 15–19-nerved, acute; prophyll 1–1.2 mm long, usually split into 2 parts, 2-keeled, many-nerved; upper bracts 3 or rarely 4, 2–2.3 mm long, 1.2–1.6 mm wide, herbaceous, ovate, acute, 9–11-nerved, acute, each subtending an axillary spikelet and surrounding a central, terminal female spikelet; axillary spikelets sterile or female, 2–3.2 mm long including the pedicel, when sterile composed of a 2-keeled prophyll and 1–3 bracts, when fertile, bearing 3 bracts above the prophyll, each bract subtending a solitary, axillary spikelet, and surrounding a central, terminal female spikelet; female spikelet a solitary female flower; achenes 1–1.2 mm long, 0.8–1 mm wide, lenticular; utricle with the base elliptic in outline, slightly thickened and forming a low, trilobed collar around the achene, the upper part a hyaline, pale brown, puberulent sac closely appressed to the smooth stramineous achene; beak 0.1 mm long; stigmas 2.

Calyptrocarya delascioi is known only from the type collection. It grew in shallow water of a small stream in the shade of a low gallery forest through the *Trachypogon* savanna that covers most of the mesa top. At the time of the collection, the leaves and culms were mostly floating on the surface of the water.

This species is named for Mr. Francisco Delascio Chitty, a co-collector of the type collection.

Calyptrocarya delascioi differs from all other species in the genus in the development of long, slender rhizomes; all other species are cespitose. In *C. irwiniana* Koyama, however, lateral culms are produced that eventually arch and bend toward the ground. Spikelets often become proliferated and produce new shoots that take root (Koyama, 1969b). This species is thus functionally stoloniferous. The central culms of *C. glomerulata* (Brongn.) Urban also occasionally reproduce plantlets in the inflorescence through proliferation of spikelets.

Calyptrocarya delascioi may be most closely related to *C. montesii*. See the discussion of that species for a comparison.

INFLORESCENCE MORPHOLOGY

The inflorescence morphology of *Calyptrocarya* has been consistently misinterpreted in recent years (Eiten, 1976; Koyama, 1967, 1969a, b, 1971). For example, Koyama (1967) described the spikelets as "compound, sessile or short-peduncled; glumes 6 (including a prophyll); prophyll and the lower 2 empty; the upper 3 bearing an axillary staminate floret; fructification solitary, terminal." A similar interpretation was accepted by Eiten (1976).

The typical compound spikelet, such as in *Calyptrocarya glomerulata*, that is borne toward the tip of a globose head and that matures an achene bears, in fact, 5 bracts (Fig. 4). The lowest bract subtends a reduced axillary branch system that bears a 2-keeled prophyll as its first foliar bract. Both the lowest bract and prophyll do not subtend flowers. Three multinerved bracts are borne successively above the prophyll, each subtending an axillary sterile spikelet. Koyama (1967) considered these axillary spikelets to be staminate spikelets but, after examining spikelets of all species except *C. irwiniana*, of which we have not seen authentic material, we have never observed any stamens or even the remains of filaments in these spikelets. Even *C. irwiniana*, judging from the published illustration (Koyama, 1969b), appears to conform to the general pattern in the other species. The sterile axillary spikelets consist of a pedicel bearing a basal two-keeled prophyll, usually followed by two or three bracts. These two or three bracts are clearly separate in some species (e.g., some specimens of *C. poeppigiana* Kunth, *C. delascioi*, and *C. bicolor* (Pfeiffer) Koyama, and many specimens of *C. luzuliformis* and *C. monocephala*); however, in certain species (e.g., *C. montesii*, *C. glomerulata*) and some specimens of most other species, the upper two bracts appear to have their margins

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FIGURE 2. Calyptrocarya delascioi *Davidse & Kral (from holotype).—a. Habit sketch.—b. Leaf tip.—c. Lower side of mid blade of leaf.—d. Node from mid culm with attached leaf sheath, adaxial view.—e. Inflorescence head composed of globose clusters of compound spikelets.*

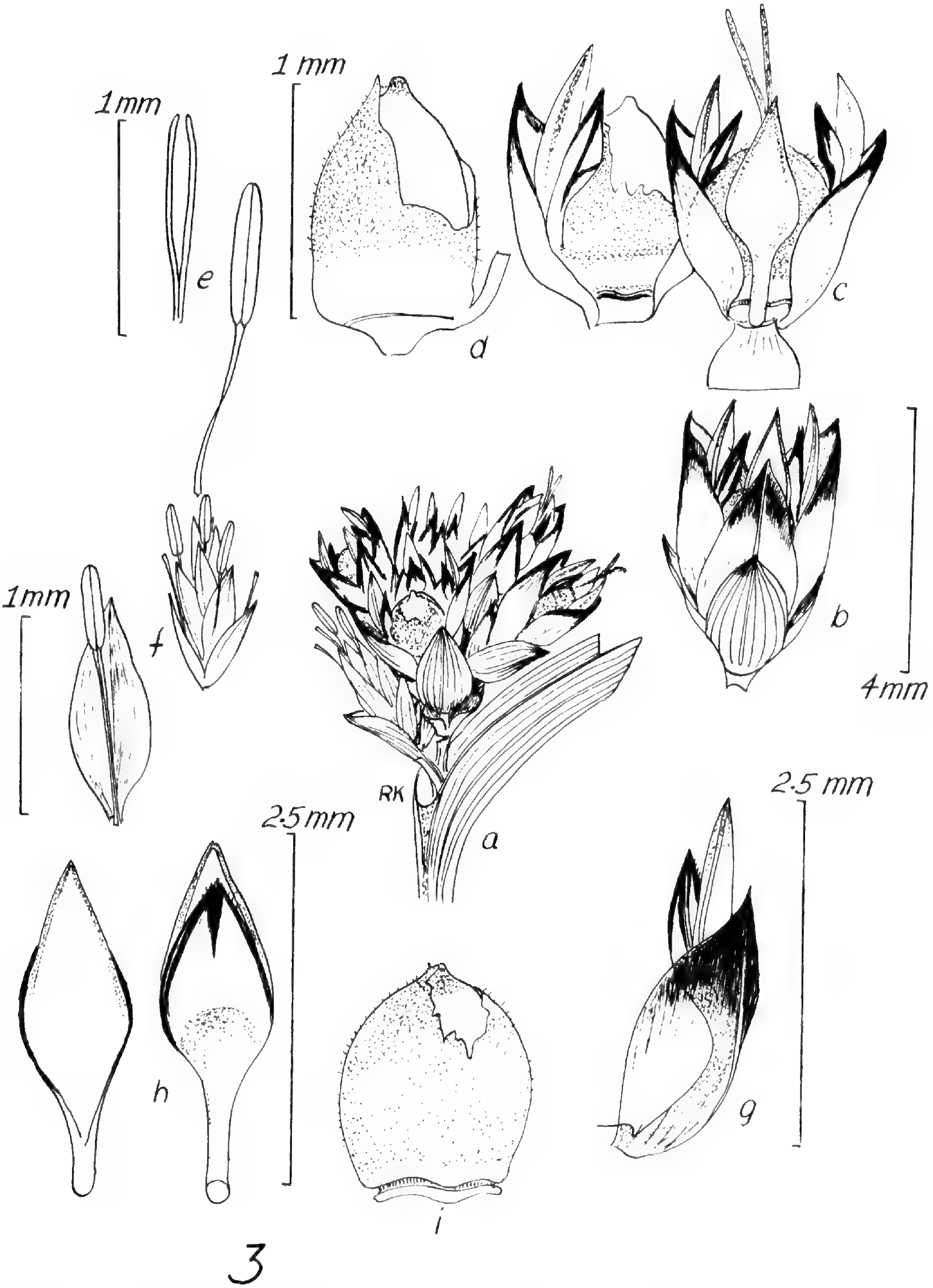


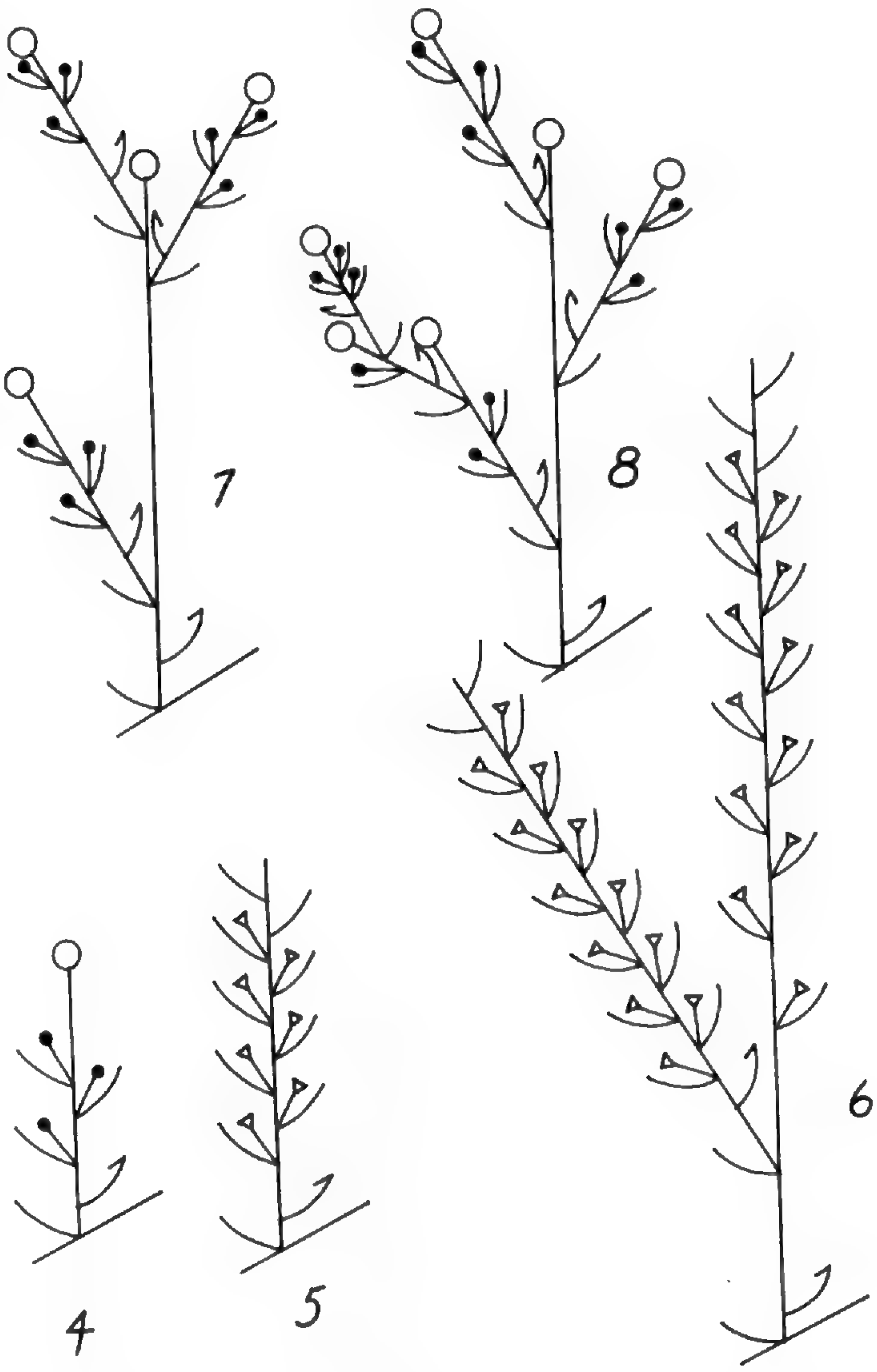
FIGURE 3. Calyptrocarya delascioi *Davidse & Kral (from holotype).—a. Inflorescence head with male branch at lower left.—b. Female compound spikelet.—c. Female compound spikelet: left, showing upper pseudowhorl of bracts, sterile spikelet whorl, fruit; right, figure with base of one upper bract pulled downward to show the abaxial side of the sterile spikelet which it subtends.—d. Utricle and enclosed achene.—e. Stigma apparatus, left; stamen, right.—f. Staminate bract and its stamens, left; reduced male compound spikelet, right.—g. Side-oblique view of an inner pistillate bract and a sterile spikelet.—h. Abaxial view of sterile spikelet (from g), left; adaxial view of sterile spikelet, right.—i. Mature fruit.*

fused, thus appearing to be a single two-keeled structure. In any case, the compound spikelets near the tip of the globose heads are functionally female with never any evidence of stamens.

The functionally male compound spikelets are borne separately at the base of each inflorescence head and often also near the tip of each head, depending on the species. The number of parts is much more variable in the male compound spikelets than in their female counterparts. As in the female compound spikelets, the typical male compound spikelet is borne in the axil of a bract and the first bract on the axis is a two-keeled prophyll. The axis beyond the prophyll may be branched or not. When it is unbranched (Fig. 5), the bracts are spirally arranged, and each subtends a solitary stamen which represents the male flower. Typically, the uppermost one to six bracts in a male compound spikelet are reduced or rudimentary. There is no morphological evidence of a pistil in any of the male compound spikelets that we have observed.

In branched male compound spikelets (Fig. 6), the branch within the spikelet is borne in the axil of a bract, and the first bract on the branch is a two-keeled prophyll. All subsequent bracts except the uppermost subtend solitary stamens. In some male spikelets of *C. poeppigiana* that are branched once again, the distinction between the lowest basal bract and prophyll from the bracts subtending stamens is difficult to observe, because the bracts become smaller and narrower towards the tip of each compound spikelet. An additional difficulty is that either the lowest basal bract or prophyll may sometimes be absent.

It is unlikely, as maintained by Eiten (1976) and Koyama (1967, 1969a, b, 1971), that the axillary spikelets borne below the terminal pistil in the female compound spikelet of *Calyptrocarya* (Fig. 4) are staminate or rudimentary staminate spikelets. Rather, it seems certain that these sterile axillary spikelets represent rudimentary female spikelets of a branched female compound spikelet. This interpretation is based on three observations: (1) We have not been able to confirm the presence of stamens in such spikelets, contrary to the assertions of Koyama (1967, 1969a, b, 1971) and Eiten (1976). (2) The branched male compound spikelets are morphologically equivalent to the branched female compound spikelets. The main difference is that almost all female compound spikelets uniformly contain three branches, whereas the male compound spikelets are commonly two-branched, less uncommonly unbranched, and least commonly more than two-branched. (3) Comparison of a gradation series of female compound spikelets in different *Calyptrocarya* species shows that the axillary spikelets represent female spikelets. That the relatively simple structure of the female compound spikelet in *C. glomerulata* (Fig. 4) and *C. montesii* (Fig. 1g) represents a reduction may be seen by comparing them with the female compound spikelets of *C. bicolor*, *C. delascioi*, *C. monocephala*, and *C. luzuliformis*. In *C. bicolor* and *C. delascioi*, the axillary spikelets commonly bear larger and additional bracts compared with those of *C. glomerulata*. Such axillary spikelets in *C. bicolor* are still nonfunctional and usually do not bear a pistil. In *C. delascioi*, *C. luzuliformis*, and *C. monocephala*, on the other hand, the ax-



FIGURES 4–8. *Schematic diagrams of compound spikelets of* Calyptrocarya *species.—4. Simple female compound spikelet of* C. glomerulata.—*5. Simple male compound spikelet of* C. montesii.—*6. Branched male compound spikelet of* C. monocephala.—*7, 8. Branched female compound spikelets of* C. luzuliformis. *Symbols: large open circles = fertile female flowers; small closed circles = sterile female spikelets; open triangles = fertile male flowers; curved lines = bracts; hooked curved lines = prophylls.*

illary spikelets that surround the solitary terminal pistil are frequently fully developed, each in turn bearing a fully developed functional terminal pistil surrounded by three lateral bracts, and each of these bearing a solitary axillary sterile spikelet (Fig. 7). Instances in which these third-order axillary spikelets are functional may also be observed in *C. luzuliformis* (Fig. 8). However, in such cases of third-order branching, the number of branches is often less than three, as in Figure 8 where there are two third-order branches with one of them fertile.

From these three lines of evidence, but especially the last where we have demonstrated intergrading series of axillary spikelets in female compound spikelets from rudimentary to fully developed, the conclusion is inescapable that the axillary spikelets borne below the terminal pistil always represent female spikelets. This means that the female and male compound spikelets of *Calyptrocarya* are always borne on completely separate units of the inflorescence, exactly as in many species of *Scleria* Bergius, a closely related genus in the tribe Sclerieae.

The major feature of this interpretation, namely, that the male and female spikelets of *Calyptrocarya* are borne on separate inflorescence units, is not new, since Nees (1842) had already correctly described and illustrated the genus as having separate male and female partial inflorescences. His characterization seems to have been misinterpreted by many subsequent students of the genus, probably through false analogy with other sclerioid and mapanioid genera.

Eiten's diagnosis of *Calyptrocarya* was slightly different from Koyama's interpretation in that she noted and, in fact, illustrated (Eiten, 1976, fig. 14) axillary spikelets lacking male flowers. However, she also indicated that these axillary spikelets usually bear male flowers composed of one stamen.

At anthesis, prophylls in male and female spikelets are often torn and sometimes appear to be two distinct structures. However, this seems to result from the expansion and growth of spikelets at anthesis, and in the female spikelets especially from expansion of the achene. This commonly torn prophyll seems to be responsible for the assertion by Nees (1842), Koyama (1967, 1969a, 1971), and Eiten (1976) that the ultimate unit of the *Calyptrocarya* inflorescence is composed of six bracts. In fact, the intact prophyll can be observed readily in very young spikelets of all species and is even easily visible intact in the narrow, postanthesis male compound spikelets of *C. luzuliformis* and *C. monocephala*. It is true, as in an unusual spikelet of *C. delascioi* that we observed, that four rather than three bracts may rarely subtend the central, terminal pistil. But such cases are clearly anomalous and do not affect our interpretation of the structure of the prophyll.

KEY TO THE SPECIES OF *CALYPTROCARYA*

1a. Inflorescence composed of headlike, sessile, or nearly sessile clusters of spikelets.
    2a. Heads solitary per culm .... *C. monocephala*
    2b. Heads several per culm.
        3a. Stigmas 3; plants cespitose; involucral bracts conspicuous, longer than the head; heads usually 2 per culm .... *C. montesii*
        3b. Stigmas 2; plants rhizomatous with elongated rhizomes; involucral bracts inconspicuous, shorter than the head; heads 3–8 per culm .... *C. delascioi*
1b. Inflorescence composed of some peduncled globose clusters of spikelets arranged in a cymose panicle.
    4a. Stigmas 3; leaf blades less than 5 mm wide; utricle pubescent .... *C. luzuliformis*
    4b. Stigmas 2; leaf blades sometimes wider than 5 mm; utricle puberulent.
        5a. Culms lateral .... *C. irwininana*
        5b. Culms central.
            6a. Achenes 1.2–1.5 mm wide, 1–1.5 mm long .... *C. glomerulata*
            6b. Achenes 1.6–2.2 mm wide, 1.7–2.2 mm long.
                7a. Upper basal leaves 5–9(–12) mm wide, attenuate at the apex, mostly longer than 25 cm .... *C. poeppigiana*
                7b. Upper basal leaves (8–)10–28 mm wide, abruptly acute at the apex, mostly shorter than 25 cm .... *C. bicolor*

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NIGERIAN *SOLANUM* SPECIES OF ECONOMIC IMPORTANCE

Z. O. Gbile[1] *and S. K. Adesina*[2]

Abstract

Many Solanum *species that occur in Nigeria are sources of food and medicinal products. The domesticated species especially serve as sources of edible fruits and vegetables. Many of the species remain good sources of diosgenin and solasodine, chemicals of great importance in the steroid industry.*

The genus *Solanum* is represented by some 25 species in Nigeria, including five introductions: *S. mammosum, S. tuberosum, S. melongena, S. wrightii,* and *S. seaforthianum* var. *disjunctum* (Gbile, 1987). *Solanum macrocarpon, S. aethiopicum, S. scabrum, S. melongena, S. gilo, S. indicum, S. anomalum, S. americanum, S. nigrum,* and others are domesticated, and their leaves or fruits or both are eaten as vegetables and used in traditional medicine. Many other *Solanum* species grow wild and are less known or used.

Chemical information on the Nigerian *Solanum* species is scanty and it is difficult to assess the values of these species in this regard.

The present article reports on the protein content of some domesticated *Solanum* species and also reviews the economic importance of the Nigerian *Solanum*.

SOLANUM SPECIES AS FOOD PLANTS

The common *Solanum* species that are used for food include *S. tuberosum*, "Irish potato," which grows well in the highlands; *S. melongena*, "aubergine" or "eggplant," which flourishes in the lowlands; *S. americanum*; *S. nigrum*; and the additional species listed in Table 1. *Solanum anomalum, S. gilo,* and *S. melongena* provide edible fruits. Fruits and leaves of *S. aethiopicum* and *S. macrocarpon* are edible, and only the leaves of *S. scabrum, S. nigrum, S. americanum* are eaten as vegetables. While the fruits of *S. aethiopicum* and *S. gilo* are usually eaten raw or are steamed before eating, the leaves of *S. aethiopicum, S. americanum, S. macrocarpon, S. nigrum,* and *S. scabrum* are usually boiled. The relative bitterness of the leaves and fruits dictates to a great extent which is edible vs. poisonous. Bitterness has been attributed to steroidal alkaloids in these plant parts.

DETERMINATION OF PROTEIN AND ASH (MG, P) IN *SOLANUM* EDIBLE SPECIES

MATERIALS AND METHODS

The *Solanum* species were interplanted in the same experimental plot behind the Forestry Research Herbarium, in Ibadan. After fruiting, each species was sampled and separated into edible leaves and fruits. Plant materials were dried in an oven to constant weight at 60°–70° C and ground to pass through a 1-mm sieve in a Thomas-Wiley meal in preparation for chemical analyses. All determinations were prepared in duplicates.

Nitrogen was determined by the semi-micro Kjeldahl procedure using selenium as catalyst. Percentage of crude protein content was obtained by multiplying N_2 content by 6.25. In the determination of phosphorus and magnesium, samples of 0.5 g were digested using a mixture of nitric acid and perchloric acid. Phosphorus was determined by colorimetry using vanadomolybdate yellow color development, while magnesium was also determined colorimetrically by the titan-yellow method. The results are detailed in Table 1.

SOLANUM SPECIES AS MEDICINAL AGENTS

Many *Solanum* species are used in indigenous medicine to counter ailments as listed in Table 2.

Many of these species are employed as tonics, antirheumatics, remedies for colds, fevers, and dizziness, and are eaten as vegetables for their high nutritive values or as potherb as mild anticonvulsants. Modern research has shown that some *Sola-*

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TABLE 1. *Protein and ash content of some edible* Solanum *species.*

Species	Organ	% Crude Protein	% P	% Mg
Solanum macrocarpon L.	fruit	1.4	0.25	0.12
S. macrocarpon	leaf	2.4	0.44	0.40
S. aethiopicum L.	fruit	1.6	0.38	0.26
S. aethiopicum	leaf	3.2	0.37	0.38
S. scabrum Miller	fruit	1.8	0.36	0.16
S. scabrum	leaf	2.9	0.40	0.44
S. melongena L.	fruit	1.6	0.25	0.08
S. gilo Raddi	conical fruit	1.2	0.47	0.17
S. gilo	spherical fruit	1.3	0.45	0.22
S. indicum L. subsp. *distichum* Thonn.	fruit	1.4	0.46	0.27

num species have antiviral, anticancer, anticonvulsant, and anti-infective agents.

Antiviral activity has been demonstrated in extracts of *Solanum melongena*, *S. nigrum*, and *S. tuberosum* (Roychoudhury, 1980). Weak anticonvulsant activity has also been demonstrated in extracts of *S. dasyphyllum* fruit (Adesina, 1985), *S. aethiopicum* leaf, *S. americanum* leaf and unripe fruit, *S. melongena* root, and *S. scabrum* leaf and fruit (Adesina et al., 1985). Besides, all the extracts examined for anticonvulsant activity exhibited an interference on the functions of the CNS to varying degrees. Anticonvulsant activity has been related to the presence and concentration of scopoletin and related coumarins found present in most *Solanum* species examined (Adesina et al., 1985). The anticonvulsant, sedative, hypotensive, and antipyretic properties of scopoletin and scoparone have been reported before by many workers (Jamwal et al., 1972; Adesina et al., 1981; Ojewole & Adesina, 1983a, b; Adesina et al., 1985).

Chemical and biological work on immature berries of *Solanum nigrum* showed that the berries possess anticancer activity. 3-O-β-lyco-tetraoside, desgalactotigonin, and solamargine isolated from the berries showed inhibitory activity against JTC-26 (100, 97.9, 100%, respectively in concentration of 15 μg/ml) (Saijo et al., 1982). It has also been shown that the crude alkaloid fraction isolated from the leaves of *Solanum melongena* exhibited significant analgesic effect and some CNS depression in mice but no anticonvulsant action (Vohora et al., 1984). This effect was also noted for *S. scabrum* alkaloidal fraction (Adesina & Gbile, 1984).

Molluscicidal activity was examined in some *Solanum* species. All the parts of *S. americanum* were found toxic to *Biomphalaria glabrata* and *B. globosus* used as test snails and could possibly be used to check schistosomiasis.

SOLANUM SPECIES AS SOURCES OF PHARMACEUTICALLY IMPORTANT CHEMICALS

Some *Solanum* species have recently assumed great importance as rich sources of precursors of steroid drugs. Steroidal raw materials have been found useful in cardiovascular therapy, as human abortifacients, as anti-inflammatory agents, and as menopause regulants and are now known to influence the CNS. Many researchers have investigated *Solanum* species for their steroidal sapogenin and alkaloid content with a view to determining the quantities of these compounds.

Indrayanto et al. (1985) recently examined the fruit of *Solanum wrightii* chemically for its solasodine content.

Pharmaceutically important compounds diosgenin and solasodine were isolated from the tissue samples of *Solanum verbascifolium* in appreciable amounts (Jain & Sahoo, 1981a, b). The leaf was found to contain solasodine (0.26%), tomatidine (0.05%), solaverbascine (0.01%), progesterone (0.001%), 16-pregnenolone, and other compounds (Adam et al., 1979, 1980). Telek (1979) found a very good yield of crude solasodine, suitable for the commercial synthesis of 3β-acetoxy-5, 16-pregnadiene-20-one, in *S. mammosum*.

Studies on *Solanum nigrum* berries by Bose & Ghosh (1980) revealed that solasodine content of the berries varies from 5–6% in ripe berries to 4–5% in unripe berries and that this could be exploited for commercial synthesis of new drugs. Tigogenin and diosgenin have also been reported from the plant. The unripe fruit of *S. incanum*, on examination by Segal et al. (1977), led to the identifi-

TABLE 2. *Some medicinal and food uses of* Solanum *species.*

Species	Medicinal and Food Values
Solanum aculeatissimum Jacq.	Fruit used in enema, constipation
S. aethiopicum	Ripe fruits edible raw or when cooked, fruits remedy for colic and flatulence; potherb
S. americanum (L.) Jacq.	Fruit and leaf used as digestive tonic, diuretic, depurative, and antiparasitic; plant has high nutritive values and eaten as vegetable or in soup after cooking; whole plant used to remove dizziness due to epilepsy and other disorders
S. anomalum Thonn.	Serves as vegetable, laxative, and treatment of ear sores and infections
S. erianthum G. Don	Roots and fruits deliriant, purge, diuretic, and cholagogue
S. gilo	Restorative, fruit eaten raw as vegetable, has high nutritive values; remedy for fevers and dizziness, weak anticonvulsant
S. incanum L.	Used to treat syphillis, fruit for patients with high blood pressure
S. macrocarpon	Bitter fruit edible when cooked; plant cultivated as potherb, fruit and leaf eaten in soups and sauces
S. melongena	Root and boiled fruit used as antirheumatic, digestive tonic, and for veterinary purposes; all three varieties of fruit with high nutritive values as vegetable when cooked; plant used for various skin diseases and infections and to relieve excitement in nervous diseases
S. nigrum L.	Anticonvulsant, African remedy for malaria, fever, dysentery; antispasmodic, diaphoretic, and sedative; ripe fruit and leaf eaten after cooking as digestive tonic; whole plant used as medicine for eye, heart, and liver
S. scabrum L.	Anticonvulsant, digestive tonic, leaf boiled and eaten as vegetable; has high nutritive values. Whole plant sedative, depressant, anticonvulsant and antiparasitic
S. torvum Sw.	Ripe fruits edible (eaten in India) and used medicinally for liver and spleen complaints; fruits expectorant and sedative

cation of diosgenin and yamogenin in fairly large concentrations suitable for chemical development. *Solanum macrocarpon* furnished solasodine, tomatidine, diosgenin, and sitosterol on chemical hydrolysis. Recent chemical examination of some other Nigerian *Solanum* by Adesina & Gbile (1984) and Adesina (1985) revealed large amounts of solasodine, diosgenin, and tomatidenol in *S. scabrum* and *S. dasyphyllum* fruits.

CONCLUSION

From Table 1, it can be seen that the edible tissues examined contain a high percentage of protein and remain a good source of ash for use as vegetables.

Wild *Solanum* species are less studied than domesticated species. Despite this, the Nigerian *Solanum* remains a good source of pharmaceutically important chemicals and of vegetable for the teeming population.

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CHROMOSOME NUMBERS OF GRASSES (POACEAE) FROM SOUTHERN AFRICA. I.[1]

Takuji Hoshino[2] *and Gerrit Davidse*[3]

ABSTRACT

Chromosome numbers and meiotic behavior are reported for 8 Namibian and 55 South African grass collections representing 30 genera and 45 species. First chromosome counts are reported for the following 13 species: Andropogon amethystinus, n = *ca. 30;* Anthephora argentea, n = *9;* Brachiaria chusqueoides, n = *9;* B. glomerata, n = *9;* Centropodia glauca, n = *24;* Danthoniopsis parva, n = *12;* Digitaria diversinervis, n = *18;* Ehrharta longigluma, n = *12;* Miscanthidium capense, n = *15;* Panicum monticolum, n = *27;* P. schinzii, n = *9;* Triraphis fleckii, n = *10;* T. ramosissima, n = *10. Chromosome counts differing from any previously reported numbers were obtained for six species. Of the 45 species, 57% are polyploid and 43% are diploid.*

This paper is part of a series contributing to a broader knowledge of chromosome numbers of African grasses. In the first we reported new chromosome counts for Zimbabwean grasses (Davidse et al., 1986). In this report we present chromosome counts for 63 collections representing 45 species and 30 genera of South African and Namibian grasses.

The major studies dealing with chromosome numbers of South African grasses are those of Moffett & Hurcombe (1949), Pienaar (1955), De Wet (1954a, b, 1958, 1960), De Wet & Anderson (1956), Spies & Du Plessis (1986a, b, 1987a, b, 1988), and Spies & Jonker (1987), although other smaller scattered reports, mostly dealing with individual genera, have also been made.

MATERIALS AND METHODS

All cytological samples studied were collected and fixed in the field January to March 1974. The methodology is the same as explained in Davidse et al. (1986). Voucher specimens (Table 1) are deposited at MO and PRE. The suprageneric classification used in this paper follows the one of Clayton & Renvoize (1986) except that we recognize the tribe Brachypodieae.

RESULTS AND DISCUSSION

A complete list of the species studied, their chromosome numbers, the generic base number derived from the determined number, and the voucher specimens is given in Table 1, where totally new counts and counts differing from any previous count for the same taxon are also identified. We illustrate only new counts (Figs. 1–4, 7, 9, 10, 15–20) and counts different from any other for a given taxon (Figs. 5, 6, 8, 11, 13, 14). Unless otherwise indicated, meiosis was regular for all taxa listed in Table 1. Comments on chromosome or base numbers without reference to original sources are based on the indices of Fedorov (1969), Moore (1973, 1974, 1975), and Goldblatt (1981, 1984, 1985).

TRIBE ANDROPOGONEAE

Diheteropogon amplectens was previously reported to be tetraploid $2n = 40$ from a Zimbabwean population (Moffett & Hurcombe, 1949). We found two collections from the Transvaal to be diploid with $n = 10$ (Fig. 13).

Heteropogon melanocarpus was previously known only as an aneuploid ($2n = 22$) from Zimbabwe (Moffett & Hurcombe, 1949). Our count establishes the existence of a eudiploid population ($n = 10$; Fig. 14) in the Transvaal.

We determined both *Miscanthidium capense* (Fig. 15) and *M. junceum* to have $n = 15$. This confirms earlier counts for *M. junceum* (De Wet & Anderson, 1956; De Wet, 1958; De Wet, 1960, as *M. teretifolium*). In addition, Brett (1954) reported *M. violaceum* to have $2n = 28$. This strong-

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TABLE 1. *Chromosome numbers of South African (without country designation) and Namibian (South West African) grasses.*

Taxon	Chromosome (n) and Generic Base Number (x)	Locality and Voucher
ANDROPOGONEAE		
Andropogon	$x = 10$	
amethystinus Steud.	$n =$ ca. 30[a]	Orange Free State: 33 km SW of Witsieshoek, *Davidse 6993*
Cymbopogon	$x = 10$	
excavatus (Hochst.) Stapf ex Burtt Davy	$n = 10$	Transvaal: 5 km NE of Haenertsburg, *Davidse & Ellis 5839*
validus (Stapf) Stapf ex Burtt Davy	$n = 10$	Transvaal: 5 km NE of Haenertsburg, *Davidse & Ellis 5840*
Diheteropogon	$x = 10$	
amplectens (Nees) Clayton	$n = 10$[b]	Transvaal: 0.5 km NE of Haenertsburg, *Davidse & Ellis 5832*; 15 km NE of Cullinan, *Davidse 6005*
Eulalia	$x = 10$	
villosa (Thunb.) Nees	$n = 10$	Natal: 33 km S of Nqutu, *Davidse 6852*. Transvaal: 5 km NE of Haenertsburg, *Davidse & Ellis 5836*
Heteropogon	$x = 10$	
melanocarpus (Ell.) Benth.	$n = 10$[b]	Transvaal: Kruger National Park, Dzundwini Hills, 20 km N of Babalala, *Davidse 5853*
Hyparrhenia	$x = 10$	
hirta (L.) Stapf	$n = 20$	Natal: Belelasberg, 6 km S of Wakkerstroom, *Davidse 6758*
Ischaemum	$x = 10$	
afrum (J. F. Gmel.) Dandy	$n = 10$	Transvaal: Kruger National Park, Babalala, *Davidse 5843*
Miscanthidium	$x = 15$	
capense (Nees) Stapf	$n = 15$[a]	Natal: 7 km N of Kranskop, *Davidse 6923*
junceum (Stapf) Stapf	$n = 15$	Natal: 11 km NW of Utrecht, *Davidse 6803*
Monocymbium	$x = 10$	
ceresiiforme (Nees) Stapf	$n = 10$	Transvaal: Magoebaskloof, 3 km NE of Haenertsburg, *Davidse & Ellis 5812*
ARUNDINEAE		
Centropodia	$x = 12$	
glauca (Nees) T. A. Cope	$n = 24$[a]	Cape Province: 59 km W of Olifantshoek, *Davidse & Loxton 6436*. Namibia: Gibeon District, 41 km E of Gochas, *Davidse & Loxton 6367*
ARUNDINELLEAE		
Danthoniopsis	$x = 12$	
parva (J. B. Phipps) Clayton	$n = 12$[a]	Transvaal: Zoutpansberg, *Davidse & Ellis 5930*
AVENEAE		
Agrostis	$x = 7$	
lachnantha Nees	$n = 21$[b]	Transvaal: 2.5 km NW of Wakkerstroom, *Davidse 6742*. Orange Free State: 33 km SW of Witsieshoek, *Davidse 6988*
Helictotrichon	$x = 7$	
turgidulum (Stapf) Schweick.	$n = 14$	Orange Free State: 33 km SW of Witsieshoek, *Davidse 6967*

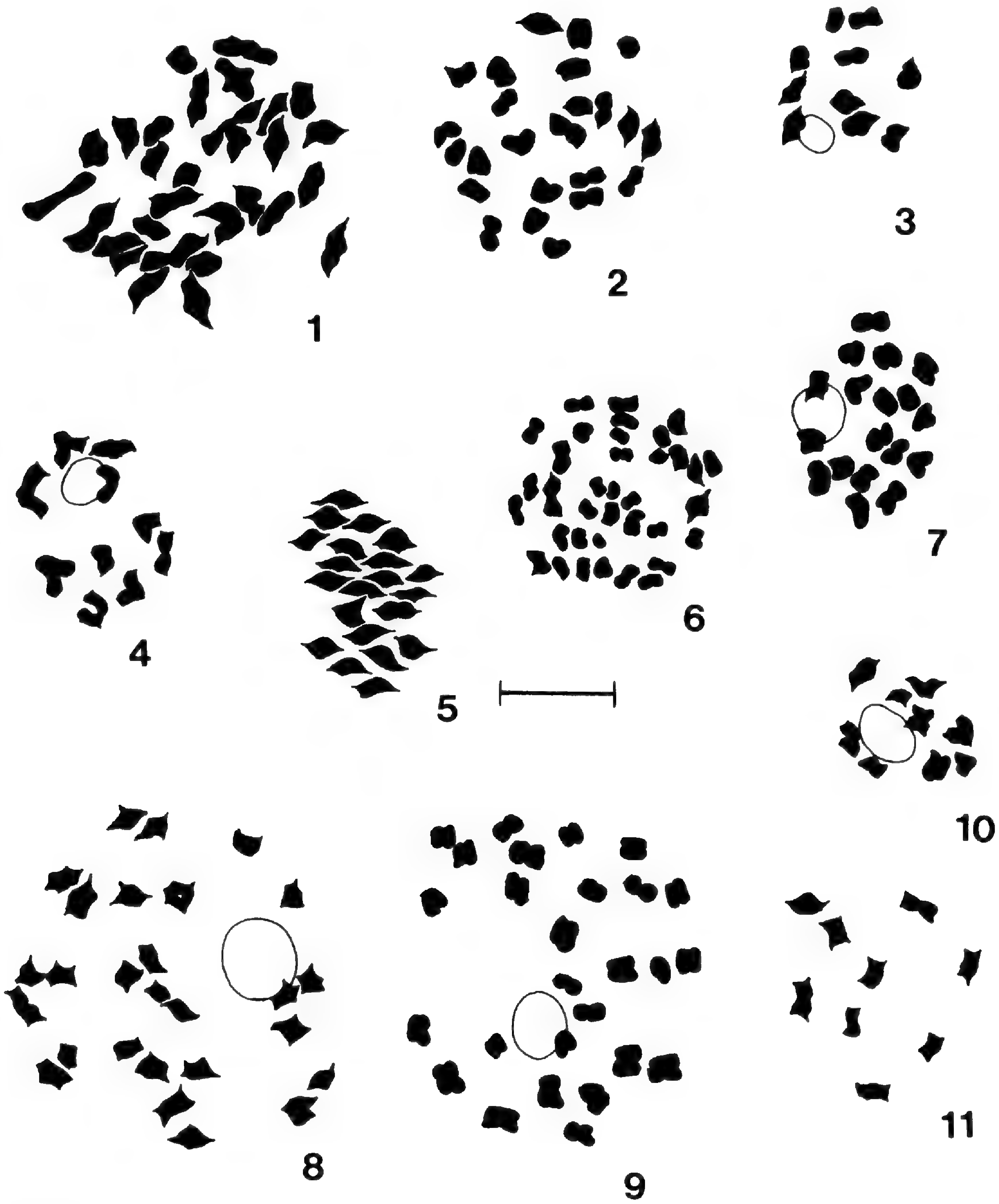
TABLE 1. *Continued.*

Taxon	Chromosome (n) and Generic Base Number (x)	Locality and Voucher
Koeleria	$x = 7$	
capensis (Steud.) Nees	$n = 7$	Orange Free State: 33 km SW of Witsieshoek, *Davidse 6981*
BRACHYPODIEAE		
Brachypodium	$x = 9$	
flexum Nees	$n = 9$	Transvaal: 6 km NE of Haenertsburg, *Davidse & Ellis 5825.* Natal: Belelasberg, 6 km S of Wakkerstroom, *Davidse 6787*
EHRHARTEAE		
Ehrharta	$x = 12$	
erecta Lam.	$n = 12$	Transvaal: Magoebaskloof, 3 km NE of Haenertsburg, *Davidse & Ellis 5810*
longigluma C. E. Hubb.	$n = 12$[a]	Orange Free State: 33 km SW of Witsieshoek, *Davidse 6974*
ERAGROSTIDEAE		
Triraphis	$x = 10$	
fleckii Hack.	$n = 10$[a]	Namibia: Gibeon District, 74 km E of Gochas, *Davidse & Loxton 6381*
ramosissima Hack.	$n = 10$[a]	Namibia: Keetmanshoop District, 2–3 km E of Groot Karasberge, *Davidse & Loxton 6252*; Warmbad District, 36 km W of Ariamsvlei, *Davidse & Loxton 6416*
ORYZEAE		
Leersia	$x = 12$	
hexandra Swartz	$n = 24$	Transvaal: 11 km WSW of Koster, *Davidse & Loxton 6012*; 2 km S of Vanderyst, *Davidse 6691*
Prosphytochloa	$x = 12$	
prehensilis (Nees) Schweick.	$n = 12$	Transvaal: Magoebaskloof, 3 km NE of Haenertsburg, *Davidse & Ellis 5811.* Natal: 42 km S of Silutshana, *Davidse 6898*
PANICEAE		
Alloteropsis	$x = 9$	
semialata (R. Br.) Hitchc.	$n = 9$	Transvaal: Magoebaskloof, 3 km NE of Haenertsburg, *Davidse & Ellis 5813*
Anthephora	$x = 9$	
argentea Goossens	$n = 9$[a]	Cape Province: 34.4 km NE of Kuruman, *Davidse & Loxton 6063*
Brachiaria	$x = 9$	
chusqueoides (Hack.) Clayton	$n = 9$[a]	Natal: Tinley Manor Beach, 55 km NE of Durban, *Davidse 6938*
deflexa (Schumach.) C. E. Hubb. ex Robyns	$n = 9$	Transvaal: Kruger National Park, 8 km N of Babalala, *Davidse & Ellis 5847*
eruciformis (J. E. Sm.) Griseb.	$n = 9$	Transvaal: 27 km SE of Bethal, *Davidse 6708*
glomerata (Hack.) A. Camus	$n = 9$[a]	Cape Province: 21 km WSW of Keimoes, *Davidse & Loxton 6124.* Namibia: Gibeon District, 25 km E of Gochas, *Davidse & Loxton 6358*
nigropedata (Munro ex Fical. & Hiern) Stapf	$n = 36$[b]	Transvaal: Kruger National Park, Dzundwini Hills, 20 km N of Babalala, *Davidse & Ellis 5852*

TABLE 1. *Continued.*

Taxon	Chromosome (*n*) and Generic Base Number (*x*)	Locality and Voucher
Digitaria	$x = 9$	
diversinervis (Nees) Stapf	$n = 18$[a]	Natal: Tinley Manor Beach, 55 km NE of Durban, *Davidse 6949*
eriantha Steud.	$n = 9$	Cape Province: 25 km SW of Olifantshoek, *Davidse & Loxton 6102*. Namibia: Keetmanshoop District, 2–3 km E of Groot Karasberge, *Davidse & Loxton 6279*
	$n = 18$	Cape Province: 75 km SW of Vryburg, *Davidse & Loxton 6040*
longiflora (Retz.) Pers.	$n = 9$	Natal: 3 km S of Kingsley, *Davidse 6839*. Transvaal: Kruger National Park, 12 km NW of Punda Milia, *Davidse & Ellis 5924*
ternata (A. Rich.) Stapf	$n = 18$	Transvaal: 27 km SE of Bethal, *Davidse 6712*
Echinochloa	$x = 9$	
haploclada (Stapf) Stapf	$n = 9$	Transvaal: Kruger National Park, 14 km SE of Punda Milia, *Davidse & Ellis 5856*
	$n = 27$[b]	Transvaal: Kruger National Park, Machayi Pan, *Davidse & Ellis 5869*; Kruger National Park, 14 km SE of Punda Milia, *Davidse & Ellis 5857*
Panicum	$x = 9$	
coloratum L. var. *coloratum*	$n = 9$	Namibia: Keetmanshoop District, 2–3 km E of Groot Karasberge, *Davidse & Loxton 6226*
	$n = 18$	Namibia: Gibeon District, Nosob River, 100 km E of Gochas, *Davidse & Loxton 6392*
maximum Jacq.	$n = 16$	Transvaal: Kruger National Park, Dzundwini Hills, 20 km N of Babalala, *Davidse & Ellis 5854*
monticolum Hook f.	$n = 27$[a]	Transvaal: Woodbush Forest Reserve, *Davidse & Ellis 5826*
schinzii Hack.	$n = 9$[a]	Transvaal: 2 km S of Vanderyst, *Davidse 6692*; 2 km NE of Haenertsburg, *Davidse & Ellis 5820*; 5 km SE of Morgenzon, *Davidse 6719*
stapfianum Fourc.	$n = 9$[b]	Cape Province: 75 km SW of Vryburg, *Davidse & Loxton 6043*
Paspalidium	$x = 9$	
obtusifolium (Del.) Simpson	$n = 18$	Transvaal: Kruger National Park, Machayi Pan, *Davidse & Ellis 5868*
Pennisetum	$x = 9$	
villosum R. Br. ex Fresen	$n = 27$	Transvaal: just SE of Amersfoort, *Davidse 6731*
Rhynchelytrum	$x = 9$	
nerviglume (Franch.) Chiov.	$n = 18$	Natal: 11 km NW of Utrecht, *Davidse 6806*; 33 km S of Nqutu, *Davidse 6861*
Setaria	$x = 9$	
megaphylla (Steud.) Dur. & Schinz	$n = 27$	Transvaal: 2 km NE of Haenertsburg, *Davidse & Ellis 5817*
Urochloa	$x = 9$	
panicoides Beauv.	$n = 18$	Natal: 39 km S of Utrecht, *Davidse 6825*

[a] First chromosome count for the species.
[b] Chromosome count differing from any previous count for the species.



FIGURES 1–11. *Camera lucida drawings of meiotic chromosomes of South African grasses.*—1. Andropogon amethystinus, n = *ca. 30, diakinesis.*—*2.* Centropodia glauca, n = *24, diakinesis.*—*3.* Triraphis fleckii, n = *10, diakinesis.*—*4.* Triraphis ramosissima, n = *10, diakinesis.*—*5.* Agrostis lachnantha, n = *21, metaphase I.*—*6.* Brachiaria nigropedata, n = *36, diakinesis.*—*7.* Digitaria diversinervis, n = *18, diakinesis.*—*8.* Echinochloa haploclada, n = *27, diakinesis.*—*9.* Panicum monticolum, n = *27, diakinesis.*—*10.* Panicum schinzii, n = *9, diakinesis.*—*11.* Panicum stapfianum, n = *9, diakinesis. Scale line = 10 µm.*

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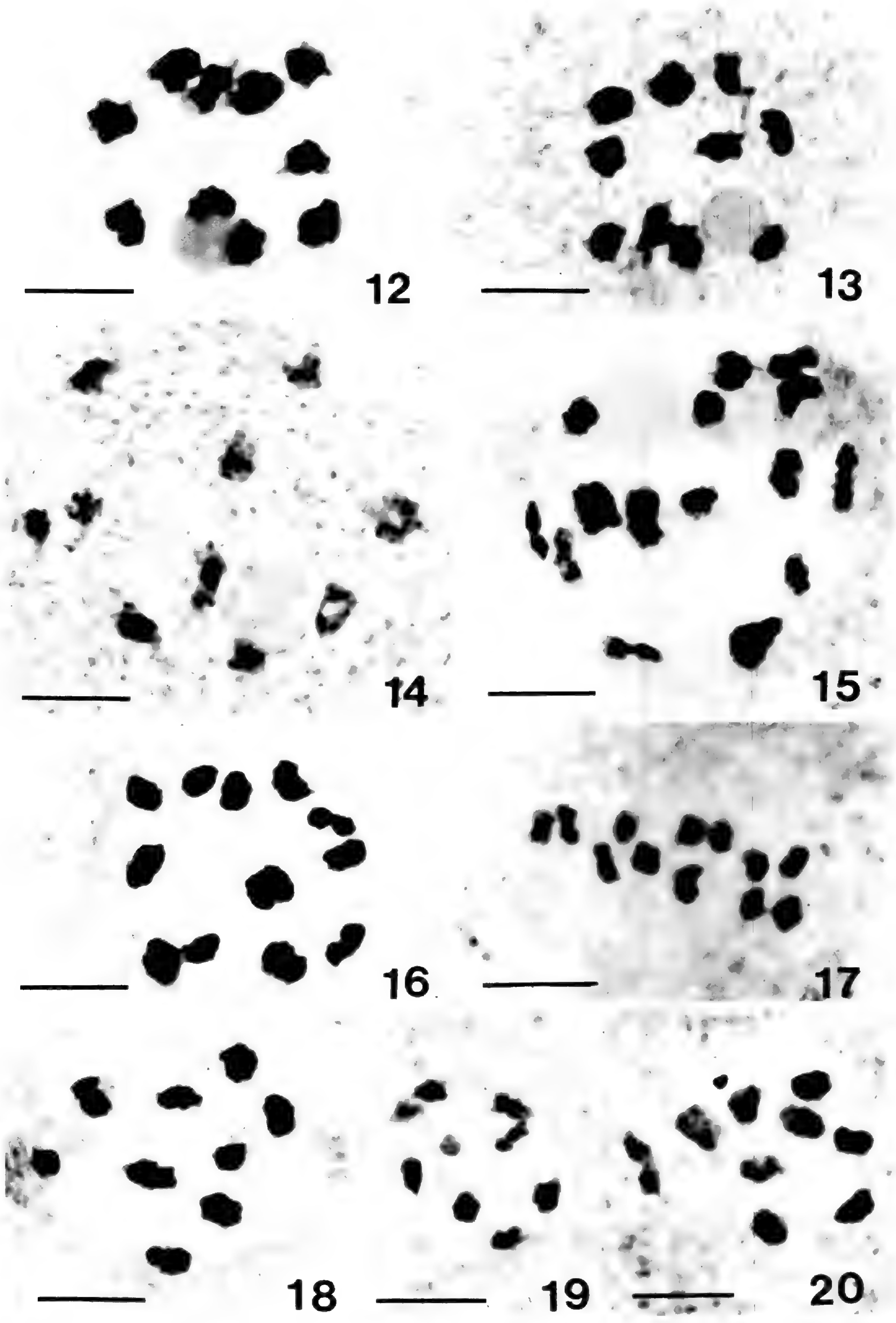
FIGURES 12–20. *Photomicrographs of meiotic chromosomes of South African grasses.*—*12.* Cymbopogon excavatus, n = *10, diakinesis.*—*13.* Diheteropogon amplectens, n = *10, diakinesis.*—*14.* Heteropogon melanocarpus, n = *10, diakinesis.*—*15.* Miscanthidium capense, n = *15, diakinesis.*—*16.* Danthoniopsis parva, n = *12, diaki-*



nesis.—*17.* Ehrharta longigluma, n = *12, metaphase I.*—*18.* Anthephora argentea, n = *9, diakinesis.*—*19.* Brachiaria chusqueoides, n = *9, diakinesis.*—*20.* Brachiaria glomerata, n = *9, diakinesis. Scale lines = 10 μm.*

ly indicates that the genus has a base number of $x = 15$, which itself was probably derived by polyploidization from $x = 5$, the base number for the tribe (Clayton & Renvoize, 1986). The number in *M. violaceum*, if it can be confirmed, was probably derived by secondary aneuploidy from $n = 15$. It also gives support for the continued recognition of this genus from the related *Miscanthus*, which has $x = 19$ (Clayton & Renvoize, 1986).

TRIBE ARUNDINEAE

The $n = 24$ (Fig. 2) count for one population of *Centropodia glauca* is consistent with the $2n = 24$ reported by De Wet (1954a) and Sokolovskaya & Probatova (1978) for *C. forskalii* (Vahl) Trin., as well as with the prevalent base number $x = 6$ for the tribe (Davidse, 1988).

TRIBE AVENEAE

De Wet (1958) reported a Transvaal population of *Agrostis lachnantha* to be tetraploid with $2n = 28$, but our sample had $n = 21$ (Fig. 5) and is thus hexaploid. Meiosis in *Helictotrichon turgidulum* ($n = 14$) was slightly irregular with the common occurrence of a single quadrivalent. All other chromosomes paired as bivalents.

TRIBE PANICEAE

Brachiaria nigropedata has been reported as diploid from South Africa (De Wet, 1954b; De Wet & Anderson, 1956) and tetraploid from Zimbabwe (Moffett & Hurcombe, 1949). We now add an octoploid count ($n = 36$) based on our analysis of a Transvaal population (Fig. 6).

Echinochloa haploclada has up to now been known as a diploid with $2n = 18$ from Tanzania (Tateoka, 1965) and as diploid (Malik & Tripathi, 1969) and tetraploid ($2n = 36$) from Kenya (Yabuno, 1966). We confirmed the diploid number for a Transvaal population and also found two nearby populations to be hexaploid ($n = 27$; Fig. 8). As presently circumscribed, *E. haploclada* is morphologically variable, and broadly based cytotaxonomic studies may help interpret this variation. Since diploids have never been found outside Africa in *Echinochloa*, Yabuno (1973) considered Africa to be one of the centers of origin for the genus. Our results strengthen this interpretation.

Spies & Du Plessis (1988) reported *Panicum stapfianum* as tetraploid ($n = 18$) from a population in the southern Cape Province, whereas we determined a northern population to be diploid ($n = 9$; Fig. 11).

Pennisetum villosum, a native of northern Africa, now widely naturalized in the tropics and subtropics, has been reported as a eudiploid to euhexaploid. Bridges and fragments were observed at anaphase I in the hexaploid ($n = 27$) plant that we examined. The occurrence of triploids, pentaploids, and hexaploids with irregular meiosis suggests the likelihood of apomixis in this species.

CONCLUSIONS

The basic chromosome numbers calculated for all the genera sampled in this study agree with those previously reported. Aneuploid numbers turned up in seven species.

Based on this report and chromosome numbers previously published for South African grasses, ploidy levels were determined for all the species included in this study from any part of their distributional range. On this basis 24 species (53%) of the 45 are polyploid in some part of their range. This is somewhat on the low side for grasses in general since most estimates for polyploidy among grasses are higher than 60% (Davidse et al., 1986). Analyzing this further, 47% of the species we studied are known only as diploids, 24% only as polyploids, and 29% as both diploids and polyploids. Although this sample is small (7% of the 895 species listed by Gibbs Russell et al., 1985) and may therefore not be very representative of the southern African grass flora, the percentages of species only known as diploids and only as polyploids are the reverse of that found in the Zimbabwean grass flora (Davidse et al., 1986). Whether this represents a real geographical trend or is random variation awaits further intensive sampling of the rich African grass flora.

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A PRELIMINARY LIST OF THE MOIST FOREST ANGIOSPERM FLORA OF MWANIHANA FOREST RESERVE, TANZANIA[1]

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ABSTRACT

A preliminary survey of the Mwanihana Forest Reserve, Tanzania, has yielded 440 angiosperm species. These are listed systematically, and by habitat and habit. The forests are rich in species of restricted distribution, and have affinities to the Guineo-Congolian forests of western Africa.

The Mwanihana Forest Reserve has been the focus of biological study since the discovery of a new taxon of the primate *Cercocebus galeritus* there in 1979 (Homewood & Rodgers, 1981), which prompted a proposal for the area to be given national park status (Rodgers & Homewood, 1982a). In the course of further study, a new species of sunbird (*Nectarinia rufipennis*) has been recorded from the forest (Jensen, 1983), and more than 40 new species of plants have been found. These include *Seychellaria africana*, which represents the first record of the family Triuridaceae from East Africa, and new species in the genera *Uvariopsis* and *Omphalocarpum*, which were not previously known from eastern Africa.

The following account is the result of botanical exploration of the forest in 1984 as part of a National Geographic Society expedition to the area in collaboration with the World Wildlife Fund Tanzania Forest Habitat Evaluation Project. Other aspects of the botany of the forest have been treated elsewhere (Lovett & Thomas, 1986).

The main area of study was the forest on the steep east-facing escarpment slopes above Sanje village at latitude 7°50′S and longitude 36°55′E. These slopes are the eastern edge of the Gologolo Mountains, which are the northern end of the Uzungwa range. In the study area the continuous altitudinal range of the forest is from 450 m to 1,760 m, but it is greater elsewhere on the escarpment. The rainfall is approximately 2,000–2,500 mm a year, with one wet season from November to May, when on average more than 100 mm of rain a month is received. There is a four-month dry season from July to October, when each month receives 50 mm of rain on average, and months of no rain are frequent. At higher altitudes there is a rich epiphytic bryophyte cover, indicating that a mist effect may be important in the water balance. The escarpment is dissected by steep-sided valleys separated by sharp ridge tops. The ridge tops are exposed, and so species normally occurring outside the forest habitat can be found within it. Some of the valley bottoms are flat, though nowhere particularly broad, and it is here that the forest is best developed. Elephant damage is common in the higher altitudes, and buffaloes are also present. Timber is being extracted by pit sawing, and in some areas there is considerable disturbance.

The angiosperm species recorded in the forest are arranged below according to habitat, habit, and in a systematic list. The habitat is divided into four types. The first three—Zanzibar–Inhambane Lowland Forest, Zanzibar–Inhambane Transitional Forest, and Afromontane Rain Forest—correspond to White's (1983) phytogeographic vegetation classification. The fourth division, Ridge Top Forest, is a specific vegetation type of restricted extent,

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being the highest ridge investigated in this study. This habitat is treated separately, as there are a number of species found only there, and it indicates which species of the Afromontane Rain Forest tend towards areas of greater exposure. The systematic list is divided into dicotyledons and monocotyledons, with families arranged alphabetically. Species and genera are arranged alphabetically within the families.

The list of species is far from complete, particularly for herbaceous and shrubby species. Many of the large trees were identified from sterile material gathered during the course of a quantitative ecological survey, and the determinations are included here because the canopy species are not often collected.

SPECIES ARRANGED ACCORDING TO HABITAT AND HABIT

The habitats follow the phytogeographical definitions given by White (1983) with the exception of Ridge Top Forest. Each habitat is given an altitudinal range and a short description of forest structure. The habit of each species is self-explanatory, except that it should be noted that a tree is a single-stemmed woody plant 10 m tall or at least 20 cm in diameter at breast height. The species are arranged alphabetically.

ZANZIBAR–INHAMBANE LOWLAND FOREST

Altitudinal range 450–750 m, canopy height 25–30 m with emergents to 40 m tall. Middle and shrub layer well developed. Herb layer sparse except in disturbed areas, where it is dominated by *Olyra latifolia.*

TREES: *Afrosersalisia cerasifera, Albizia adianthifolia, A. glaberrima* var. *glabrescens, A. zimmermannii, Allophylus melliodorus, Angylocalyx braunii, Aningeria pseudoracemosa, Anthocleista grandifolia, Antiaris toxicaria, Baphia semseiana, Bequaertiodendron natalense, Brachystegia microphylla, Calycosiphonia spathicalyx, Campylospermum sacleuxii, Casearia battiscombei, C. ?runssorica, Celtis durandii, Chaetacme aristata, Chionanthus mildbraedii, Craibia brevicaudata* subsp. *brevicaudata, Croton macrostachyus, C.* cf. *megalocarpoides, Dialium holtzii, Dichapetalum stuhlmannii, Diospyros brucei, D. mespiliformis, D. zombensis, Dracaena usambarensis, Drypetes natalensis, Elaeis guineensis, Enantia kummeriae, Erythrophleum suaveolens, Ficus cyathistipula* subsp. *cyathistipula, F. kirkii, F. lutea, F. quibeba, F. sur, F. thonningii, Filicium decipiens, Funtumia africana, Garcinia buchananii, Haplocoeliopsis africana, Haplocoelum foliolosum, Harungana madagascariensis, Homalium longistylum, Inhambanella henriquesii, Khaya nyasica, Lagynias pallidiflora, Lecaniodiscus fraxinifolius, Lettowianthus stellatus, Ludia mauritiana, Macaranga capensis* var. *capensis, Malacantha alnifolia, Milicia excelsa, Monodora grandidieri, Newtonia paucijuga, Odyendea zimmermannii, Pachystela brevipes, Paramacrolobium coeruleum, Parinari excelsa, Parkia filicoidea, Phyllanthus inflatus, Placodiscus* aff. *amaniensis, Pteleopsis myrtifolia, Pterocarpus milbraedii* subsp. *usambarensis, Rhodognaphalon schumannianum, Ricinodendron heudelotii, Rothmannia fischeri* subsp. *fischeri, R. manganjae, Sapium ellipticum, Schefflerodendron usambarense, Sorindeia madagascariensis, Stereospermum kunthianum, Suregada zanzibariensis, Tabernaemontana pachysiphon, Terminalia sambesiaca, Treculia africana, Trichoscypha ulugurensis, Trilepisium madagascariense, Uvariodendron gorgonis, Vangueriopsis longiflora, Vitellariopsis cuneata, Ziziphus pubescens.*

SMALL TREES AND SHRUBS: *Achyrospermum carvalhi, Allophylus pervillei, Campylospermum sacleuxii, Carvalhoa campanulata, Chytranthus prieurianus* subsp. *longiflorus, Clerodendrum capitatum* var. *capitatum, Cremaspora triflora* subsp. *confluens, Crotonogynopsis usambarica, Didymosalpinx norae, Dorstenia kameruniana, Ixora tanzaniensis, Justicia interrupta, Leptactina platyphylla, Maytenus undata, Memecylon* aff. *myrtilliodes, Olax gambecola, Pavetta ?mzeleziensis, P. stenosepala* subsp. *kisarawensis, Pleioceras orientale, Psychotria schliebenii, Psydrax livida, Rhus natalensis, Rinorea arborea, R. ferruginea, R. subintegrifolia, Sclerochiton obtusisepalus, Sloetiopsis usambarensis, Tarenna pavettiodes* subsp. *affinis, Tricalysia pallens.*

LIANES AND CLIMBERS: *Cissus producta, Cnestis confertiflora, Culcasia orientalis, Entada pursaetha, Oncinotis tenuiloba, Rhoicissus revoilii, Salacia lovettii, Strychnos angolensis, Tetracera* cf. *litoralis.*

HERBS: *Aeolanthus holstii, Begonia wakefieldii, Brillantaisia madagascariensis, Bulbophyllum concatenatum, Cheirostylis lepida, Chlorophytum sparsiflorum, Coelachne africana, Crassocephalum crepidiodes, Diodia sarmentosa, Disperis uzungwae, Geophila obvallata* subsp. *iodes,* *Habenaria trilobulata, Impatiens joachimii, I. walleriana, Justicia glabra, J. interrupta, Lobelia cymbalariodes, L. inconspicua, Marantochloa leucantha, Mellera lobulata, Oldenlandia affinis, O. corymbosa* var. *caespitosa, Olyra latifolia, Pentas longituba, Phaulopsis imbricata, Pseuderanthemum tunicatum, Puelia olyriformis, Saintpaulia ionantha, Scadoxus multiflorus, Scleria isostephana, S. racemosa, Sclerochiton obtusisepalus, Sida urens, Solanecio angulatus, Streptocarpus glandulosissimus, Utricularia striatula.*

ZANZIBAR–INHAMBANE TRANSITIONAL RAIN FOREST

Altitudinal range 750–1,200 m. Canopy height 25–30 m with emergents to 40 m tall. Taller trees are found in the valley bottoms than on the ridge tops. Middle and shrub layer well developed. Herb layer sparse except in disturbed areas, where it is dominated by a dense growth of Zingiberaceae and Piperaceae.

TREES: *Afrosersalisia cerasifera, Aidia micrantha* var. *msonju, Albizia adianthifolia, A. gummifera, Allanblackia stuhlmannii, Aningeria pseudoracemosa, Anisophylla obtusifolia, Annonaceae* gen. nov., *Anthocleista grandifolia, Antiaris toxicaria, Antidesma vogelianum, Beilschmiedia kweo, Cassia angolensis, Cassipourea gummiflua, Celtis africana, Cephalosphaera usambarensis, Chrysophyllum gorungosanum, C.* cf. *lanceolatum, Cleistanthus polystachyus, Cola uloloma, Croton sylvaticus, Dalbergia boehmii* subsp. *boehmii, Dialium holtzii, Diospyros amaniensis, D.* cf. *troupinii, Dracaena usambarensis, Drypetes* cf. *arguta, D. reticulata, D.* cf. *roxburghii, D. usambarica* var. *trichogyna, Eugenia capensis, Funtumia africana, Garcinia volkensii, Glenniea africana, Grewia* cf. *barombiensis, Heinsenia diervilleoides, Homalium longistylum, Isolona hexaloba, Ixora scheffleri, Lagynias rufescens* subsp. *angustilobus, Leptactina platyphylla, Macaranga capensis* var. *capensis, Maesa lanceolata, Maranthes goetzeniana, Maytenus acuminata, Memecylon ?brenanii, Memecylon* sp. nov., *Mesogyne insignis, Milicia excelsa, Milletia ?elongistyla, Mimusops aedificatoria, Myrianthus holstii, Newtonia buchananii, Ochna holstii, Octoknema orientalis, Odyendea zimmermannii, Omphalocarpum* sp. nov., *Pancovia golungensis, Parinari excelsa, Parkia filicoidea, Phyllanthus inflatus, Polyceratocarpus scheffleri, Porterandia penduliflora, Rawsonia lucida, Rothmannia urcelliformis, Sapium ellipticum, Sibangea pleioneura, Sorindeia madagascariensis, Strombosia scheffleri, Syzygium guineense* subsp. *afromontanum, Tabernaemontana pachysiphon, Tarenna pavettoides* subsp. *affinis, Trichilia dregeana, Trichoscypha ulugurensis, Trilepisium madagascariense, Uapaca paludosa, Vangueriopsis longiflora, Xylopia aethiopica, X. parvifolia, Xymalos monospora, Zanha golungensis.*

SMALL TREES AND SHRUBS: *Acalypha psilostachya* var. *psilostachya, Alchornea laxiflora, Allophylus pervillei, Baissea* sp., *Brachystephanus africanus, Campylospermum reticulatum, Carpolobia* cf. *goetzei, Chassalia discolor, Clausena anisata, Dicranolepis usambarica, Dracaena laxissima, Erythrococca polyandra, Lagynias rufescens* subsp. *angustiloba, Lasianthus* sp. nov., *Leptonychia usambarensis, Lobelia longisepala, Mostuea brunonis* var. *brunonis, Ormocarpum* sp. nov., *Oxyanthus pyriformis* subsp. *tanganyikensis, O. speciosus* subsp. *stenocarpus, Pancovia holtzii, Pauridiantha* sp. nov., *Pavetta* sp., *Piper capense, P. umbellatum, Psychotria lauracea, P. schliebenii, P. tanganyicensis* var. *ferruginea, Pyrostria* sp. nov., *Rauvolfia mannii, Rhus longipes, Rinorea ferruginea, R. ilicifolia* var. *amplexicaulis, R. subintegrifolia, Schizozygia coffaeoides, Tricalysia pallens, T.* sp. nov.

LIANES AND CLIMBERS: *Agelaea heterophylla, Baissea myrtifolia, Culcasia falcifolia, Keetia venosa, Monanthotaxis buchananii, Salacia lovettii, S. madagascariensis, Tetracera* cf. *litoralis, Uncaria africana* var. *africana, Uvaria tanzaniae.*

HERBS: *Alectra kirkii, Begonia oxyloba* var. *kummeriae, Cheirostylis lepida, Costus subbiflorus, Dorstenia tayloriana* var. *laikipiensis, D. warneckei, Geniosporum africanum, Impatiens confusa* subsp. *longicornu, Isoglossa lactea, Justicia* aff. *nyassana, J. pseudorungia, Leptaspis cochleata, Lobelia baumannii, L. inconspicua, Peperomia molleri, P. rotundifolia, Plectranthus* sp. = *Schlieben 4215, Pollia condensata, Rungia* sp. ?nov., *Solenostemon* sp. = *Mwasumbi 2720, Sphaerostephanos arbuscula* subsp. *africanus, Stenandriopsis warneckei, Streptocarpus caulescens* var. *pallescens, Utricularia livida.*

HEMIPARASITES: *Englerina inaequilatera.*

AFROMONTANE RAIN FOREST

For ease of data presentation, Afromontane Rain Forest is taken here to include the forest type defined as Afromontane Undifferentiated Forest by White (1983). Altitudinal range 1,200–1,700 m. In valleys and sheltered areas canopy height 25–30 m with emergents to 35 m tall. On ridges and exposed sites canopy height 15–25 m. Middle and shrub layers well developed in tall forest, middle layer not pronounced in exposed forest. Herb layer sparse in tall forest, dominated by Acanthaceae and Gramineae in more open areas.

TREES: *Agauria salicifolia* var. *pyrifolia, Albizia gummifera, Allanblackia stuhlmannii, A. ulugurensis, Alsodeiopsis schumannii, Aphloia theiformis, Beilschmiedia kweo, Bequaertiodendron magalismontanum, Bersama abyssinica, Brachylaena huillensis, Bridelia brideliifolia, Caloncoba welwitschii, Canthium captum, Casearia battiscombei, Cassipourea gummiflua, C. malosana, Chrysophyllum gorungosanum, Cleistanthus polystachyus, Coffea mongensis, Cola greenwayi, Craibia brevicaudata* subsp. *brevicaudata, Craterispermum longipedunculatum, Cryptocarya liebertiana, Diospyros amaniensis, Drypetes* cf. *arguta, Faurea saligna, Ficalhoa laurifolia, Garcinia kingaensis, G. volkensii, Heinsenia diervilleoides, Hirtella megacarpa, Isoberlinia scheffleri, Isolona hexaloba, Ixora scheffleri* subsp. *scheffleri, Lasiodiscus usambarensis* var. *usambarensis, Macaranga capensis* var. *kilimandscharica, Maesa lanceolata, Maranthes goetziana, Maytenus acuminata, Memecylon ?brenanii, M.* aff. *semsei, Myrianthus holstii, Myrica salicifolia, Mystroxylon aethiopicum, Newtonia buchananii, Ochna holstii, O. kenyensis, Ocotea usambarensis, Olea capensis, Olinia rochetiana, Ouratea schusteri, Parinari excelsa, Pauridiantha paucinervis* subsp. *holstii, Phoenix reclinata, Polyceratocarpus scheffleri, Polyscias fulva, Psychotria* aff. *trichoclada, Psydrax parviflora* subsp. *rubrocostata, Rapanea melanophloeos, Rawsonia reticulata, Schrebera alata, Strombosia scheffleri, Strychnos mellodora, S. mitis, Syzygium cordatum, S. guineense* subsp. *afromontanum, S. masukuense, Trichocladus goetzei, Trichoscyphya ulugurensis, Uvariodendron* sp. nov., *Uvariopsis bisexualis, Vepris stolzii, Xylopia aethiopica, Xymalos monospora, Zanha golungensis, Zanthoxylum* sp.

SMALL TREES AND SHRUBS: *Acanthopale pubescens, Aidia micrantha* var. *msonju, Allophylus macrobotrys, Apodytes dimidiata* subsp. *acutifolia, Bertiera pauloi, Brillantaisia nyanzarum, Casearia gladiiformis, Chassalia parvifolia, Clutia abyssinica* var. *abyssinica, Coffea mufindiensis, Craterispermum longipedunculatum, Crotalaria unicella, Crotonogynopsis usambarica, Dissotis princeps* var. *princeps, Erythrococca sanjensis, E. ulugurensis, Garcinia volkensii, Isoglossa bracteosa, Lasianthus kilimandscharicus* subsp. *kilimandscharicus, L. peduncularis, Lasiodiscus usambarensis* var. *usambarensis, Leptonychia usambarensis, Maytenus mossambicensis* subsp. *mossambicensis, M. undata, Memecylon* aff. *amaniense, Memecylon* sp. nov., *Micrococca* cf. *holstii, Mimulopsis arborescens, M. kilimandscharica, Pauridiantha paucinervis* subsp. *holstii, P.* sp. nov., *Pavetta lynesii, P. mshigeniana, P. nitidissima, P. stenosepala* subsp. *kisarawensis, Peddiea polyantha, Pseuderanthemum campylosiphon, Psychotria cryptogrammata, P. faucicola, P. goetzei, P. megalopus, P. zombamontana, P.* sp. nov., *Rauvolfia mannii, Rinorea arborea, Rytigynia caudatissima, R. hirsutiflora, R. lichenoxenos* subsp. *glabrituba, Sclerochiton obtusisepalus, Sericanthe odoratissima* var. *ulugurensis, Solanum* aff. *schumannianum, Strychnos myrtoides, Tarenna uzungwaensis, Teclea nobilis, Tricalysia pallens, Trichilia* sp. nov., *Turrea holstii, Uvariopsis* sp. ?nov., *Xymalos monospora.*

LIANES AND CLIMBERS: *Asparagus asparagoides, Embelia schimperi, Schefflera myriantha, Tiliacora funifera.*

HERBS: *Aframomum laxiflorum, Alectra kirkii, Anisosepalum humbertii, Ardisiandra sibthorpioides, Begonia* sp. ?nov., *Bulbophyllum* cf. *imbricatum, Cheirostylis lepida, Cincinnobotrys oreophila, Cyperus pseudoleptocladus, Disperis elaphoceras, Dissotis polyantha, Dorstenia denticulata, D. holstii, D. schliebenii, Gladiolus rupicola, Gymnosiphon usambaricus, Impatiens joachimii, I. kentrodonta, I. rubromaculata* subsp. nov., *I.* sp. nov. aff. *rubromaculata, Isoglossa lactea, Justicia pseudorungia, Liparis* sp. ?nov., *Lobelia baumannii, Medinilla engleri, Oldenlandia rupicola, Plectranthus* sp., *Polystachya ulugurensis, Saintpauliopsis lebrunii, Sclerochiton obtusisepalus, Seychellaria africana, Solenostemon* sp., *Streptocarpus glandulosissimus.*

HEMIPARASITES: *Englerina inaequilatera.*

RIDGE TOP FOREST

Altitude 1,760 m. Canopy height 3–6 m. Middle layer absent, the shrub layer composed of many small-diameter poles when under the canopy. Herb layer sparse under canopy, in open areas domi-

TABLE 1. *Taxa recently described from Mwanihana Forest Reserve.*

Disperis elaphoceras Verdc.
D. uzungwae Verdc.
Drypetes usambarica (Pax) Hutch. var. *trichogyna* A. R.-Sm.
Erythrococca sanjensis A. R.-Sm.
Lagynias rufescens (E. A. Bruce) subsp. *angustiloba* Verdc.
Pavetta nitidissima Bridson
Rytigynia caudatissima Verdc.
R. hirsutiflora Verdc.
Salacia lovettii Halle & B. Mathew
Seychellaria africana Vollesen
Tarenna uzungwaensis Bridson
Uvaria tanzaniae Verdc.
Uvariopsis bisexualis Verdc.

nated by Gramineae and Pteridophyta. Rich epiphytic bryophyte cover.

TREES: *Afrosersalisia* sp. ?nov., *Allanblackia ulugurensis, Aphloia theiformis, Apodytes dimidiata* subsp. *acutifolia, Bequaertiodendron magalismontanum, Cryptocarya liebertiana, Diospyros whyteana, Faurea saligna, Garcinia kingaensis, Isoberlinia scheffleri, Maytenus acuminata, Newtonia buchananii, Ochna holstii, Ocotea kenyensis, O. usambarensis, Olea capensis, Olinia rochetiana, Rapanea melanophloeos, Strychnos mitis, Syzygium cordatum, Ternstroemia polypetala* var. ?nov., *Trichocladus goetzei.*

SMALL TREES AND SHRUBS: *Agauria salicifolia* var. *pyrifolia, Clutia abyssinica* var. *abyssinica, Inula stuhlmannii, Pauridiantha paucinervis* subsp. *holstii, Phyllanthus hutchinsonianus.*

LIANES AND CLIMBERS: *Schefflera myriantha.*

HERBS: *Cryptotaenia calycina, Cynorkis anacamptoides, C. buchwaldiana* subsp. *braunii, C. pleistadenia, Polystachya cultriformis, P. ?goetzeana, P. melantha, P. transvaalensis, Saintpauliopsis lebrunii, Solanecio epidendricus, Stolzia leedalii, S. nyassana, Streptocarpus caulescens* var. *pallescens, Tridactyle* sp. nov., *T.* sp. nov. = *Leedal 6138.*

HEMIPARASITES: *Thesium triflorum.*

DISCUSSION

The moist forests of eastern Tanzania and southeastern Kenya are well known for the high number of species that are found only in that area (Lovett, 1988; Rodgers & Homewood, 1982b). The Mwanihana Forest Reserve is no exception, and a number of new species have been described recently from the locality (Table 1). Many other species are inadequately known and more material is needed (Table 2). Undoubtedly further exploration will reveal still more novelties.

TABLE 2. *Taxa in the Mwanihana Forest Reserve currently inadequately known to be described, or taxonomic research not yet completed. The following abbreviations are used to refer to collectors: DT = Duncan Thomas, DB = Diane Bridson, RP = Roger Polhill, JL = Jon Lovett. sn =* sine numero *sterile collections from the ecological survey.*

Afrosersalisia sp. ?nov., JL sn
Annonaceae ?gen. nov. = Ede 65, JL sn
Begonia sp. ?nov., DT 3797
Bulbophyllum cf. *imbricatum,* DT 3876
Carpolobia cf. *goetzei,* DT 3758
Diospyros cf. *troupinii,* JL sn
Drypetes aff. *arguta,* DT 3913
Grewia cf. *barombiensis,* DT 3747
Impatiens joachimii var. ?nov., DB 602, DT 3798, JL 271
I. aff. *rubromaculata,* DT 3846
Justicia aff. *nyassana,* DB 644
Lasianthus sp. nov., DB 650, DT 3759, JL 235
Liparis sp. ?nov., DT 3874
Memecylon aff. *amaniense,* DT 3850
M. aff. *brenanii,* DT 3760, DT 3916
M. aff. *myrtilloides,* RP 5118
M. aff. *semsei,* DT 3702
M. sp. nov., DT 3773
M. sp. nov., JL 215
Omphalocarpum sp. nov., DT 3652
Ormocarpum sp. nov., JL 384
Pauridiantha sp. nov., DB 648, DT 3680B, DT 3778, DT 3826, DT 3841
Pavetta sp. nov., JL 291
Placodiscus aff. *amaniensis,* DT 3724
Plectranthus sp., DT 3823
P. sp. = Schlieben 4215, DB 640
Psychotria aff. *trichoclada,* DT 3836
P. sp. nov., JL 294
Rawsonia aff. *lucida,* DT 3638, DT 3966
Rinorea aff. *arborea,* DT 3894
Rungia sp. ?nov., DT 3625
Solanum aff. *schumannianum,* DT 3896
Solenostemon sp. = Mwasumbi 2720, DB 641, DT 3771
Tricalysia sp. nov., DB 647
Trichilia sp. nov,. JL 232
Tridactyle sp. nov., DT 3763A
T. sp. nov. = Leedal 6138, DT 3764
Uvariodendron sp. nov., JL 222
Uvariopsis sp. nov., DT 3921

The occurrence of species in the Mwanihana Reserve that are only found on other similar mountains demonstrates that the forests of the ancient crystalline mountains of eastern Tanzania form a distinct floristic unit. Examples include *Anglyocalyx braunii, Aningeria pseudoracemosa, Anisophyllea obtusifolia, Cephalosphaera usambarensis, Allanblackia stuhlmannii, Beilschmiedia kweo, Isoberlinia scheffleri, Newtonia pau-*

cijuga, *Polyceratocarpus scheffleri*, and *Saintpaulia ionantha*.

The forests also have links with west and central Africa. For example, the species *Cincinnobotrys oreophila*, *Crotonogynopsis usambarica*, *Isolona hexaloba*, *Olax gambecola*, *Puelia olyriformis*, *Rinorea subintegrifolia*, *Saintpauliopsis lebrunii*, *Schefflerodendron usambarense*, and *Uapaca paludosa* are also found west of the arid corridor that separates the moist forests of eastern Tanzania from the Guineo-Congolian region. At a generic level *Enantia kummeriae*, *Uvariopsis bisexualis*, *Octoknema orientalis*, and *Polyceratocarpus scheffleri* are all restricted to eastern Tanzania but are of predominantly Guineo-Congolian genera.

Links to forests in the south are found in species such as *Diospyros whyteana* and *Syzygium masukuense*, while affinities with Madagascar and the Indian Ocean islands are found in the genera *Aphloia*, *Ludia*, and *Seychellaria*.

The reason for the high level of endemism in the eastern Tanzanian moist forests on ancient crystalline mountains is not difficult to explain. The mountains have probably been in existence since the Cretaceous (Sowerbutts, 1972), and Africa reached its present latitudinal position by the Oligocene (Axelrod & Raven, 1978). The area would therefore have been under the influence of a moist tropical climate for at least 40 million years. During the last 500,000 years there have been periods of pronounced aridity in continental Africa that correspond to glacial maxima (Imbrie & Imbrie, 1980; Pokras & Mix, 1987). During the last glacial maximum (18,000 years B.P.), the temperature of the equatorial Atlantic dropped 4–5°C (van Zinderen Bakker, 1982), whereas that of the Indian Ocean in the area of eastern Tanzania was similar to that at present (Prell et al., 1980). This suggests that during the last glacial maximum the climate of eastern Tanzania was similar to that at present, whereas west and central Africa went through a period of pronounced aridity with a corresponding reduction of forest area (Hamilton, 1982). If this situation reflects that of earlier glacial maxima, then the forests of eastern Tanzania have been remarkably stable in comparison with most of the Guineo-Congolian forests.

Consequently the high level of endemism can be explained by either the extinction of species over much of their range during periods of aridity but their survival in the eastern Tanzanian forests, or by evolution by isolation in the climatically stable eastern forests.

More difficult to explain are the affinities of the eastern Tanzanian forests with the Guineo-Congolian region and Madagascar. It is unclear how far these are the results of long-distance dispersal or relicts of continuous forest links.

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APPENDIX I

Systematic list of collections. The following abbreviations are used to refer to collectors: DT = Duncan Thomas, DB = Diane Bridson, RP = Roger Polhill, JL = Jon Lovett. sn = *sine numero* sterile collections from the ecological survey.

ANGIOSPERMAE, DICOTYLEDONS

ACANTHACEAE

Acanthopale pubescens C. B. Cl., RP 5147
Anisosepalum humbertii (Mildbr.) E. Hossain, DT 3825, JL 299
Brachystephanus africanus S. Moore, DT 3684

Brillantaisia madagascariensis Lindau, DB 610
B. nyanzarum Burkhill, DT 3790
Isoglossa bracteosa Mildbr., RP 5146
I. lactea Lindau s.l., DB 643, DT 3839
I. sp. ?nov., JL 194
Justicia glabra Roxb., JL 281
J. interrupta (Lindau) C. B. Cl., DT 3664, RP 5124
J. aff. *nyassana* Lindau, DB 644
J. pseudorungia Lindau, DB 646, JL 316
Mellera lobulata S. Moore, DB 592, RP 5156
Mimulopsis arborescens C. B. Cl., DT 3789
M. kilimandscharica Lindau, RP 5149
M. solmsii Schweinf., RP 5148
Phaulopsis imbricata (Forsskal) Sweet, DB 593
Pseuderanthemum campylosiphon Mildbr., RP 5145
P. tunicatum (Afzl.) Milne-Redh., DT 3671, JL 186, RP 5115
Rungia sp. ?nov., DT 3625
Saintpauliopsis lebrunii Staner, DT 3805, DT 3898, JL 310
Sclerochiton obtusisepalus C. B. Cl., DB 591, DB 618, DT 3674, DT 3905, JL 315, RP 5114
Stenandariopsis warneckei (S. Moore) Napper, JL 274
Whitfieldia elongata (P. Beauv.) C. B. Cl., DT 3663, RP 5120

ANACARDIACEAE

Rhus longipes Engl., DT 3653, DT 3953
R. natalensis Krauss, DT 3669
Sorindeia madagascariensis DC., DB 639, DB 639A, DT 3610, DT 3639, JL 190
Trichoscypha ulugurensis Mildbr., JL 180

ANNONACEAE

Enantia kummeriae Engl. & Diels, JL sn
Isolona hexaloba (Pierre) Engl. & Diels, RP 5143
I. sp., DT 3899
Lettowianthus stellatus Diels, DT 3753, DT 3937
Monanthotaxis buchananii (Engl.) Verdc., DT 3624, DT 3644
Monodora grandidieri Baill., JL sn
Polyceratocarpus scheffleri Engl. & Diels, DT 3656, DT 3698
Uvaria tanzaniae Verdc., DT 3641
Uvariodendron gorgonis Verdc., JL sn
U. sp. nov., JL 222
Uvariopsis bisexualis Verdc., DT 3921, JL 233
Xylopia aethiopica (Dunal) A. Rich., JL sn
X. parviflora (A. Rich.) Benth., JL sn
Annonaceae gen. nov. = Ede 65, JL sn

APOCYNACEAE

Baissea myrtifolia (Benth.) Pichon, DT 3645
Carvalhoa campanulata K. Schum., JL 183
Funtumia africana (Benth.) Stapf, DT 3741
Oncinotis tenuiloba Stapf, DT 3718
Pleioceras orientale Vollesen, JL 179
Rauvolfia mannii Stapf, DT 3791, JL 212
Schizozygia coffaeoides Baill., DB 645, DT 3754
Strophanthus petersianus Klotzsch, DB sn
Tabernaemontana pachysiphon Stapf, JL 211

ARALIACEAE

Polyscias fulva (Hiern) Harms, JL sn
Schefflera myriantha (Baker) Drake, JL sn

BALSAMINACEAE

Impatiens confusa Grey-Wilson subsp. *longicornu* Grey-Wilson, DT 3618
I. joachimii G. M. Schulze var. ?nov., DB 602, DT 3798, JL 271
I. kentrodonta Gilg, DT 3672, DT 3772
I. rubromaculata Warb., subsp. nov., DT 3769
I. aff. *rubromaculata* Warb., DT 3846
I. walleriana Hook. f., DB 603

BEGONIACEAE

Begonia oxyloba Welw. var. *kummeriae* (Gilg) Irmscher, DT 3617
B. wakefieldii Gilg, JL 272
B. sp. ?nov., DT 3797

BIGNONIACEAE

Stereospermum kunthianum Cham., JL sn

BOMBACACEAE

Rhodognaphalon schumannium A. Robyns, JL sn

CELASTRACEAE

Maytenus acuminata (L. f.) Loess, DT 3643, DT 3810
M. mossambicensis (Klotzsch) Blakelock var. *mossambicensis*, DT 3903
M. undata (Thunb.) Blakelock, DB 601, DB 628, RP 5152, JL 187
Mystroxylon aethiopicum (Thunb.) Loes, DT 3879, DT 3902
Salacia erecta (G. Don) Walp., DB sn
S. lovettii Halle & B. Mathew, DB 638, DB 655, JL 216
S. madagascariensis (Lam.) DC., DT 3642

CHRYSOBALANACEAE

Hirtella megacarpa R. Graham, DT 3901
Maranthes goetzeniana (Engl.) Prance, JL sn
Parinari excelsa Sabine, JL sn

COMBRETACEAE

Pteleopsis myrtifolia (Laws.) Engl. & Diels, JL sn
Terminalia sambesica Engl. & Diels, DT 3719

COMMELINACEAE

Pollia condensata C. B. Cl., JL 279

COMPOSITAE

Brachylaena huillensis O. Hoffm., JL sn
Crassocephalum crepidioides (Benth.) S. Moore, DB 621
Inula stuhlmannii O. Hoffm., DT 3928
Solanecio angulatus (Vahl) C. Jeffrey, DB 620
S. epidendricus (O. Hoffm.) C. Jeffrey, DT 3840, DT 3847B

CONNARACEAE

Agelaea heterophylla Gilg, JL sn
Cnestis confertiflora Gilg, JL sn

DICHAPETALACEAE

Dichapetalum stuhlmannii Engl., DT 3728

DILLENIACEAE

Tetracera cf. *litoralis* Gilg, DB 594, DT 3632

EBENACEAE

Diospyros amaniensis Guerke, DT 3788
D. brucei F. White, JL sn
D. mespiliformis Hochst. ex A. DC., JL sn
D. cf. *troupinii* F. White, JL sn
D. whyteana (Hiern) F. White, DT 3927
D. zombensis (B. L. Burtt) F. White, JL sn

ERICACEAE

Agauria salicifolia (Lam.) Oliver var. *pyrifolia* (Pers.) Oliver, DT 3926, JL 3096

EUPHORBIACEAE

Acalypha psilostachya Hochst. ex A. Rich. var. *psilostachya*, DT 3690
Alchornea laxiflora (Benth.) Pax & K. Hoffm., DT 3636
Antidesma vogelianum Muell. Arg., DT 3752
Bridelia brideliifolia (Pax) Fedde, DT 3900
Cleistanthus polystachyus Hook. f. ex Planchon, JL sn
Clutia abyssinica Jaub. & Spach var. *abyssinica*, DT 3707, DT 3708, JL 300
Croton macrostachyus Hochst. ex Del., JL sn
C. cf. *megalocarpoides* Friis & M. Gilbert, DT 3727
C. sylvaticus Hochst. ex Krauss, DT 3756
Crotonogynopsis usambarica Pax, DT 3761, DT 3924, RP 5129
Drypetes natalensis (Harvey) Hutch., JL sn
D. reticulata Pax, JL sn
D. usambarica (Pax) Hutch. var. *trichogyna* A. R.-Sm., JL 219
D. ?arguta (Muell. Arg.) Hutch., DT 3913
D. cf. *roxburghii* (Wall.) Hurusawa, JL sn
Erythrococca polyandra (Pax & K. Hoffm.) Prain, DT 3751
E. sanjensis A. R.-Sm., DT 3677, DT 3774, DT 3775, DT 3782, DT 3783
E. ulugurensis A. R.-Sm., DT 3762, DT 3770
Macaranga capensis Baill. var. *capensis*, DT 3739
M. capensis Baill. var. *kilimandscharica* (Pax) Friis & M. Gilbert, JL sn
Micrococca cf. *holstii* (Pax) Prain, DT 3833
Phyllanthus hutchinsonianus S. Moore, DT 3803
P. inflatus Hutch., DT 3609, JL 181
Ricinodendron heudelotii (Baill.) Pierre ex Pax, JL sn
Sapium ellipticum (Hochst.) Pax, JL sn
Sibangea pleioneura A. R.-Sm., DT 3651, JL 221
Suregada zanzibariensis Baill., DT 3613
Uapaca paludosa Aubrév. & Léandri, JL sn

FLACOURTIACEAE

Aphloia theiformis (Vahl.) Benn., DT 3705
Caloncoba welwitschii (Oliver) Gilg, JL sn
Casearia battiscombei R. E. Fr., JL sn
C. gladiiformis Mast., DT 3776
C. ?runssorica Mildb., DT 3773, DT 3755
Homalium longistylum Mast., JL sn
Ludia mauritiana Gmelin, Dt 3936
Rawsonia lucida Harvey & Sonder, DT 3650
R. aff. *lucida* Harvey & Sonder, DT 3638, DT 3966
R. reticulata Gilg, DT 3835, JL 290

GESNERIACEAE

Saintpaulia ionantha H. Wendl., RP 5130
Streptocarpus caulescens Vatke var. *pallescens* Engl., DT 3620, DT 3847
S. glandulosissimus Engl., DB 604, DT 3848, RP 5155

GUTTIFERAE

Allanblackia stuhlmannii (Engl.) Engl., JL sn
A. ulugurensis Engl., JL sn
Garcinia buchananii Baker, JL sn
G. kingaensis Engl., DT 3853
G. volkensii Engl., DT 3649, DT 3912
Harungana madagascariensis Poiret, JL sn

HAMAMELIDACEAE

Trichocladus goetzei Engl., JL sn

ICACINACEAE

Alsodeiopsis schumannii (Engl.) Engl., DT 3915
Apodytes dimidiata E. Meyer ex Arn. subsp. *acutifolia* (Hochst. ex A. Rich.) Cuf., DT 3715, DT 3766

LABIATAE

Achyrospermum carvalhi Guerke, DB 598
Aeolanthus holstii Guerke s.l., DB 617
Geniosporum africanum P. Beauv., DB 635
Plectranthus sp., DT 3823
P. sp. = Schlieben 4215, DB 640
Solenostemon sp. ?= Mwasumbi 2720, DB 641, DT 3771

LAURACEAE

Beilschmiedia kweo (Mildbr.) A. Robyns & Wilczek, DT 3882
Cryptocarya liebertiana Engl., JL sn
Ocotea kenyensis (Chiov.) A. Robyns & Wilczek, DT 3907
O. usambarensis Engl., JL 301

LEGUMINOSAE

Caesalpinioideae

Brachystegia microphylla Harms, DT 3612
Cassia angolensis Hiern, JL sn
Dialium holtzii Harms, DT 3732, DT 3740
Erythrophleum suaveolens (Guill. & Perr.) Brenan, JL sn
Isoberlinia scheffleri (Harms) Greenway, JL sn
Paramacrolobium coeruleum (Taubert) Leonard, JL sn

Mimosoideae

Albizia adianthifolia (Schumach.) W. F. Wight, DT 3646
A. glaberrima (Schumach. & Thonn.) Benth. var. *glabrescens* (Oliver) Brenan, DT 3734
A. gummifera (J. Gmelin) C. A. Sm., DT 3735A, DT 3736
A. zimmermannii Harms, DT 3640, DT 3731
Entada pursaetha DC., JL sn
Newtonia buchananii (Baker) Gilb. & Bout., JL sn
N. paucijuga (Harms) Brenan, DT 3723
Parkia filicoidea Welw. ex Oliver, DT 3735

Papilionoideae

Angylocalyx braunii Harms, DT 3729
Baphia semseiana Brummitt, DT 3668
Craibia brevicaudata (Vatke) Dunn subsp. *brevicaudata*, DT 3730
Crotalaria unicella Lam., RP 5139
Dalbergia boehmii Taub. subsp. *boehmii*, DT 3623
Millettia ?elongatistyla Gillett, DT 3746
Ormocarpum sp. nov., JL 384
Pterocarpus mildbraedii Harms subsp. *usambarensis* (Verdc.) Polh., JL sn
Schefflerodendron usambarense Harms, JL sn

LENTIBULARIACEAE

Utricularia livida E. Meyer, DT 3648
U. striatula Sm., DB 605, RP 5121

LOBELIACEAE

Lobelia baumannii Engl., DB 642, DT 3804
L. cyambalarioides Engl., DB 606
L. inconspicua A. Rich., DB 607, DT 3621
L. longisepala Engl., DT 3616

LOGANIACEAE

Anthocleista grandiflora Gilg, JL sn
Mostuea brunonis Didr. var. *brunonis*, DT 3637
Strychnos angolensis Gilg, JL 276
S. mellodora S. Moore, JL sn
S. mitis S. Moore, JL sn
S. myrtoides Gilg & Busse, DT 3829

LORANTHACEAE

Englerina inaequilatera (Engl.) Balle ex Polh. & Wiens, DT 3830, JL 288, JL 299

MALVACEAE

Sida urens L., DB 633

MELASTOMATACEAE

Cincinnobotrys oreophila Gilg, DT 3877
Dissotis polyantha Gilg, DT 3794
D. princeps (Kunth.) Triana var. *princeps*, RP 5141
Medinilla ?engleri Gilg, DT 3832
Memecylon ?brenanii A. & R. Fernandes, DT 3760, DT 3916
M. aff. *amaniense* (Gilg) A. & R. Fernandes, DT 3850
M. aff. *myrtilloides* Markgraf, RP 5118
M. aff. *semsei* A. & R. Fernandes, DT 3702
M. sp. nov. DT 3773
M. sp. nov. JL 215

MELIACEAE

Khaya nyasica Stapf ex Baker f., JL sn
Trichilia dregeana Sonder, JL sn
T. sp. nov., JL 232
Turraea holstii Guerke, DT 3714

MELIANTHACEAE

Bersama abyssinica Fresen., JL sn

MENISPERMACEAE

Tiliacora funifera (Miers) Oliver, DT 3914

MONIMIACEAE

Xymalos monospora (Harvey) Baill., DT 3786, DT 3787, DT 3843

MORACEAE

Antiaris toxicaria Lesch., JL sn
Dorstenia denticulata A. Peter, RP 5151
D. holstii Engl., RP 5153
D. kameruniana Engl., RP 5119
D. schliebenii Mildbr., DT 3796
D. tayloriana Rendle var. *laikipiensis* (Rendle) Hijman, JL 213
D. warneckei Engl., DT 3660
Ficus cyathistipula Warb. subsp. *cyathistipula*, DT 3666
F. kirkii Hutch., JL sn
F. lutea Vahl, JL sn
F. quibeba Welw. ex Ficalho, JL 184
F. sur Forsskal, JL sn
F. thonningii Blume, JL sn
Mesogyne insignis Engl., JL 231
Milicia excelsa (Welw.) Berg, JL sn
Myrianthus holstii Engl., DT 3757
Sloetiopsis usambarensis Engl., DT 3670, DT 3726
Treculia africana Decne., JL sn
Trilepisium madagascariensis DC., JL sn

MYRICACEAE

Myrica salicifolia Hochst. ex A. Rich., JL sn

MYRISTICACEAE

Cephalosphaera usambarensis (Warb.) Warb., DT 3619

MYRSINACEAE

Embelia schimperi Vatke, JL sn
Maesa lanceolata Forsskal, DT 3897
Rapanea melanophloeos (L.) Mez, JL sn

MYRTACEAE

Eugenia capensis (Ecklon & Zeyher) Sonder, JL sn
Syzygium cordatum Hochst. ex Krauss, JL sn
S. guineense (Willd.) DC. subsp. *afromontanum* F. White, JL sn
S. masukuense (Baker) R. E. Fries, JL sn

OCHNACEAE

Campylospermum reticulatum (P. Beauv.) Farron, JL 214
C. sacleuxii (Tieghem) Farron, DT 3939, JL 217, RP 5122
Ochna holstii Engl., DT 3738, DT 3922
Ouratea schusteri Gilg ex Engl., DT 3834

OLACACEAE

Octoknema orientalis Mildbr., JL 287
Olax gambecola Baill., RP 5117
Strombosia scheffleri Engl., JL sn

OLEACEAE

Chionanthus mildbraedii (Gilg & Schellenb.) Stearn, RP 5123
Olea capensis L., JL sn
Schrebera alata (Hochst.) Welw., DT 3904

OLINIACEAE

Olinia rochetiana A. Juss., JL sn

PIPERACEAE

Peperomia molleri C. DC., DT 3692, RP 5142
P. rotundifolia (L.) Kunth., DT 3622
Piper capense L. f., JL sn
P. umbellatum L., JL 234

POLYGALACEAE

Carpolobia cf. *goetzei* Guerke, DT 3758

PRIMULACEAE

Ardisiandra sibthorpioides Hook. f., DT 3799

PROTEACEAE

Faurea saligna Harvey, DT 3703

RHAMNACEAE

Lasiodiscus usambarensis Engl. var. *usambarensis*, DT 3828
Ziziphus pubescens Oliver, JL sn

RHIZOPHORACEAE

Anisophyllea obtusifolia Engl. & Brehm., JL sn
Cassipourea gummiflua Tul., JL sn
C. malosana (Baker) Alston, JL sn

RUBIACEAE

Aidia micrantha (K. Schum.) F. White var. *msonju* (Krausse) Petit, DT 3679
Bertiera pauloi Verdc., DT 3842, DT 292
Calycosiphonia spathicalyx (K. Schum.) Robbrecht, DB 658, JL 269
Canthium captum Bullock, JL sn
Chassalia discolor K. Schum., JL 220
C. parviflora K. Schum., DT 3838
Coffea mongensis Bridson, JL sn
C. mufindiensis Hutch. ex Bridson, DT 3819, DT 3914A
Craterispermum longipedunculatum Verdc., DT 3784, DT 3827
Cremaspora triflora (Thonn.) K. Schum. subsp. *confluens* (K. Schum.) Verdc., DB 624
Didymosalpinx norae (Swynnerton) Keay, DB 623
Diodia sarmentosa Sm., DB 632
Geophila obvallata (Schumach.) F. Didr. subsp. *iodes* K. Schum., JL 275
Heinsenia diervilleoides K. Schum., DT 3822
Ixora scheffleri K. Schum. & K. Krausse subsp. *scheffleri*, DT 3852
I. tanzaniensis Bridson, DB 626, RP 5116
Keetia venosa (Oliver) Bridson, DT 3608
Lagynias pallidiflora Bullock, DB 612
L. rufescens (E. A. Bruce) Verdc. subsp. *angustiloba* Verdc., DB 649, JL 289
Lasianthus kilimandscharicus K. Schum. subsp. *kilimandscharicus*, JL sn
L. pedunculatis E. A. Bruce, DT 3777
L. sp. nov., DB 650, DT 3759, JL 235
Leptactina platyphylla (Hiern) Wernham, DB 653, DT 3721
Oldenlandia affinis (Roemer & Schultes) DC., DB 597
O. corymbosa L. var. *caespitosa* (Benth.) Verdc., DB 616
O. rupicola (Sonder) Kuntze, DT 3800
Oxyanthus pyriformis (Hochst.) Skeels subsp. *tanganyikensis* Bridson, DB 636, DT 3745
O. speciosus DC. subsp. *stenocarpus* (K. Schum.) Bridson, DB 651
Pauridiantha bridelioides Verdc., DB sn
P. paucinervis (Hiern) Bremek. subsp. *holstii* (K. Schum.) Verdc., DB 569, DT 3831
P. sp. nov., DB 648, DT 3680B, DT 3778, DT 3826, DT 3841
Pavetta lynesii Bridson, DT 3717, DT 3837
P. mshigeniana Bridson, DT 8678
P. nitidissima Bridson, DT 3851
P. stenosepala K. Schum. subsp. *kisarawensis* (Bremek.) Bridson, DB 599, JL 210, JL 308
P. ?mzeleziensis Bridson, DB 625
P. sp., JL 291
Pentas longituba K. Schum., DB 596
Porterandia penduliflora (K. Schum.) Keay, DT 3611
Psychotria cryptogrammata Petit, JL 227
P. faucicola K. Schum., DT 3844
P. goetzei (K. Schum.) Petit, DT 3716
P. lauracea (K. Schum.) Petit, DB 637
P. megalopus Verdc., DT 3910
P. meridiano-montana Petit var. *angustifolia* Petit, DT 3710
P. schliebenii Petit, DB 627
P. tanganyicensis Verdc. var. *ferruginea* Verdc., JL 278
P. aff. *trichoclada* Petit, DT 3836
P. sp., JL 294
Psydrax livida (Hiern) Bridson, DB 586, DB 587, DB 588
P. parviflora (Afz.) Bridson subsp. *rubrocostata* (Robyns) Bridson, JL sn
Pyrostria sp. nov., DT 3942
Rothmannia fischeri (K. Schum.) Bullock subsp. *fischeri*, JL 178
R. manganjae (Hiern) Keay, JL sn
R. urcelliformis (Schweinf. ex Hiern) Bullock ex Robyns, DT 3748
Rytigynia caudatissima Verdc., DT 3781
R. hirsutiflora Verdc., DT 3811
R. lichenoxenos (K. Schum.) A. Robyns subsp. *glabrituba* Verdc., DT 3779
R. pseudolongicaudata Verdc., DT 3780
Sericanthe odoratissima (K. Schum.) Robbrecht var. *ulugurensis* Robbrecht, DT 3680A, DT 3711
Tarenna pavettiodes (Harvey) Sim subsp. *affinis* (K. Schum.) Bridson, DB 629, DT 3614, DT 3750
T. uzungwaensis Bridson, DT 3785
Tricalysia pallens Hiern, DB 595, DB 595A, DB 600, DB 611, DB 630, DT 3607, DT 3615, DT 3712, DT 3737
T. sp. nov., DB 647
Uncaria africana G. Don var. *africana*, DT 3758A
Vangueriopsis longiflora Verdc., JL sn

RUTACEAE

Clausena anisata (Willd.) Benth., DT 3941
Teclea nobilis Del., DT 3906
Vepris stolzii Verdoorn, DT 3713
Zanthoxylum sp., JL sn

SANTALACEAE

Thesium triflorum Thunb., DT 3809, JL 309

SAPINDACEAE

Allophylus macrobotrys Gilg, DT 3792
A. melliodorus Gilg ex Radlk., JL sn
A. pervillei Blume, DB 656, DT 3635
Chytranthus prieurianus Baill. subsp. *longiflorus* (Verdc.) Halle, DT 3940, JL 189
Deinbollia sp., JL sn
Filicium decipiens (Wight & Arn.) Thw., JL sn
Glenniea africana (Radlk.) Leenh., DT 3749
Haplocoelopsis africana F. Davis in MS, JL sn
Haplocoelum foliolosum (Hiern) Bullock, JL sn
Lecaniodiscus fraxinifolius Baker, JL sn
Pancovia golungensis (Hiern) Excell & Mendonca, JL sn
P. holtzii Radlk., DT 3633
Placodiscus aff. *amaniensis* Radlk., DT 3724
Zanha golungensis Hiern, JL sn

SAPOTACEAE

Afrosersalisia cerasifera (Welw.) Aubrév., DT 3628
Afrosersalisia sp. ?nov., JL sn
Aningeria pseudoracemosa J. Hemsley, DT 3725
Bequaertiodendron magalismontanum (Sonder) Heine & J. Hemsley, JL sn
B. natalense (Sonder) Heine & J. Hemsley, DT 3606
Chrysophyllum gorungosanum Engl., JL sn
C. cf. *lanceolatum* (Bl.) DC., JL sn
Inhambanella henriquesii (Engl. & Warb.) Dubard, JL sn
Malacantha alnifolia (Baker) Pierre, JL sn
Mimusops aedificatoria Mildbr., DT 3845
Omphalocarpum sp. nov., DT 3652
Pachystela brevipes (Baker) Engl., JL sn
Vitellariopsis cuneata (Engl.) Aubrév., DT 3662

SCROPHULARIACEAE

Alectra kirkii Hemsley, DT 3631, RP 5140

SIMAROUBACEAE

Odyendea zimmermannii Engl., JL sn

SOLANACEAE

Solanum aff. *schumannianum* Dammer, DT 3896

STERCULIACEAE

Cola greenwayi Brenan, JL sn
C. uloloma Brenan, JL sn
Leptonychia usambarensis K. Schum., DT 3657, DT 3795

THEACEAE

Ficalhoa laurifolia Hiern, JL sn
Ternstroemia polypetala Melchior, var. ?nov., DT 3767

THYMELAEACEAE

Dicranolepis usambarica Gilg, JL sn
Peddiea polyantha Gilg, DT 3701

TILIACEAE

Grewia cf. *barombiensis* K. Schum., DT 3747

ULMACEAE

Celtis africana Burm. f., JL sn
C. durandii Engl., JL sn
Chaetacme aristata Planchon, JL sn

UMBELLIFERAE

Cryptotaenia calycina C. C. Townsend, DT 3806

VERBENACEAE

Clerodendrum capitatum Schum. & Thonn. var. *capitatum*, DB 631

VIOLACEAE

Rinorea arborea (Thouars) Baill., DB 654, DT 3665, JL 296
R. aff. *arborea* (Thouars) Baill., DT 3894
R. ferruginea Engl., DB 609, DB 622, DB 652, JL 185
R. ilicifolia (Welw. ex Oliver) Kuntze var. *amplexicaulis* Grey-Wilson, DT 3691
R. subintegrifolia (P. Beauv.) Kuntze, DT 3634, DT 3938, JL 223

VITACEAE

Cissus producta Afz., DB 614
Rhoicissus revoilii Planchon, DT 3720

ANGIOSPERMAE, MONOCOTYLEDONS

AGAVACEAE

Dracaena laxissima Engl., JL sn
D. usambarensis Engl., JL 181

AMARYLLIDACEAE

Scadoxus multiflorus (Martyn) Raf., JL sn

ARACEAE

Amorphophallus sp., JL sn
Callopsis volkensii Engl., Carmichael 127
Culcasia falcifolia Engl., JL sn
C. orientalis Mayo, JL sn

BURMANNIACEAE

Gymnosiphon usambaricus Engl., JL 298

CYPERACEAE

Cyperus pseudoleptocladus Kukenthal, DT 3897A
Scleria iostephana Nelmes, DB 613
S. racemosa Poiret, DB 619

GRAMINEAE

Coelachne africana Pilger, DT 3935
Leptaspis cochleata Thwaites, JL sn
Olyra latifolia L., JL sn
Puelia olyriformis (Franch) Clayton, DT 3722

IRIDACEAE

Gladiolus rupicola Vaupel, DT 3706

LILIACEAE

Asparagus asparagoides (L.) Wight, DT 3704

Chlorophytum sparsiflorum Baker, DB 608
C. sp., DT 3892, DT 3893

MARANTACEAE

Marantochloa leucantha (K. Schum.) Milne-Redh., DB 615, RP 5127

ORCHIDACEAE

Bulbophyllum concatenatum Cribb & P. Taylor, DB 590
B. cf. *imbricatum* Lindl., DT 3876
Cheirostylis lepida (Reichb. f.) Rolfe, DB 589, DT 3647, DT 3700
Cynorchis anacamptoides Kraenzl., JL 304
C. buchwaldiana Kraenzl. subsp. *braunii* (Kraenzl.) Summerh., DT 3763
C. pleistadenia (Reichb. f.) Schltr., JL 303
Disperis elaphoceras Verdc., DT 3682A
D. uzungwae Verdc., JL 270
Habenaria trilobulata Schltr., JL 277
Liparis sp. ?nov., DT 3874
Polystachya cultriformis (Thou.) Spreng, DT 3875
P. ?goetzeana Kraenzl., DT 3873
P. melantha Schltr., DT 3872
P. transvaalensis Schlechter, DT 3768, DT 3812, JL 302
P. ulugurensis Cribb & Podz., DT 3793
Stolzia leedalii Cribb, DT 3871
S. nyassana Schltr., DT 3870
Tridactyle sp. nov., DT 3763A
T. sp. nov. = Leedal 6138, DT 3764

PALMAE

Elaeis guineensis Jacq., JL sn
Phoenix reclinata Jacq., JL sn

SMILACACEAE

Smilax kraussiana Meisen., JL sn

TRIURIDACEAE

Seychellaria africana Vollesen, DB 634, JL 226

ZINGIBERACEAE

Aframomum angustifolium (Sonn.) K. Schum., JL sn
A. laxiflorum Loes ex Lock, JL 228
Costus subbiflorus K. Schum., JL sn

EXPERIMENTAL STUDIES ON SPECIES RELATIONSHIPS IN *ERYTHRINA* (LEGUMINOSAE: PAPILIONOIDEAE)[1]

David A. Neill[2]

ABSTRACT

Erythrina *L. comprises about 112 species distributed throughout the tropics and subtropics. Most species are trees or shrubs, and most are diploids with* n = *21. All are adapted to bird pollination, some by passerine birds and others by hummingbirds.* Erythrina *is subdivided into five subgenera and 27 sections. Research concentrated on sect.* Erythrina, *with 36 species centered in Mexico and Central America; selected species in other sections were also studied. Experimental interspecific hybridizations and self-compatibility trials were conducted using cultivated trees at several botanical gardens in Hawaii. Comparative morphological analyses were made of the hybrids and their parents. Studies of population structure and natural hybridization were carried out in natural populations of hummingbird-pollinated sect.* Erythrina. Erythrina *species are self-compatible, but some inbreeding depression is associated with selfing. Within sect.* Erythrina, *interspecific hybrids are obtained just as readily as are progeny from within-species outcrosses. The hybrids are vigorous, fertile, and by several measures exhibit interspecific heterosis. At greater taxonomic distances between the parental species (between sections and subgenera), crossability, viability, and fertility of the hybrid progeny are generally lower than in intrasectional hybridizations. Some hybrids were obtained between species of different subgenera indigenous to different continents. There are probably no absolute internal barriers to hybridization among all the diploid species of* Erythrina. *The genus may be characterized taxogenetically as a homogamic complex. Interspecific hybrids are intermediate between their parental species in morphological traits, including macroscopic features of the inflorescence and flower and microscopic features of the leaf epidermis. The inheritance of particular features of the male parent in the progeny allows for confirmation of hybridity. Species of sect.* Erythrina *are generally allopatric, but field studies of natural populations in southern Mexico revealed several localities where two species do occur sympatrically and where natural hybrids are found. Traplining hummingbirds, the pollinators of sect.* Erythrina, *are implicated as the agents of interspecific hybridization among sympatric species. The results of experimental hybridization, together with studies of comparative morphology and distribution patterns, suggest that some species of* Erythrina *are stabilized hybrid derivatives.*

Experimental hybridization studies have been a cornerstone of research in plant biosystematics since the emergence of this synthetic field. Much of the work of early biosystematists was directed toward efforts to define taxa and taxonomic categories on the basis of reproductive barriers as revealed by experiment, an approach exemplified by the studies of Clausen et al. (1939, 1940) and their proposal

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[1] *This study was undertaken as part of a doctoral dissertation at Washington University, St. Louis, Missouri. Peter Raven first suggested the research on* Erythrina *biosystematics as a dissertation topic and helped in innumerable ways during the research. His ideas on plant evolution and the role of hybridization in the evolutionary process provided the conceptual framework upon which this study is based. Rupert Barneby and the late B. A. Krukoff introduced me to the the systematics of* Erythrina *and suggested relationships among the taxa of particular interest for the experimental studies. This work was made possible by the generous support of the three Hawaiian botanical gardens, and especially by the efforts of their respective directors and chief horticulturists: William Theobald and Scott Lucas at Pacific Tropical Botanical Garden; Keith Woolliams and Cecilia Ufano at Waimea Arboretum; and Paul Weissich and Daniel McGuire at Ho'omaluhia Botanic Garden. Gerald Carr at the University of Hawaii provided use of his cytological laboratory and excellent advice on the handling of chromosomes. Michael Veith provided assistance and advice with the scanning electron microscope at Washington University. Hiroshi Tobe prepared the leaf sections illustrated in Figures 19, 21, and 23. Conversations with and comments by Héctor Hernández and Peter Hoch helped to improve the manuscript. Alina Chacón and Mary Merello assisted in the preparation of the manuscript and figures. As a graduate student I was supported by fellowships from the Danforth Foundation, Washington University Division of Biology and Biomedical Sciences, and Missouri Botanical Garden. The research was funded by grants from the National Science Foundation (DEB 81-20386) and Elizabeth Neill.*

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to establish ecotypes, ecospecies, coenospecies, and comparia as universal units of classification to replace the traditional ones. The criteria used to define taxa on the basis of fertility relationships and the enormous labor required to obtain the experimental results on a broad scale proved impractical for a general-purpose classification system, and most present-day biosystematists have rightly abandoned the earlier efforts to "meddle" with the traditional taxonomic hierarchy.

Experimental hybridization studies continue to play a central role in research on the nature of species relationships, however, and their usefulness extends far beyond the requirements of formal taxonomy. They provide the material for a broad spectrum of integrated studies in the genetics of evolutionary divergence. Research on long-lived perennials, although it requires patience and a long-term commitment of labor and resources, is particularly amenable to hybridization programs because the parentals and several generations of offspring can be grown side-by-side, and many comparative studies can be carried out with the living plants.

This paper describes the results of experimental investigations into the biosystematics and reproductive biology of *Erythrina* (Phaseoleae), a widespread genus comprising more than 110 species, most of them tropical trees. The research was concentrated on species of sect. *Erythrina*, a complex of 36 species centered in southern Mexico and Central America (Mesoamerica), but other taxa of *Erythrina* were included in some phases of the investigation. The results of the research are used to establish a series of hypotheses regarding species relationships and evolutionary history of *Erythrina*. The hypotheses are presented here in sequence: each is dependent on the validity of the previous hypotheses.

Hypothesis 1. The species of sect. *Erythrina* can all hybridize freely with each other, and the resulting hybrids are as fertile as the parents. The section is a homogamic complex, and internal, post-mating isolating barriers between the species are absent.

Hypothesis 2. The interfertile homogamic complex encompassing sect. *Erythrina* extends, to a greater or lesser degree, to species in other sections and other subgenera of the genus. Any diploid *Erythrina* species can mate with any other to form a viable F_1 hybrid, but hybrids between widely divergent species may exhibit varying degrees of sterility. The genus as a whole may be characterized taxogenetically as a series of interfertile homogamic complexes with weak to moderate reproductive barriers between the complexes.

Hypothesis 3. The widely foraging hummingbirds that pollinate trees in sect. *Erythrina* ensure effective outcrossing even in the isolated populations of small neighborhood size and low density characteristic of these species. Self-compatibility and occasional autogamy allow establishment of a population from a single founder individual. When two species of sect. *Erythrina* are sympatric, the pollinating birds do not discriminate between them, and interspecific pollen transfer is likely.

Hypothesis 4. The species in sect. *Erythrina* are mostly restricted in geographic range and are usually allopatric, separated by habitat differences. For the most part, these factors are effective barriers to interspecific gene flow. However, sometimes different species do come into contact in nature, and then fertile hybrids are formed.

Hypothesis 5. Patterns of distribution and phenetic variation in sect. *Erythrina* indicate that some distinct forms recognized as species are stabilized derivatives resulting from hybridization of two parental species. In the changing climates and dynamic geomorphologic landscape that have characterized Mesoamerica since the Miocene, and with the consequent migration of vegetation types and mixing of floristic elements, formerly allopatric species may have come into contact a number of times. With the temporary breakdown of external isolating barriers, the interfertile species hybridized, and the subsequent segregation and stabilization of hybrid derivatives has contributed to the proliferation of *Erythrina* species in Mesoamerica.

The first two hypotheses can be tested directly by experimental hybridization programs. The third and fourth can be substantially confirmed by observations of mating behavior and patterns of variation in natural populations. The fifth hypothesis is historical and can only be inferred by drawing on information obtained by testing the first four. The "level of confidence" (Gottlieb, 1972) in the final hypothesis of hybrid speciation in *Erythrina* is dependent upon the strength of the evidence presented in this paper in support of the four antecedent hypotheses.

This research was made possible by the existence of the extensive living collections of *Erythrina* at three botanical gardens in Hawaii: Pacific Tropical Botanical Garden in Lawai, Kauai; Waimea Arboretum in Haleiwa, Oahu; and Ho'omaluhia Botanic Garden in Kanehohe, Oahu. The cultivated *Erythrina* collections were assembled, beginning in the early 1970s, through the efforts of the *Erythrina* monographer B. A. Krukoff. The gardens collectively now have in cultivation more than 90 of the 112 recognized species in the genus, and the remaining species are gradually being obtained through requests to botanists around the world for seed.

SECTION 1. EVOLUTION IN HOMOGAMIC COMPLEXES: A REVIEW

The following section provides an overview of the conceptual framework of the experimental work on *Erythrina* and a literature review of the role of hybridization in the evolution of homogamic complexes.

Grant (1953) coined the term "hybrid complex" for groups of related species linked by occasional or frequent hybridization, and he classified different types of hybrid complex based on their reproductive mode and the means of stabilization of the hybrids. In two of these complexes the hybrid derivatives are mostly or entirely apomictic: in a clonal complex the hybrids are sterile and reproduce vegetatively, and in an agamic complex they reproduce by agamospermy. In the remaining three types of hybrid complexes, the hybrid derivatives reproduce sexually: (1) in a heterogamic complex they are permanent structural heterozygotes or permanent odd polyploids; (2) in a polyploid complex they are amphiploid with respect to the parental species; and (3) in a homogamic complex the hybrid derivatives exhibit normal meiosis and are sexual diploids, homoploid with respect to the parental species.

In some groups forming homogamic complexes, internal reproductive barriers may be present and the hybrid derivatives may be partially intersterile with the parents and with each other, as revealed by Grant's studies of annual *Gilia* (summarized in Grant, 1981). More frequently, though, particularly in complexes of perennials and woody plants, the derivatives are highly interfertile with the parents, with each other, and with all the other species in the complex: the only barriers to gametic exchange between any populations or any pair of taxa in the group are external.

Grant (1953) and Gottlieb (1972) pointed out a paradox inherent in the recombinational system of the homogamic complex that sets it apart from the other types of hybrid complex. In clonal, agamic, heterogamic, and polyploid complexes, the cytogenetic features or reproductive systems of the hybrid derivatives are important criteria of hybridity and distinguish them from the parents. In homogamic complexes the derivatives are fertile and cytogenetically homogeneous with the parents, so these criteria cannot be used as a test of hybridity. Consequently, homogamic complexes are more difficult to analyze and may pass undetected.

Grant (1953) contended that in the long term the "evolutionary potential" of homogamic complexes is much greater than in other types of hybrid complex. In the clonal, agamic, and heterogamic complexes, and to a lesser extent in polyploid complexes, favorable gene combinations are stabilized in the hybrid derivatives at the cost of a severe restriction in recombination. When environmental conditions change, the derivatives are less flexible in their capacity for genetic adaptation than are sexual diploids. Should the progenitors of the complex, the original sexual diploids, become extinct, an important source of new variation in the complex is lost.

These restrictions do not apply to homogamic complexes, however. Since the derivatives are sexual diploids, recombination is unrestricted. They are able to backcross freely with the parentals, and the original species may become extinct without jeopardizing the evolutionary potential and flexibility of the complex. Relative to the other types of hybrid complex, the homogamic complex is, in the words of Grant, an "open-ended genetic system."

The maintenance of the ability to hybridize gains importance because it extends the pool of natural variation available for recombination and selection far beyond that present in any single species. In environments undergoing climatic and/or geologic change, that "extra" genetic pool may be crucial for adaptive adjustment of the organisms, and hybrid recombinants from two or more species may have greater fitness in the newly created habitats than either of the parental species. Evolution in an open-ended homogamic complex may follow a reticulate pattern, with cycles of divergence and differentiation alternating with hybridization and recombination as environmental conditions change (Raven & Raven, 1976; Raven, 1980).

The paradox is that while hybridization is most difficult to detect and analyze in homogamic complexes, on a broad scale homogamic complexes may be much more important in plant evolution than other types of hybrid complex. Grant (1953) even speculated that hybridization in homogamic complexes may account for much of the diversity of the angiosperms, and for the reticulate nature of variation and lack of clear discontinuities between the major phyletic lines of flowering plants. Grant concluded that "the ancestral stocks may have been hybridizing on the diploid (or diploidized) level since the earliest stages of angiosperm evolution."

Whether or not homogamic complexes have played such an important role in the evolutionary history of flowering plants, it is now well accepted that they are characteristic of the genetic structure of many large and ecologically dominant genera of trees and shrubs, at least in temperate regions. The only really thorough biosystematic study of a homogamic complex in a genus of woody plants, combining fossil evidence, experimental hybridizations, and careful field studies, is Nobs's (1963) exemplary work on *Ceanothus* in California. Many species of *Ceanothus* are dominant shrubs in the chaparral vegetation of that region, and all are diploid with $n = 12$. Nobs showed that since the Miocene, certain wide-ranging species in *Ceanothus* sect. *Cerastes* have formed hybrid swarms in areas where they have intermixed. In novel habitats created by an increasingly arid climate and by the exposure of new substrates such as serpentine outcrops, some of the hybrid derivatives have become stabilized as new self-perpetuating species.

Numerous studies have also been carried out on natural hybridization in *Quercus*, and this enormous homoploid genus ($n = 12$), which dominates the forests of much of the north-temperate zone, is generally agreed to comprise a homogamic complex (Muller, 1952; Hardin, 1975; Van Valen, 1976) or, perhaps more accurately, several homogamic complexes corresponding to its subgenera, with strong but incomplete barriers between them. The results of Cottam's long-term *Quercus* hybridization program (Cottam et al., 1982) considerably strengthen the experimental evidence (most of the previous hybridization studies in the genus merely analyzed morphological variation in natural populations).

Among other genera of trees and shrubs that probably comprise extensive homogamic complexes are *Eucalyptus* (Pryor, 1959), *Prosopis* (Simpson, 1977), and *Ribes* (Keep, 1962).

Most of the world's flora is made up of tropical woody plants, and the role of hybridization and the presence of homogamic complexes in these groups is largely unknown and remains a matter of dispute. Many systematists who work on tropical woody genera evidently believe that hybridization is absent or unimportant in the organisms they study, e.g., Ashton's (1969) comments on Dipterocarpaceae in Southeast Asia. Ehrendorfer (1970) thought that narrower "niche width" restricted gene flow, and a higher incidence of polyploidy and apomixis in tropical tree species made them much less likely to hybridize than their temperate-zone counterparts. It does appear logical that in species-rich tropical forests population density is low and neighborhood size is small for any one species, as well as for groups of sympatric congeners, so the opportunities for hybridization may be fewer and the hybrids harder to detect than, for example, in a temperate forest with large populations of sympatric *Quercus* species.

At any rate, the critical experimental hybridization trials have not been carried out for tropical woody plants, except for a few economically important genera. For example, strong sterility barriers have been found between Amazonian species of *Theobroma* (Addison & Tavares, 1952). In contrast, *Hevea* in the same region is probably a homogamic complex. In this homoploid genus ($n = 18$), fertile hybrids were easily obtained in experimental gardens, and numerous natural hybrids were reported (Seibert, 1947).

In many genera of tropical woody plants, all or most species share the same relatively high chromosome number and may be considered diploidized paleopolyploids. Thus, most genera of Bignoniaceae have the same chromosome number of $n = 20$; they are probably paleohexaploids based on $x = 7$ (Goldblatt & Gentry, 1979). Such plant groups may be prime candidates for the formation of homogamic complexes. Until the present study, however, a thorough biosystematic investigation on the scale of Nobs's work on *Ceanothus* had not been carried out on any large tropical woody genus or, in fact, on any other woody genus.

SECTION 2. HISTORY AND RELATIONSHIPS OF THE GENUS

Erythrina L. comprises about 112 species distributed throughout the tropical regions of the world and extending into warm-temperate areas such as South Africa, the Himalayas and southern China, the Rio de La Plata region of Argentina, and the southern United States (Krukoff & Barneby, 1974) (Fig. 1). Most species are trees or shrubs, but about 10 species occurring in climates with pronounced dry and/or cool seasons are perennial herbs with large woody rootstocks. *Erythrina* species occur in a very wide variety of habitats, from lowland tropical rainforest to very arid subtropical deserts to highland coniferous forests above 3,000 m.

The distinctiveness of *Erythrina* has long been recognized by legume systematists. Following Bentham (1865), the genus has been placed traditionally in the subtribe Erythrininae of the tribe Phaseoleae, a relationship based principally on the characteristic trifoliolate leaves that *Erythrina*

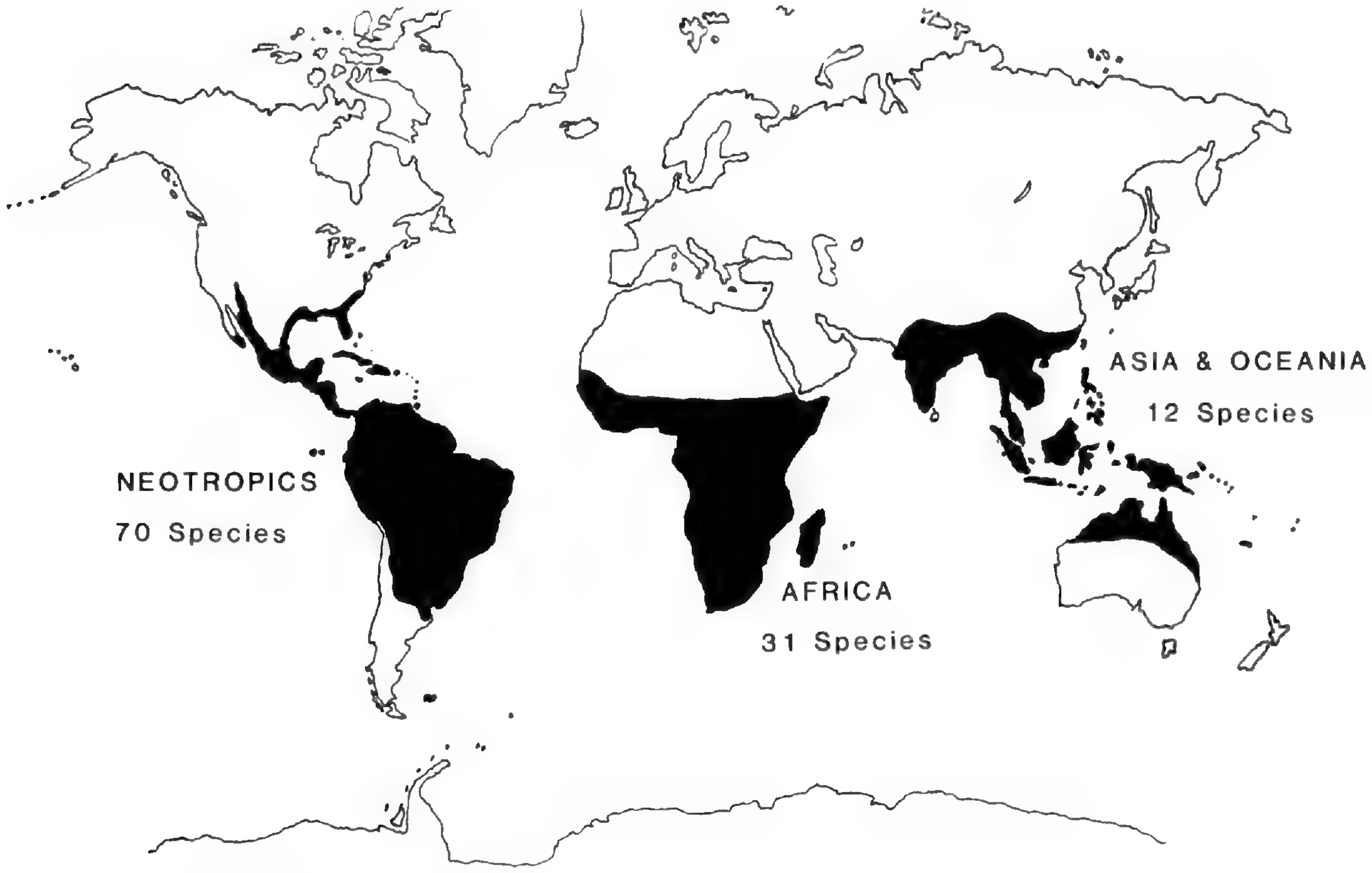


FIGURE 1. *Distribution of* Erythrina.

shares with the rest of the Phaseoleae. In a recent generic treatment of Phaseoleae, Lackey (1981) maintained the traditional classification but remarked that "the relationship of [*Erythrina*] to the remainder of the Papilionoideae is an absolute mystery . . . the genus would have long ago been accommodated outside the Phaseoleae had not the foliage suggested this tribe. In many significant characters, *Erythrina* stands alone among the Phaseoleae."

Besides *Erythrina*, the subtribe Erythrininae contains the genera *Mucuna*, *Strongylodon*, *Butea*, *Apios*, *Spatholobus*, *Cochlianthus*, *Rhodopsis*, and *Neorudolphia*. The relationships among these genera are not close and the erection of the subtribe is largely a matter of convenience to accommodate a loose assortment of genera not easily placed in other subtribes of the Phaseoleae.

Butea alone, the only other arborescent genus in the Phaseoleae, appears to have some true affinities with *Erythrina*. Baretta-Kuipers (1982) found that the unusual wood anatomy of *Erythrina* is very similar to that of *Butea*. In many other important traits, however, *Erythrina* is distinct from *Butea* and from all other legumes. The base chromosome number of $x = 21$, shared by all 86 *Erythrina* species that have been counted, is unique in the Leguminosae and indicates no direct relationship with *Butea* with $n = 9$. The unusual, high activity–low affinity nitrate reductase system present in all *Erythrina* species that have been examined differs in some respects from known nitrate reduction patterns in other angiosperms (Orebamjo et al., 1982). Neither *Mucuna* nor *Butea* (G. R. Stewart, pers. comm. to P. Raven, 1984) shares this trait with *Erythrina*. The *Erythrina* alkaloids, structurally complex isoquinolines nearly universal in the seeds of the genus, are found in no other legumes (Mears & Mabry, 1971).

Although *Erythrina* is quite distinct from the rest of the Leguminosae, and despite its great ecological and morphological diversity, the cytological and phytochemical evidence cited above and the interfertility relationships presented in this paper indicate that the genus is unusually close-knit for its size (Raven, 1974), and there is no doubt that it is monophyletic. As such, the genus is an ideal subject for the biosystematic study of diversification of an entire evolutionary clade.

The origin of *Erythrina*, like its relationship to the rest of the Leguminosae, is obscure. No fossil record of the genus has been reported. In the light of its distribution patterns, pollination, and dispersal mechanisms, and the known history of Leguminosae as a whole, Raven (1974) postulated an Upper Eocene to Upper Oligocene origin for the genus (40–30 m.y. BP), followed by ocean-drift and/or other long-distance dispersal among the three principal tropical regions of America, Africa, and Asia–Oceania. Much diversification of *Erythrina* has occurred independently in Africa and America and to a lesser extent in Asia.

The place of origin of *Erythrina* is unknown, but South America appears most likely since the majority of the putative ancestral groups (as considered by Krukoff & Barneby, 1974) within the genus are found there. Africa is also a possible candidate, since it likewise contains a number of endemic groups. Although *Erythrina* almost certainly originated well after the breakup of West Gondwanaland, it has a basically South American–African distribution that is shared by many angiospermous groups, including the Leguminosae itself (Raven & Axelrod, 1974). The *Erythrina* taxa in "tropical Laurasia," i.e., Asia and Mesoamerica, are clearly derived groups. In Mesoamerica the genus has undergone extensive recent speciation within a single lineage.

PATTERNS OF DIVERSIFICATION: POLLINATION

Erythrina species exhibit a great diversity in floral structure, inflorescence orientation, fruit morphology, seed coat coloration, and vestiture and epidermal ornamentation of foliage and calyces. The infrageneric classification of *Erythrina* is based principally on these characters.

The diversity of floral structure reflects adaptive radiation in *Erythrina* with respect to pollination mechanisms. All *Erythrina* species have red or orange flowers and copious nectar, and are adapted to pollination by nectarivorous birds. There are two distinct syndromes of ornithophily in the genus. All 42 Old World species and 15 of the 70 New World species are pollinated by "perching birds" of several families in the order Passeriformes. Passerine birds cannot hover efficiently or for any length of time, and the inflorescences of passerine-pollinated *Erythrina* are oriented in such a way that the birds can perch while feeding on floral nectar. The corolla standard is usually broad, and the flowers are open, with exposed reproductive parts. Pollen is deposited on the feeding bird's breast. The flowers of passerine-pollinated species of *Erythrina* are diverse in size, form, and orientation, which appears to reflect the variation in size, morphology, and behavior of the pollinators, which range from sunbirds and white-eyes weighing 8–10 g to orioles weighing over 35 g.

The remaining 55 New World species of *Erythrina* (nearly half the genus) are pollinated by hummingbirds (Trochilidae). Hummingbirds are the most specialized of nectarivorous birds and the only ones that hover while feeding. The corolla standard of hummingbird-pollinated *Erythrina* is narrow and conduplicately folded to form a "pseudotube," concealing the wing and keel petals as well as the reproductive parts. The flower resembles the tubular corollas of many gamopetalous hummingbird-pollinated plants, but in *Erythrina* the pseudotube is not sealed on the ventral side where the margins of the corolla standard meet. The inflorescence axis of the hummingbird-pollinated species is erect, and the flowers are oriented outward, providing no perch for the hovering hummingbirds.

Only a small number of the 315 neotropical hummingbird species are *Erythrina* pollinators, and these are all similar in size, bill length, and behavior. The *Erythrina* pollinators are principally specialized "high-reward trapliners," nonterritorial species that follow regular daily foraging routes between widely separated individual plants (Neill, 1987). The flowers of the hummingbird-pollinated *Erythrina* species are much more uniform in size and shape than those of the passerine-pollinated species, and this probably reflects the relative uniformity of pollination mechanisms among the former group.

FRUITS, SEEDS, AND DISPERSAL

The diverse fruit and seed characteristics of *Erythrina* species are indicative of adaptation for different dispersal mechanisms. The putative ancestral species (Krukoff & Barneby, 1974) inhabit coastal, estuarine, or riverine environments and have dull brown floating seeds transported by oceanic or fluvial currents. These species are effective colonizers: *Erythrina fusca* and *E. variegata* both became established on the island of Krakatoa a few years after the cataclysmic eruption of 1883 (Guppy, 1906). Since the review of Raven (1974), new anecdotal evidence has come to light concerning the dispersal of these seeds and their viability following long exposure to salt water. A drift seed of *Erythrina variegata* was recorded after a storm on the beach of Canton Island, a low coral atoll at 3°S latitude in the western Pacific, where *Erythrina* does not occur. The nearest possible source for the drift seed is Samoa, 700 km to the south. The seed, planted in Hawaii, grew into a 20-m tree (from herbarium label of *Degener 35066*, BISH).

Alone in *Erythrina*, *E. subumbrans* of Asia–Oceania has winged, wind-dispersed fruits. The Tanzanian endemic *E. greenwayi* has unusual fruits with narrow winglike ridges, but the fruits are heavy and do not appear to be effectively wind dispersed.

Most of the putative derived species of *Ery-*

thrina have bright red seeds, which persist in conspicuous display on the pods after dehiscence. Red seeds have evidently evolved independently in several lineages of *Erythrina*; one or two species in each lineage have bicolored red and black seeds. The red or red-and-black seeds are presumed to be "imitation arils" (Ridley, 1930) or mimetic berries. According to this theory, they are eaten by frugivorous birds attracted by the bright colors and are dispersed when they pass through the digestive tract unharmed, but there are few actual reports of such "mistake" dispersals. Skutch (1971) recorded an overwintering yellow-throated vireo (*Vireo flavifrons*) eating red *Erythrina* seeds in Costa Rica. I have seen this phenomenon on only one occasion, when in March 1983 in Chiapas, Mexico, I observed a migrant wood thrush (*Hylocichla mustellina*) ingest several red seeds of *Erythrina folkersii* displayed on the pods. A major autumn food item of this bird in eastern North America, before it migrates south, is the bright red, fleshy fruit of *Cornus florida*, which *Erythrina* seeds resemble quite closely (E. Morton, pers. comm.). Thus the dispersal of *Erythrina* seeds as mimetic berries by "naive" migrant birds does seem to be a real, though perhaps infrequent, phenomenon.

The "mimetic berry" theory is fraught with all of the conceptual difficulties common to considerations of the evolution of mimicry. The alkaloids in the seeds of *Erythrina* are toxic, and the deceived bird must survive the passage of the seed through its gut if it is to produce subsequent generations of birds that will disperse subsequent generations of *Erythrina*. (The alkaloids are not released unless the seed coat is broken, and frugivorous birds do not have strong gizzards to grind seeds.) Additionally, the mimic should be rare relative to the model, and the deception must occur frequently enough so that natural selection can act upon it. The question of mimetic seed coloration in *Erythrina* and other legumes is discussed in McKey (1975).

FEATURES OF THE EPIDERMIS

A great variety of special epidermal structures occurs in *Erythrina*, particularly on the abaxial leaf surfaces. These include hairs of many types, epidermal papillae and various "lamellae," and epicuticular wax deposits. The adaptive significance of these features is not known, but they are often diagnostic for particular species or species groups and often aid in identification of sterile material. Patterns of leaf epidermal features and their inheritance in interspecific hybrids are discussed later.

SUBDIVISIONS OF *ERYTHRINA*

The first formal subdivision of *Erythrina* was established by Harvey (1861), with subsequent treatments by Harms (1915), Louis (1935), and Krukoff (1939a, for the American species; 1939b, for the Asiatic–Polynesian species). In the 19th century a number of generic segregates were proposed based on the distinctive floral morphs of certain groups of species: e.g., *Chirocalyx* Meisn., *Micropteryx* Walp., *Duchassaingia* Walp., and *Hypaphorus* Hassk. These segregates were treated as sections or subgenera of *Erythrina* by later monographers. The modern classification of the genus was established by Krukoff & Barneby (1974), who recognized 5 subgenera and 26 sections. I accept their treatment as the systematic basis for the present work; a few taxonomic changes to be published later are anticipated in this paper prior to their formal designation. The infrageneric classification of *Erythrina* is summarized in Table 1. A list of the currently recognized species, with authorities and with changes in synonymy made since Krukoff & Barneby's (1974) conspectus of the genus, is included in Appendix I.

The sections of *Erythrina* are well delimited morphologically and biogeographically, and each appears to be monophyletic. The subgenera also are delimited by several good characters and appear monophyletic, except for the large and heterogeneous subg. *Erythrina*, which includes 70% of the species in the genus. The relationships of the sections comprising subg. *Erythrina* to one another still present a number of unresolved taxonomic and phylogenetic questions.

The following is a short narrative synopsis of the infrageneric classification of *Erythrina* and an outline of evolutionary and biogeographical trends; in the discussion, the taxa used in the experimental studies are emphasized.

Subgenus *Micropteryx* is restricted to South America, except for *Erythrina fusca* in the monotypic sect. *Duchassaingia*. With floating seeds dispersed by ocean currents, *E. fusca* is the only species in the genus to occur in both the Old World and the New World. It is widely distributed along coasts and rivers in the Neotropics and Asia–Oceania, as well as in Madagascar and the Mascarene Islands, but its present native range does not include continental Africa. It often occurs in extensive pure stands in seasonal swamps. With its

TABLE 1. *Infrageneric classification of* Erythrina.

	Sections	Number of Species	Distribution		
			America	Africa	Asia–Oceania
I.	Subg. *Micropteryx*				
	1. *Duchassaingia*	1	X	X (Madagascar)	X
	2. *Cristae-galli*	2	X		
	3. *Micropteryx*	4	X		
II.	Subg. *Erythrina*				
	4. *Suberosae*	4			X
	5. *Arborescentes*	1			X
	6. *Hypaphorus*	1			X
	7. *Breviflorae*	4	X		
	8. *Edules*	2	X		
	9. *Stenotropis*	1	X		
	10. *Pseudo-edules*	2	X		
	11. *Leptorhizae*	4	X		
	12. *Erythrina*	36	X		
	13. *Gibbosae*	1	X		
	14. *Corallodendra*	9	X		
	14a. *Fidelenses*	1	X		
	15. *Cubenses*	1	X		
	16. *Olivianae*	1	X		
	17. *Caffrae*	2		X	
	18. *Humeanae*	2		X	
	19. *Acanthocarpae*	1		X	
III.	Subg. *Tripterolobus*				
	20. *Tripterolobus*	1		X	
IV.	Subg. *Chirocalyx*				
	21. *Bruceanae*	1		X	
	22. *Macrocymbium*	2		X	
	23. *Dilobochilus*	1		X	
	24. *Dichilocraspedon*	1		X	
	25. *Chirocalyx*	14		X	
V.	Subg. *Erythraster*				
	26. *Erythraster*	13	X	X	X

wide distribution and presumably primitive features (Krukoff & Barneby, 1974), *E. fusca* or a *fusca*-like ancestor may represent the original progenitor of the entire genus.

Section *Cristae-galli* includes two species, *E. crista-galli*, which forms extensive populations along the estuary of the Río de La Plata in extratropical South America, and *E. falcata*, which inhabits the "Yungas" forest of the eastern Andean foothills and similar subtropical forest vegetation in southeast Brazil. The four species of sect. *Micropteryx* inhabit riverine or upland forests of the Amazon and Orinoco basins and the Planalto of Brazil.

Subgenus *Erythrina*, with 79 species in 17 sections, is distributed throughout the three major tropical regions of America, Africa, and Asia, but no single section occurs in more than one of these areas. The subgenus includes all 55 of the American hummingbird-pollinated species in six different sections which I believe to have been derived from passerine-pollinated groups by convergent evolution in several independent lineages.

Erythrina speciosa of coastal Brazil, in the monotypic sect. *Stenotropis*, is geographically and phylogenetically isolated from the rest of the hummingbird-pollinated species. The herbaceous, hummingbird-pollinated species of sect. *Leptorhizae*, endemic to central Mexico, are probably derived directly from the passerine-pollinated shrubby/ar-

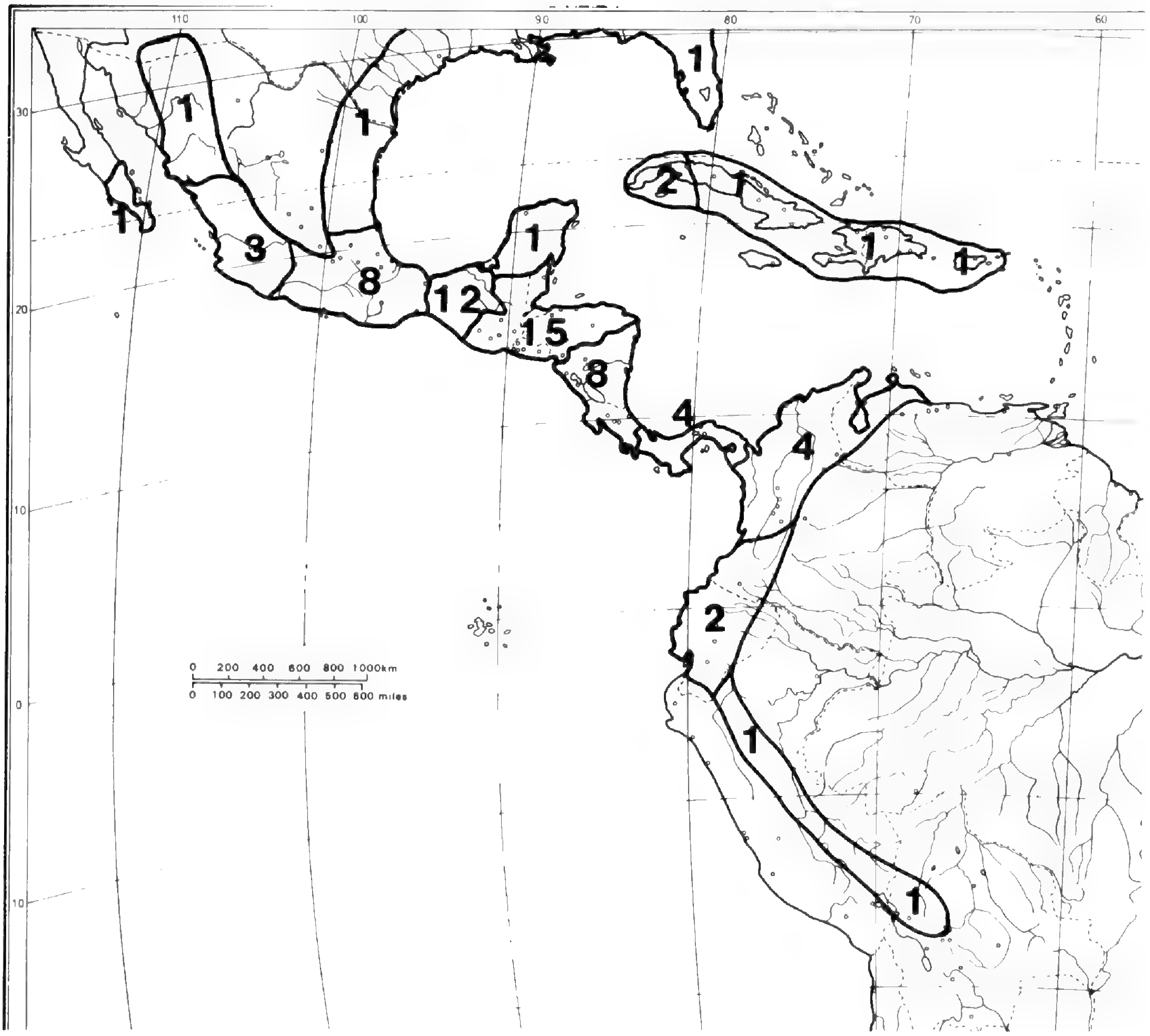


FIGURE 2. *Distribution of* Erythrina *sect.* Erythrina. *The numbers indicate the numbers of species known to occur in each geopolitical region bounded by the heavy black lines.*

borescent sect. *Breviflorae* endemic to the same region. In a parallel manner, the Andean hummingbird-pollinated sect. *Pseudo-edules* may be derived from the Andean passerine-pollinated sect. *Edules*.

The large Mesoamerican-centered, hummingbird-pollinated sect. *Erythrina* (36 species) is closely allied with the remaining hummingbird-pollinated sections; *Corallodendra*, with 9 species in South America and the Antilles, and the monotypic sections *Gibbosae* in southern Central America, and *Cubenses* endemic to Cuba. The relationship of these advanced arborescent hummingbird-pollinated groups to the rest of the genus is not clear, however.

Figure 2 shows the distribution of sect. *Erythrina* and the number of species known to occur in geomorphologically and politically delimited subregions of its range. The greatest concentration of species is in nuclear Central America, particularly in the Mexican state of Chiapas and in Guatemala. Geologically, nuclear Central America is much older than southern Central America. It has been connected to the North American continent since the Cretaceous, whereas southern Central America was only a chain of volcanic islands until the close of the Panamanian isthmus in the Pliocene (Raven & Axelrod, 1974; Coney, 1982). It is most probable that sect. *Erythrina* originated in nuclear Central America following migration of its progenitor from South America, an event that could have occurred either before or shortly after the final formation of the southern Central American land bridge. Species of this section, which comprises nearly one-third of the entire genus, inhabit nearly every forested habitat in the geologically active and climatically complex Mesoamerican region. In contrast to *Erythrina fusca* and other species that form extensive monospecific stands, the species of sect. *Erythrina* generally occur at low population densities. Many have a restricted geographic range and occur in a single vegetation type, in a rather narrow altitudinal belt, or only on particular substrates, such as outcrops of calcareous rock. Sympatry among species in the section is rare, but when it does occur, natural hybrids are generally found. All available evidence indicates that sect. *Erythrina* is an outstanding example of rapid adaptive radiation and speciation in the recent geological past.

The remaining sections of subg. *Erythrina* occur in the Old World, and their affinities to the American sections are not apparent. The South African endemic sects. *Caffrae*, *Humeanae*, and *Acanthocarpae* are the only representatives of the subgenus on that continent. Certain floral, fruit, and seed features of sect. *Caffrae* do suggest an affinity with the monotypic Mexican sect. *Olivianae*, but a plausible explanation of such a connection is difficult to imagine.

The Asian sects. *Suberosae*, *Arborescentes*, and *Hypaphorus* are an autochthonous group with mostly "primitive" features and do not appear to be closely allied with the American and African sections of subg. *Erythrina*. The species of sect. *Suberosae* possess one singularly "advanced" feature: complex reticulate "lamellae" formed by epidermal cells of the abaxial leaf surfaces (this paper, Section 5).

The monotypic subg. *Tripterolobus*, consisting of *E. greenwayi* and endemic to a small area in the Rift Valley of Tanzania, is an evolutionary anomaly. The three-winged follicular pod is unique in the genus, while the flower, as Krukoff & Barneby (1974) indicated, seems constructed from disparate elements of different subgenera.

Subgenus *Chirocalyx*, with 5 sections and 19 species, is restricted to sub-Saharan Africa. Section *Chirocalyx* comprises 14 species which inhabit environments as diverse as the Kalahari Desert, the lowland rainforests of Cameroon, the vast savannas of the Sahel, and the montane forests of eastern Zaire—a radiation reminiscent of sect. *Erythrina* in Mesoamerica, although with fewer species. The remaining sections in subg. *Chirocalyx* are mono- or ditypic, each quite distinct morphologically.

The final subgenus is *Erythraster*, with 13 species in the sole sect. *Erythraster*. It is basically an Old World group with two disjunct, derived species in the Neotropics. *Erythrina variegata*, the coastal-strand, ocean-dispersed species, occurs from Tanzania and Madagascar around the shores of the Indian Ocean and westward through Indonesia, New Guinea, Polynesia, and Micronesia to the Marquesas. The remaining species inhabit upland areas, including four in East Africa and one in Australia. There is one endemic species on each of the islands or island groups of Madagascar, Java-Bali, New Guinea, Tahiti, and the Hawaiian archipelago, and each of these may be derived independently from *E. variegata*. The disjunct *E. velutina*, widely distributed in dry forests of northern South America, the Galapagos, and the Antilles, and its Cuban endemic derivative, *E. grisebachii*, form a distinct species complex together with the Tahitian *E. tahitensis* and the Hawaiian *E. sandwicensis*. All the species of this Polynesian–Neotropical complex have "mimetic berry" red seeds, unlike *E. variegata* and most of the other species in sect. *Erythraster*. *Erythrina variegata* is present on Tahiti but not in Hawaii or the Neotropics. With this pattern of distribution, it appears most likely that these Polynesian–Neotropical disjuncts were established following long-distance dispersal by birds across the Pacific, and not by ocean-drift of *E. variegata* or a *variegata*-like ancestor.

SECTION 3. CHROMOSOME NUMBERS AND MEIOTIC BEHAVIOR IN DIPLOID AND POLYPLOID SPECIES

Erythrina is well known to be relatively uniform cytologically; polyploidy is rare, and aneuploidy is unknown (Lewis, 1974; Goldblatt, 1981a, 1984). The basic chromosome number of the genus is $x = 21$, unique in Leguminosae. Of the 65 species counted prior to the present study, 61 are diploid ($2n = 42$), two are tetraploid ($2n = 84$), one has reports of both diploid and tetraploid races, and one has reports of hexaploid ($2n = 126$) and octoploid ($2n = 168$) races.

The base number for Phaseoleae and probably for subtribe Erythrinineae is $x = 11$, and reduction to $n = 10$ is common in the tribe. *Erythrina* is likely either an allotetraploid based on $n = 11 + n = 10$ or a hypotetraploid $n = (11 \times 2) - 1$ (Goldblatt, 1981b), and thus a paleopolyploid genus.

MATERIALS AND METHODS

Floral buds were collected from trees in cultivation at three botanical gardens in Hawaii: Pacific Tropical Botanical Gardens in Lawai (PT); Waimea Arboretum in Haleiwa (WA); and Hoʻomaluhia Botanic Garden in Kaneohe (HO). Floral buds and/or seeds were collected from wild populations of certain species in Mexico and Costa Rica.

For gametic counts and meiotic analyses, floral buds in developmental series were fixed either in 3 : 1 ethanol : acetic acid or in 6 : 3 : 1 chloroform : ethanol : acetic acid, which generally provided better fixation. After 1–2 weeks in the fixative at room temperature, buds were transferred to 70% ethanol and stored below 5°C. Anthers were squashed in acetocarmine with Hoyer's solution added (Beeks, 1955) to make permanent slides.

For somatic counts, seeds obtained from wild populations were germinated on filter paper. The primary root tips were pretreated in 0.003 M 8-hydroxyquinoline for 4 hours at room temperature, fixed in 3 : 1 ethanol : acetic acid for 2–12 hours, and hydrolyzed in 10% HCl for 10 minutes at 60°C. Root tips were squashed in FLP orcein (Jackson, 1973).

Slides were examined under phase contrast with a Zeiss Universal microscope; chromosomal configurations were photographed with Zeiss MC63 equipment using Kodak Technical Pan film developed for high contrast.

RESULTS

Chromosome Numbers. Chromosome counts and voucher data are listed in Table 2. For cultivated material the original wild-collected voucher is cited if it exists; if not, a voucher made from the garden progeny is cited. All vouchers are deposited at Missouri Botanical Garden (MO) unless otherwise noted.

The gametic count of $n = 42$ for *E. amazonica* reconfirms earlier somatic counts of $2n = 84$ (Atchison, 1947; Goldblatt & Davidse, 1977) for this tetraploid. This species is distributed throughout the northern Amazon basin and in the Guianas, but all the chromosome counts to date have been obtained from populations in the Brazilian state of Maranhão. A more complete sampling of the species range may reveal infraspecific variation in ploidy level, as has been determined for other species with polyploid strains.

My count of $n = 21$ for the tropical Asian *Erythrina suberosa* is diploid and agrees with 13 previous reports for the species. Mehra (1976), however, reported $n = 42$ in three populations in the western Himalayas, at its geographic margin and altitudinal upper limit. As with *E. amazonica*, a cytogeographic survey of ploidy level in *E. suberosa* is desirable.

With the exception of *Erythrina macrophylla*, the remaining 22 chromosome counts listed in Table 2 are all first reports for species. All are diploid ($n = 21$ or $2n = 42$) except the octoploid *E. burana* ($n = 84$). This Ethiopian endemic is closely related to *E. burttii*, which ranges from Ethiopia south to Tanzania, and for which both hexaploid ($2n$ = ca. 126; Atchison, 1947) and octoploid ($2n$ = ca. 168; Goldblatt, 1981a) counts have been obtained.

Chromosome numbers are now known for 86 of the 112 species of *Erythrina* recognized here. Eighty-one species (94%) are diploid, with the remaining 5 species (6%) polyploid or variable in ploidy level. The polyploid species are all in different sections and are not closely related to one another, with the exception of *E. burttii* and *E. burana*. Polyploidization has thus occurred at least four times independently in *Erythrina*. Given the rarity of polyploidy in the genus, it seems likely that the closely related *E. burttii* and *E. burana* were derived from a common polyploid ancestor.

Chromosome counts have yet to be obtained from 25 species of *Erythrina*. Eleven of these are from Africa where three of the five known polyploids occur. Seven uncounted species are South American, where *E. amazonica* is the only polyploid known. Polyploidy is unknown for *Erythrina* in North and Central America, where 42 of the 45 native species have been counted.

Meiosis in Diploid Species. Chromosome size, morphology, and meiotic behavior were similar in all species examined. Observations of individuals of two typical diploid species, *Erythrina berenices* (WA 81s505) and *E. macrophylla* (PT 750420001), are described and illustrated here.

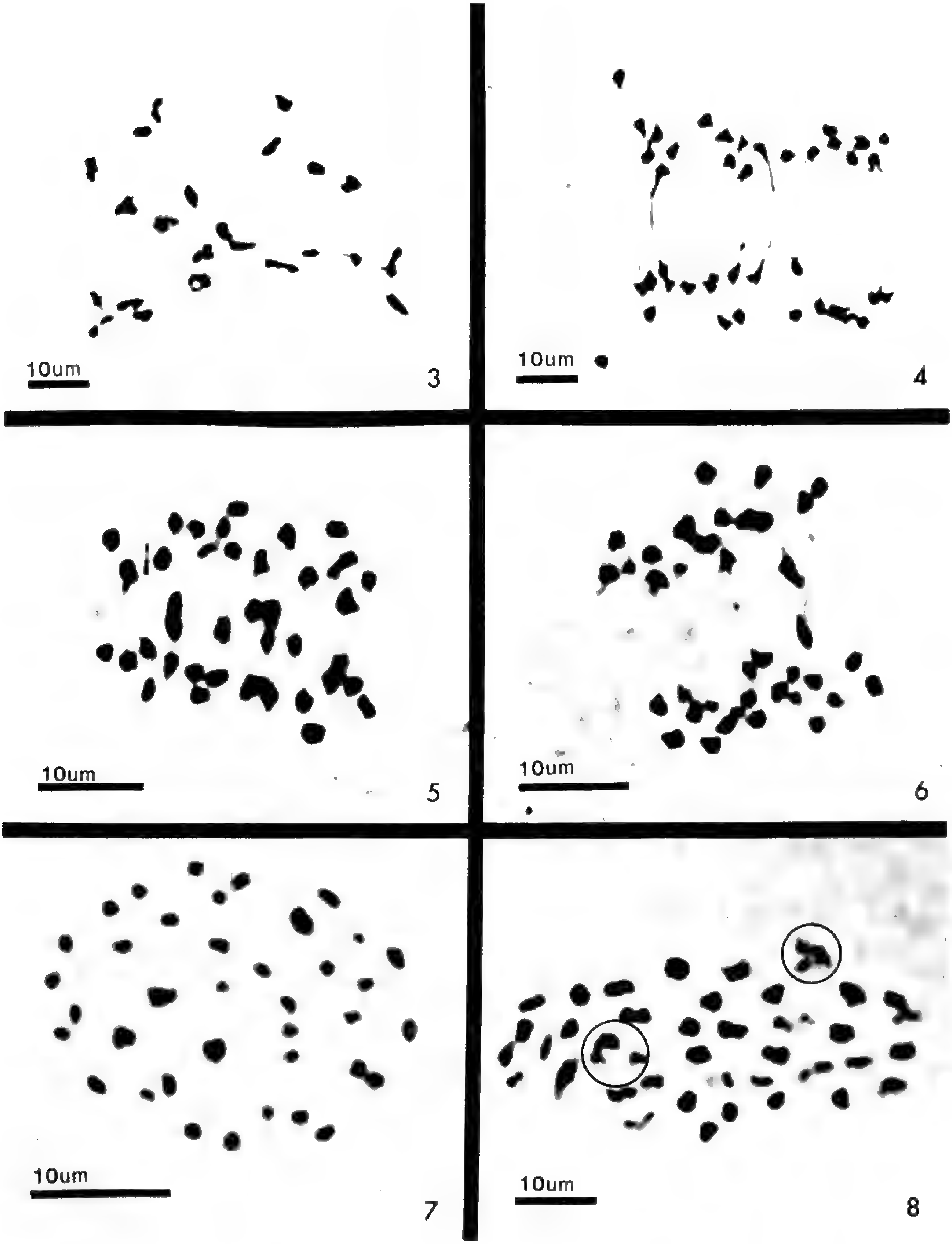
Observations of chromosome pairing at zygotene and pachytene are desirable in meiotic analyses (Jackson, 1984), but these were not feasible in *Erythrina* because of its high chromosome numbers. At diakinesis, 21 bivalents were regularly formed. Each bivalent had either one or two terminal chiasmata. In *E. macrophylla*, the average number of chiasmata per cell was 31.5 ± 1.84 out of 10 cells sampled. This accords with the figures of 31.35 ± 0.54, 31.25 ± 0.61, and 32.08 ± 0.7 chiasmata per cell reported by Jalil et al. (1982) for, respectively, *E. variegata*, *E. resupinata*, and their F_1 hybrid *E.* × *resuparcellii*.

At early to mid diakinesis, the bivalents were generally well separated, thus the gametic chromosome counts listed in Table 2 were usually made at this stage. Toward the later stages of diakinesis and as the nucleolus began to disintegrate, groups of two or more bivalents appeared clumped together in the cell (Fig. 3). Thin strands of chromatin were frequently observed to stretch between bivalents.

TABLE 2. *Chromosome counts of* Erythrina *species reported in this paper. Vouchers are housed at MO unless otherwise indicated.*

Species	*n* =	2*n* =	Voucher Data
E. amazonica Krukoff	42		WA 76s449, cultivated. Brazil. Maranhão: Lapela, *N. T. Silva 4238* (NY).
E. batolobium Krukoff & Barneby	21		Missouri Botanical Garden, cultivated (from wild-collected rootstock). Mexico. Guerrero: Filo de Caballo, 6,300 ft., oak forest, *Neill 5647*.
E. berenices Krukoff & Barneby	21		WA 81s505, cultivated. Mexico. Veracruz: Tlalnelhuayocan, *H. Perales s.n.* in 1981 (NY).
E. breviflora A. DC.	21		Mexico. Guerrero: *H. Iltis 28655*.
E. burana R. Chiovenda	84		PT 740435001, cultivated. Ethiopia. Locality unknown: *F. Meyer s.n.* in 1974. Voucher from cult.: *Neill 5716*.
E. cochleata Standley	21		Costa Rica. Heredia: La Virgen, 10 km SW of Puerto Viejo, 200 m, *Neill 5102*.
E. elenae Howard & Briggs	21		WA 80s614, cultivated. Cuba. Cienfuegos: *Centro de Investigación Forestal s.n.* Voucher from cult.: *Neill 5078*.
E. florenciae Krukoff & Barneby		42	Mexico. Chiapas: Motozintla, Cerro Mozotal, 6,600 ft., *Neill 5600*.
E. gibbosa Cuf.	21		Costa Rica. Alajuela: Cordillera de Tilarán, upper Peñas Blancas valley, below Monteverde reserve, 1,300 m, *Neill 5028*.
E. globocalyx Porsch & Cuf.	21		Costa Rica. San José: Las Nubes, 1,700 m, *Neill 5033*.
E. hondurensis Standley	21		HO 80.037, cultivated. Honduras. Tela: *Hazlett s.n.* in 1980. Voucher from cult.: *Neill 5709*.
E. horrida A. DC.		42	Mexico. Oaxaca: 2 km E of Ixtlán, road to Yavesia, 2,030 m, *M. Sousa 12634* (MEXU).
E. leptorhiza A. DC.	21		Mexico. México: Municipio Ixtapaluca, old Hwy. 190, km 25, 8,300 ft., *Neill 5646*.
E. macrophylla A. DC.	21		PT 750420001, cultivated. Guatemala. Sololá: Godinez, 6,145 ft., *B. A. Krukoff 1975-4* (NY).
E. mexicana Krukoff		42	Mexico. Oaxaca: 14 mi. SW of San Jeronimo Miahuatlán, 4,800 ft., *Neill 5423*.
E. oaxacana (Krukoff) Krukoff		42	Mexico. Oaxaca: 9 km N of Diaz Ordaz, road to Cuajimolaya, 7,700 ft., *Neill 5409*.
E. pudica Krukoff & Barneby	21		Mexico. Chiapas: 15 mi. E of Cintalapa, Hwy. 190, 2,000 ft., *Neill 5440*.
E. sacleuxii Hua	21		WA 74p1296, cultivated. Kenya: Arabuko forest, near coast, *Lavranos 11225* (NY).
E. sigmoidea Hua	21		PT 740192001, cultivated. India: locality unknown, cultivated, *D. A. Millington s.n.* in 1974. Voucher from cult.: *Neill 5715*.
E. smithiana Krukoff	21		PT 740329001, cultivated. Ecuador. Guayas: Manglaralto, *MacBryde & Herrera-MacBryde 690* (NY).
E. sousae Krukoff		42	Mexico. Oaxaca: 14 km S of San Miguel Suchixtepec, 2,100 m, *Neill 5425*.
E. suberosa Roxb.	21		WA 75s960, cultivated. India: Matrimandir Gardens, cultivated. Voucher from cult.: *Neill 5273*.
E. tahitensis Nad.	21		PT 770442001, cultivated. Tahiti: Manupa Ridge, 2,000 ft., *Perlman s.n.* in 1977. Voucher from cult.: *Neill 5177*.
E. tuxtlana Krukoff & Barneby	21		Mexico. Chiapas: 26 km N of Ocozocuautla on road to Malpaso, 2,100 ft., *Neill 5486*.

The characteristic clumping of two or three bivalents became even more common in metaphase I. At anaphase I, long strands of chromatin were frequently observed stretching between disjoining chromosomes, even after the main bodies of the chromosomes were separated by a considerable distance on either side of the equatorial plate (Fig. 4).



FIGURES 3–8. *3–6. Meiosis in pollen mother cells, diploid species of* Erythrina.—*3. Late diakinesis,* E. berenices, *WA 81s505 (n = 21). Clumping of bivalents.—4. Anaphase,* E. berenices, *WA 81s505. Sticky chromatin bridges stretch between disjoined chromosomes.—5, 6. Anaphase,* E. macrophylla, *PT 750420002 (n = 21). Late disjunction of some bivalents.—7. Mitosis in root tip cell of diploid* E. horrida, Sousa 12634 *(2n = 42). Somatic chromosomes are not clumped.—8. Diakinesis in pollen mother cell of tetraploid* E. amazonica, *WA 76s449 (n = 42). Two quadrivalents are circled.*

The chromatin connections between disjoining chromosomes appeared to be in all cases simply "matrix bridges" caused by chromosome "stickiness" (Beadle, 1932). Based on observations at subsequent stages, it is unlikely that any of the observed "bridges" were true dicentric bridges or any other configuration resulting from chromosomal inversions or translocations.

Another frequently observed phenomenon was late disjunction of one or several bivalents at anaphase I (Figs. 5, 6). One or two lagging bivalents were often present even at late anaphase I when most chromosome pairs were completely separated. However, observations of cells at later stages revealed no evidence of nondisjunction or unequal assortment of chromosomes.

In contrast to the chromosome "stickiness" and secondary association of bivalents at meiosis, somatic pairing of homologues was not observed in mitotic root-tip cells. A typical mitotic configuration of the diploid species *Erythrina horrida* ($2n = 42$) is shown in Figure 7, where there is no evidence of pairing or of sticky chromatin connections between chromosomes.

Meiosis in pollen mother cells of the Asian *E. variegata* (as *E. indica* Lam.) was depicted by Sundar Rao (1945) and in several additional Asian species by Mehra (1976). Both reported postsynaptic secondary association of chromosomes at metaphase I and subsequent stages to be common in some species. Mehra (1976) reported aberrant meiosis with 13–21 bivalents, 0–16 univalents, and 0–2 B chromosomes in a diploid strain of *E. suberosa*, while a tetraploid strain of the same species exhibited normal meiosis with 42_{II}. Jalil et al. (1982) reported normal meiosis with 21_{II} in the artificial hybrid *E.* ×*resuparcellii* (*E. resupinata* × *E. variegata*).

Pollen fertility, as estimated by Alexander's double stain technique (Alexander, 1969) was uniformly high in all *Erythrina* species examined. Seventeen individuals belonging to eight species, used as parentals in the experimental hybridization trials, had a mean pollen fertility of 95% (at least 500 grains counted per sample). Such high fertility suggests that the chromatin "bridges" and late disjunction of bivalents observed in most cells at anaphase I are not indicative of meiotic aberrations, do not result in a high frequency of aborted cells, and therefore most cells receive the correct complement of 21 chromosomes following meiosis I and II.

Meiosis in Polyploid Species. Among the tetraploid species of *Erythrina*, only a single strain of *E. amazonica* was available for analysis (WA 76s449; PT 760356001). In several individuals of this strain, 42 bivalents were observed in some cells at diakinesis and metaphase I, while in others one or two quadrivalents were clearly visible (Fig. 8). In contrast to the merely "sticky" postsynaptic associations seen in the diploids, the quadrivalents in *E. amazonica* appeared to be true multivalents resulting from synaptic pairing at prophase. The configuration of this species at meiosis I, then, is $38\text{–}42_{II}$ and $2\text{–}0_{IV}$. The formation of occasional quadrivalents did not disrupt normal disjunction, however, as no cells at telophase I or subsequent stages were observed with other than 42 chromosomes.

At diakinesis and metaphase I of the octoploid *E. burana*, considerable clumping of chromosomes was evident in all cells examined. With a large number of chromosomes crowded together, the configurations were not completely resolvable and it was not possible to determine whether synaptic multivalents were actually formed.

DISCUSSION

The postsynaptic secondary association of bivalents at meiotic metaphase observed in diploid *Erythrina* species has been reported from many other plant groups. According to a theory introduced by Darlington (1930) and amplified by Lawrence (1931), secondary pairing is due to attraction of homologous or homeologous chromosomes when the degree of homology is not close enough to result in synaptic pairing, and is presumed to be indicative of allopolyploidy. In a recently formed autotetraploid, homology between the two pairs of chromosomes will be nearly complete and a multivalent will be formed at pachytene. In an allotetraploid or in an "old" tetraploid in which the genes of homeologous chromosomes have diverged to some extent, two bivalents result; they may later form a secondary association at metaphase I or late diakinesis due to attraction between the homeologous chromosomes making up the two bivalents. Secondary pairing does not always occur, however; it is a relatively loose association and does not affect disjunction at anaphase I.

This interpretation of secondary pairing and its relation to allopolyploidy has been borne out by quantitative studies of the spatial distribution at metaphase I of marked homeologous chromosomes in the allohexaploid *Triticum aestivum* (Kempanna & Riley, 1964). In other plant groups such a rigorous quantification of secondary pairing has not been obtained, but a number of workers have inferred a history of polyploidy in groups with meiotic secondary pairing, particularly for those with high chromosome numbers suspected to be paleopolyploids. For example, Venkatasubban (1944), in a cytological study of Bignoniaceae, found a base number of $n = 20$ for the family and a presumed ancestral base number of $x = 10$, since up to 10 "secondarily associated" pairs of bivalents were present at metaphase I in many species. The evidence from secondary pairing is not unequivocal, however; in the case of Bignoniaceae, Goldblatt & Gentry (1979) believed $n = 20$ to be a paleohexaploid of a base number $x = 7$, with aneuploidy from $n = 21$.

Both Sundar Rao (1945) and Mehra (1976) noted secondary pairing in *Erythrina*, and the latter author cited it as evidence for an ancestral lower base number for the genus. On the basis of present knowledge, however, it is not possible to state unequivocally that the observed meiotic patterns in diploid *Erythrina* species are due to secondary pairing of specific homologous or homeologous chromosomes, and not simply to random nonhomologous "stickiness" of chromosomal matrix material. Multivalent formation in *E. amazonica*, a neopolyploid, does appear to be a result of true synaptic pairing of homologous chromosomes.

The hybridization trials carried out in *Erythrina* (described below) reveal a high degree of structural and genic homology in the chromosomes of all species, and it is probable that virtually any *Erythrina* genome can combine with that on the same ploidy level of any other species in the genus to form a viable F_1 hybrid. Whether tetraploid *E. amazonica* is of autoploid or alloploid origin, then, it must have two highly homologous sets of chromosomes. It is somewhat surprising that more than two quadrivalents are not usually formed in meiosis I of *E. amazonica*. It is possible that the species contains a specific gene that suppresses multivalent formation and promotes strict homologous pairing of bivalents, similar to the Ph gene which performs this function in hexaploid *Triticum aestivum* (Riley & Chapman, 1958).

SECTION 4. EXPERIMENTAL HYBRIDIZATION AND SELF-COMPATIBILITY

MATERIALS AND METHODS

Experimental hybridizations and self-compatibility trials were conducted at Pacific Tropical Botanical Garden and Waimea Arboretum February–July 1982 and February–April 1984. Although the living *Erythrina* collections at the two gardens share many accessions from the same sources, the species complement of mature, flowering individuals was different at each garden. The use of both gardens allowed a broader inclusion of taxa in the experimental studies than would have been possible otherwise.

In addition, self-compatibility trials and interspecific hybridizations were conducted with natural populations of *Erythrina chiapasana* and *E. goldmanii* at El Sumidero Canyon National Park in Chiapas, Mexico in February 1983. The two species are parapatric at El Sumidero and hybridize naturally (this paper, Section 6).

In all, 32 species were used in the interspecific hybridization trials, in 155 hybrid combinations including reciprocals. Species from throughout the worldwide distribution of *Erythrina* were used in the trials; four of the five subgenera and 12 of the 27 sections were represented. The monotypic African subg. *Tripterolobus* was the only subgenus not included. Eighteen species were tested for self-compatibility. All species used in the trials are diploids ($n = 21$) except *E. amazonica*, a tetraploid ($n = 42$). Attempts were made to hybridize *E. amazonica* as the pollen parent with several diploid species.

The hybrid combinations were selected to represent different "taxonomic distances" between the female and male parental species: "narrow hybridizations" between species of the same section, "medium hybridizations" between species of different sections in the same subgenus, and "wide hybridizations" between species of different subgenera. The narrow hybridizations involved mostly species within sect. *Erythrina*. The medium and wide hybridizations included crosses of sect. *Erythrina* to other sections and subgenera, as well as representative hybridizations not involving sect. *Erythrina*, selected to include the maximum taxonomic diversity and geographic range of the genus.

Constraints on the Experimental Protocol. Shortly after the initiation of the pollination trials, certain constraints imposed by *Erythrina* breeding systems became apparent. Other constraints were imposed by the fact that the experimental subjects were trees exposed to the vicissitudes of the weather and to local, uncontrolled variation in other factors that may affect reproductive success, such as soil fertility and moisture, and insolation. These considerations required a somewhat different experimental protocol and a different statistical treatment of the results than has been customary with biosystematic studies of greenhouse-grown herbaceous plants.

The proportion of fruit set in intraspecific and interspecific pollinations was quite low (see Results, below) and the incidence of postfertilization abortion of young fruits was very high. Pollination success and fecundity varied greatly among individuals of the same species. Some trees were effectively "female sterile": they produced no fruits either spontaneously (i.e., from "open-pollinated" flowers) or from controlled pollinations. At the same time, conspecifics and even individuals from the same accession, which were presumably at least half-siblings of the "female sterile" individuals, produced fruits spontaneously in abundance and produced fruits quite readily from both intraspecific and interspecific controlled pollinations. For many species only a single tree was available, so the use of intraspecific outcrossing success rate as a control was not possible for those species.

Another constraint was the often limited number of flowers per tree that were accessible each day. On many trees only one or a few inflorescences producing three or four new flowers each day were accessible for hand-pollination. The time required to emasculate, isolate, and pollinate each flower individually also limited the number of flowers that could be treated each day. Another practical consideration was the amount of land and labor required for growing the hybrid progeny at the Hawaiian botanical gardens. It was desirable to obtain progeny of many different hybrid combinations, so with limited resources large F_1 families of any particular combination could not be accommodated.

One positive aspect of *Erythrina* reproductive systems that influenced the experimental protocol was the relatively high viability of the seed. Among the hybrids, 45% of the seeds germinated and produced healthy F_1 plants. This high viability meant that large seed lots of any particular combination were not necessary to ensure that at least some progeny would survive to maturity.

The above considerations and constraints led to the development of procedures designed to maximize the number of "narrow," "medium," and "wide" hybrid combinations without undue emphasis on any particular combination. Once several well-formed maturing fruits were produced for any combination, pollinations of that combination were ceased and new combinations were attempted. When possible, species combinations were repeated using several different individuals as female and/or male parents. For self-compatibility trials as well, pollinations within an individual were terminated once several semimature fruits had developed.

In the course of the pollination trials it soon became apparent that certain individual trees of several species were more fecund, successful female parents than others. To the extent possible, pollination trials were concentrated on the more successful females, within the limitations imposed by the number of flowers available. Hybrid combinations or self-pollinations that failed to set fruit were repeated up to 50 times or more, but for many combinations fewer than 10 flowers were pollinated due to limitations of time and available flowers.

Pollination Techniques: Hybridization. The development of suitable techniques to emasculate, isolate, and pollinate the flowers involved considerable trial and error. Nylon mesh bags of several types were used initially to isolate the flowers, but these proved to be too unwieldy, requiring elaborate, heavy wire frames or other means of support so the mesh did not touch the flowers. Also, in rainy weather the high humidity within the mesh bags tended to cause all the flowers to abort.

A simple alternative technique that proved successful was to isolate each flower individually. Floral buds were emasculated at the latest possible stage of development, i.e., on the day before anthesis and pollen release. The tightly closed corolla standard was carefully peeled open, and the anthers were excised with dissecting scissors sterilized in 95% ethanol between each emasculation. If an anther released pollen before removal, the flower was not used in the experiment. Following emasculation, the corolla standard was folded back over the pistil and sealed with plastic Scotch tape. This effectively protected the stigma from any chance pollen deposition and also prevented it from drying out. The following day the corolla was reopened and the standard excised. After pollination a small cone of aluminum foil, formed over the point of a pencil, was placed over the stigma and pinched lightly onto the style. This helped to hold the pollen on the stigma in the face of rain and wind, and isolated the stigma from any other pollen deposition. The cap remained on the stigma throughout the development of the fruit.

For the open-corolla, homogamous species of *Erythrina* adapted to pollination by passerine birds, this technique ensured that the pollen was applied while the stigma was receptive. In most species receptivity was signalled by presence of a wet, sticky exudate on the stigmatic surface on the day of anthesis. For the closed-corolla, protandrous species (primarily sect. *Erythrina*) adapted to hummingbird pollination, the style had not elongated fully and the stigma was not yet receptive on the day following emasculation. The stigma was thus pollinated prematurely by this method, but the pollen held in place by the aluminum cap evidently remained viable at least until the next day when the stigma became receptive, and these species did set fruit with premature pollination. An alternative method, to wait two days following emasculation to pollinate the protandrous species, yielded no better results and was logistically more complicated.

Stephenson (1981) presented evidence from an extensive literature review that in many plant species, particularly massively blooming trees, only a small fraction of pollinated flowers produce mature fruits; the majority are aborted at an early stage of growth before large amounts of nutrients are channelled into them. The number of fruits that can be matured is usually limited by resource availability, not by pollination. Furthermore, flower and fruit abortion is selective: some species selectively shed self-pollinated flowers. They mature fruits from self-pollinated flowers only when fruit set is low and/or when "higher quality" fruits from cross-pollinated flowers are removed. Therefore there may be "mate competition" within a plant among fruits of different paternity.

In this study attempts were made to reduce, to the extent practical, the effects of resource limitation and competition on mating success. All flowers except the hand-pollinated ones were removed from the inflorescence. Once a few fruits were set on an inflorescence, all flower buds were removed. Until fruits were set, buds were left to develop into flowers available for further pollination trials. Most inflorescences bloomed continuously for several weeks, producing a few new flowers each day, so failed matings could be attempted repeatedly.

An individual inflorescence was treated with pollen from a single source. This eliminated mate competition among the flowers within the inflorescence. An individual tree often had several inflorescences, each pollinated with a different species of male parent, so there could have been interinflorescence competition among mates.

To further reduce resource competition and channel available nutrients into the hand-pollinated flowers, most untreated inflorescences and spontaneous, open-pollinated fruits (those accessible with clipper poles) were removed from the crowns of the trees.

In all species, seeds matured approximately 60 days after pollination. At maturity the hybrid fruit was removed and the number of mature seeds, aborted seeds, and undeveloped ovules was recorded. Length and width of each mature seed were measured for comparison with seeds produced from intraspecific matings.

Tests for Self-Compatibility, Autogamy, and Apomixis. For self-pollinations and intraspecific outcrosses, anthers were not emasculated, but the corolla standard of the flower bud was sealed with tape prior to dehiscence to prevent chance deposition of nonself pollen on the stigma. When the stigma became receptive, pollen from the same tree (for selfs) or from different conspecific trees (for outcrosses) was applied, and a cap of aluminum foil was placed over the stigmas in the same manner as in the intraspecific hybridizations.

The pollen for the outcrosses was a mixture from all available conspecific trees in the botanical garden, including individuals from the same accession as the female parent as well as from different accessions. For the self-compatibility trials carried out in the natural populations of *Erythrina chiapasana* and *E. goldmanii* at El Sumidero, the pollen for the outcrosses was a mixture of at least five different individuals in the population.

The treated flowers of an individual inflorescence were either all selfed or all outcrossed to eliminate within-inflorescence mate competition.

The abortion of young fruits during the first two to three weeks following fertilization was very high for selfs and intraspecific outcrosses, as well as for interspecific hybridizations. Fruit set data were taken at least four weeks following pollination, after which abortion of the developing fruits was negligible. Complete data on intraspecific reproductive success, including mature seed production and seed size, germination success, and viability of the progeny, were obtained only for cultivated *Erythrina guatemalensis* and *E. crista-galli*. Several individuals of these species from different accessions were available for the trials, and they were the most successful female parents in the interspecific hybridizations. For comparative analyses, then, the intraspecific data were particularly desirable for these two species. Because of space and labor limitations, intraspecific progeny could not be raised for all species.

In the flowers of sect. *Erythrina* and the other hummingbird-pollinated sections of the genus, the anthers and stigma are positioned close to one another. Initial observations indicated that, although the flowers are protandrous, autogamy may sometimes take place. Autogamy was tested by isolating entire inflorescences in wire-framed nylon mesh bags. After all the flowers had either aborted or set fruit, the mesh was removed. Six species were tested this way at Pacific Tropical Botanical

Garden during a period of relatively dry weather (May 1982) to minimize abortion of flowers caused by high humidity inside the mesh bags.

Autogamous fruits were obtained only on the most distal flowers (the last to open) on inflorescences of two individuals of *Erythrina guatemalensis* (Results, Table 4). These individuals were tested for agamospermy. On three inflorescences of each plant, all the flowers on the distal one-third of the inflorescence were emasculated before dehiscence, and the stigmas were covered with aluminum foil caps to prevent any pollen deposition on the stigma. Fruit set was monitored in the same manner as in the pollination trials.

Statistical Analysis of Results. The protocol described above was necessitated by the flowering patterns and reproductive traits of *Erythrina*, by practical limitations of breeding trees in the heterogeneous environments of open-air botanical gardens, and by the goal of obtaining viable progeny of as many "narrow," "medium," and "wide" hybrid combinations as possible. The resulting small and very unequal sample sizes for different hybrid combinations as well as for selfings and intraspecific outcrosses meant that outcomes of particular combinations could not be compared statistically. Instead, for statistical analyses hybrid combinations and intraspecific matings were pooled into broad categories based on taxonomic distance (assumed for the purposes of the study to be a true representation of relative genetic and phylogenetic distance) between the female and male parents. The five experimental treatments are: self-matings, intraspecific outcrosses, and the three categories of hybrid combinations—"narrow," "medium," and "wide" hybridizations.

For statistical analyses, mating success for each treatment was expressed as the proportion of hand-pollinated flowers producing mature fruit (i.e., a fruit with at least one fully developed, normal-sized seed). The commonly used analysis-of-variance (ANOVA) tests (e.g., Sokal & Rohlf, 1969; Statistical Analysis Institute, 1982) are designed to test the significance of differences between means of continuously variable data. ANOVA tests are inappropriate for categorical (either/or) data, such as mating success, where the outcome of a pollination attempt falls into one of only two categories. A multiple comparison test for differences between proportions, appropriate for categorical data, was devised by Alan R. Templeton for these analyses. Templeton's test allows for pairwise comparisons of all combinations of the five treatment categories; also, categories can be pooled to test various hypotheses regarding mating success (e.g., all intraspecific vs. all interspecific matings).

The null hypothesis for the test was that there is no difference in proportion of mature fruits produced among any of the pollination treatments. This is a corollary of the central hypothesis of this research: that there are no interspecific or self-incompatibility barriers to mating within *Erythrina*, that any pair of gametes from any species in the genus are equally likely to pair successfully, form a viable zygote, and grow into a healthy adult sporophyte regardless of the infrageneric taxonomic position or putative phylogenetic distance between the parents.

Templeton's test is an inequality that compares the differences between proportions with their variances. Proportions are subjected to an arcsine–square root transformation to set the variance independent of the mean; the variance is inversely proportional to the sample size. The 95% confidence limits of the proportion are:

$$X = \arcsin\sqrt{\frac{F}{N}} \pm 1.96\sqrt{\frac{1}{4N}},$$

where F = number of mature fruits (successful matings); N = number of flowers pollinated (attempted matings).

For small sample sizes ($N < 50$), the arcsine–square root transformation is corrected:

$$X = \frac{1}{2}\left(\arcsin\sqrt{\frac{F}{N+1}} + \arcsin\sqrt{\frac{F+1}{N+1}}\right).$$

For the general case, the null hypothesis is rejected at $P = 0.05$ if the inequality is true:

$$\left|\sum a_i X_i\right| > 0.98\sqrt{\frac{a_i^2}{N_i}},$$

where X_i = the arcsine–square root transformed proportion of successful matings in the ith category; N_i = sample size (total number of flowers pollinated in the ith category); and a_i = a weighting factor set so that $|\sum a_i| = 0$.

The a_i for each category is proportional to the sample size N_i.

For pairwise comparisons between categories i and j, the inequality is simplified; the H_0 is rejected at $P = 0.05$ if it is true that

$$|X_i - X_j| > 0.98\sqrt{\frac{1}{N_i} + \frac{1}{N_j}}.$$

For a test of "highly significant" difference at

$P = 0.01$, the term "0.98" on the right side of the inequality is replaced by the value "1.28."

Several individuals of *Erythrina guatemalensis* and *E. crista-galli* were the most fecund, successful females in the interspecific hybridizations as well as the intraspecific matings. For all categories employing these two species as female parents, separate multiple comparison tests were used to compare mating success. These comparisons included both selfings and intraspecific outcrosses for *E. guatemalensis* but only selfings for *E. crista-galli*, which had only one individual in flower at each garden (Pacific Tropical and Waimea) when the pollinations were conducted.

Separate statistical tests were carried out for the self-compatibility trials of individual species. For those species with analyzable data on fruit set of self-pollinations vs. intraspecific outcrosses, the data were ordered into 2 × 2 contingency tables. With small sample sizes and values of less than 5 in many cells of the contingency tables, the standard chi-square test was not appropriate; so Fisher's exact probability was computed for the outcomes (Sokal & Rohlf, 1969). For the pooled self-compatibility data including all species tested, the sample size was large enough for a chi-square test.

F_1 Hybrid Viability. The F_1 hybrid seeds were planted within a few weeks after harvest. To the extent possible, seed lots of each hybrid combination were divided for propagation at two sites. The F_1 plants were raised by the horticulturists at Pacific Tropical and Ho'omaluhia Botanical Gardens, who monitored germination success, growth, and vigor of the hybrids. Evaluations were made approximately once each six months using a standardized form. Survivorship, growth rates, and indications of chlorosis or other abnormalities were recorded.

The multiple comparison test described above for analysis of fruit set was employed for a statistical evaluation of hybrid viability, defined as the proportion of seeds in each category that germinated and survived as healthy plants for six months (after which mortality in the garden was negligible). Viability of the "narrow," "medium," and "wide" F_1 hybrids was compared, together with that of the "narrow" F_2 hybrids in sect. *Erythrina* (see below). Seeds from controlled intraspecific matings of *Erythrina guatemalensis* and *E. crista-galli* were planted along with the hybrids. For each of these species a separate multiple comparison test was conducted for viability of "intraspecific" seed vs. hybrid seed having these two species as female parents.

F_1 Hybrid Fertility. Many of the narrow hybrids between species in sect. *Erythrina*, produced in 1982, grew to be 4-m trees and produced flowers by February 1984. By several different measures of fertility, these F_1s were compared with the parental species and their meiosis examined. As an estimate of pollen fertility, percentage of stainable (nonaborted) pollen was determined for the F_1 hybrids and their parents using Alexander's double stain technique (Alexander, 1969) (at least 500 grains counted per sample) and compared with a one-tail *t*-test.

Fecundity of F_1 Hybrids. As discussed earlier, one goal of the hybridization study was to assess the relative fitness of the hybrids in comparison with their parents. The viability, vigor, meiotic regularity, and pollen fertility of the hybrids are indicators of fitness, but a more direct measure is their relative reproductive success vis-à-vis that of the parental species. During the period of this study the F_1 hybrids, although some of them produced flowers and fruits, did not grow into full-sized adult trees, so a thorough assessment of hybrid fecundity and fitness was not possible. However, a preliminary indication of reproductive success was obtained from the two-year-old narrow hybrids in sect. *Erythrina* that flowered in the spring of 1984.

Controlled self-pollination of some of these F_1 hybrids was conducted in order to obtain seed for a limited number of F_2 families. The multiple comparison test was employed for pairwise comparisons of mating success (proportion of hand-pollinated flowers producing mature fruits) between the selfed F_1s and their parental species. Different categories of parental matings varied among themselves in mating success, and several types of parental matings were compared with the selfed F_1s. The pairwise comparisons of fruit set included: 1) selfed F_1s vs. their own parental matings, i.e., the original hybridizations that produced the F_1s used in the trials; 2) selfed F_1s vs. all paired combinations of the parental species, including the reciprocals that failed to produce F_1 hybrids; 3) selfed F_1s vs. selfed parental species. The logic for using these particular groupings of parental matings in the comparative assessment of F_1 reproductive success is discussed in the Results.

Viability of F_2 Hybrids. Many of the F_1s also produced fruit and mature seed spontaneously on open-pollinated inflorescences, almost certainly the result of autogamy. F_2 seed lots from selfed flowers, and some from open-pollinated flowers, were planted along with the 1984 F_1 hybrids. The viability of the F_2 progeny was compared with that of the F_1s.

Studies of Previously Synthesized Hybrids. A few *Erythrina* hybrids have been produced in the past by horticulturists and are commonly grown in tropical and subtropical regions. Two were available at the Hawaiian gardens: *Erythrina* ×*bidwillii* and *E.* ×*sykesii.* Studies of meiosis, pollen fertility, and fruit set from controlled self-pollinations were conducted on these plants with the methods described above.

Hybrid Names. In this paper horticultural convention (Brickell et al., 1980) is followed for the hybrid names. For artificial hybrids when the female parent is known, the female parent is first in the hybrid formula name. When the female parent is not known, as in natural hybrids, the order of the constituent species names is alphabetical.

RESULTS AND DISCUSSION

The results of the experimental hybridizations, self-compatibility trials, and studies of viability and fertility of the progeny are presented in summary form for the statistical analyses of the data. In addition, more complete data sets, listing the results obtained from individual plants, are presented in certain of the tables below.

There are several reasons for this more thorough reporting of the data. The first is to provide the most complete information available on the ancestry of each individual in the F_1 and subsequent hybrid generations. The full documentation is necessary for the studies on the inheritance of various traits in the hybrids. Studies of morphological inheritance were initiated in this paper (Section 5), and research on the inheritance of micromolecular and macromolecular traits in the interspecific hybrids is anticipated for the future. In addition, some of the hybrid plants with their colorful flowers are likely to be propagated widely as ornamentals; the tables presented here serve as public documentation of the parentage of these cultivars. Finally, it is hoped that some of these experiments will be repeated with the same parental and hybrid trees in the Hawaiian botanical gardens. The documentation of the results for individual plants of traits probably indicative of reproductive success, such as pollen fertility and fruit set, will allow investigation of the possibility that such traits may change through time with the maturation of the plant.

Self-Compatibility. The results of the self-compatibility trials are shown in Table 3. The low percentage of mating success in the pooled data for all species—6% fruit set for selfings and 10% for outcrosses—is due to a high incidence of postzygotic abortion of young fruits and to failure of pollen tubes to reach the ovules, but the relative importance of these two factors is not known. For the pooled totals, the difference in fruit set between selfs and outcrosses is nonsignificant.

Statistical comparison of fruit set in selfs vs. outcrosses was possible in four species. In only one of these, the natural population of *Erythrina goldmanii* at El Sumidero, was fruit set significantly higher in outcrosses than in selfs, and then but marginally so at $P = 0.05$.

In six additional species, self-pollinated flowers set fruit, but only one individual of the species was available, so the outcrossing control was not possible. In nine species, no fruits were set from self-pollinated flowers, but in four of these the outcrossing controls yielded no fruits either. Failure of fruit set, then, is evidently a consequence of overall low fecundity in *Erythrina* and not of self-incompatibility per se.

Self-incompatibility has previously been reported for seven species of *Erythrina*: *E. senegalensis* and *E. speciosa* (East, 1940); *E. crista-galli* (Fryxell, 1957); *E. mitis* and *E. poeppigiana* (Arroyo, 1981); *E. leptorhiza* (Hernández & Toledo, 1979); and *E. montana* (Hernández, 1982). Only for *E. montana* was the assertion of self-incompatibility supported by evidence from experimental self-pollinations and outcrossing controls. Calculation of Fisher's exact probability for the data presented in Hernández (1982), however, reveals that the difference in fruit set between selfs and outcrosses in *E. montana* is nonsignificant ($P = 0.25$). My evidence for self-compatibility in *E. senegalensis* and *E. crista-galli* contradicts the earlier reports of self-incompatibility in these species, which were based merely on the failure of isolated cultivated trees to produce seed spontaneously. Feinsinger et al. (1979) provided evidence from experimentally controlled pollinations that *E. fusca* and *E. pallida* are self-compatible.

There is thus no reliable evidence for genetic self-incompatibility in any species of *Erythrina*. It appears safe to assume that genetic self-incompatibility—at least the classical single-locus, multiple S-allele, stigma- or style-mediated model of self-incompatibility (Nettancourt, 1977)—is completely absent from the 112 species in the genus. If this is true, it would invalidate some of the evidence that Arroyo (1981) advanced to support her assertion that tropical woody Papilionoideae are predominantly self-incompatible. Five of the

TABLE 3. *Self-compatibility trials in* Erythrina.

Species[1]	Self Flowers	Self Fruits[2]	Outcross Flowers	Outcross Fruits[2]	Probability, Self vs. Cross
E. berteroana (4)	27	0	9	0	—
E. chiapasana (2)	14	0	—	—	—
E. chiapasana[3] (6)	32	4 (0.13)	15	1 (0.07)	0.48*
E. crista-galli (1)	27	7 (0.26)	—	—	—
E. elenae (1)	27	0	—	—	—
E. falcata (1)	5	1 (0.20)	—	—	—
E. folkersii (1)	2	2 (1.0)	—	—	—
E. fusca (2)	82	1 (0.01)	85	1 (0.01)	> 0.05**
E. goldmanii[3] (6)	27	3 (0.11)	23	8 (0.35)	0.05*
E. guatemalensis (5)	33	3 (0.09)	28	7 (0.25)	0.09*
E. latissima (1)	10	0	—	—	—
E. lysistemon (1)	25	4 (0.16)	—	—	—
E. perrieri (2)	27	0	1	0	—
E. sandwicensis (1)	49	2 (0.04)	—	—	—
E. senegalensis (1)	28	2 (0.07)	—	—	—
E. speciosa (2)	21	0	8	0	—
E. standleyana (1)	9	0	—	—	—
E. tahitensis (2)	64	0	—	—	—
E. variegata (1)	6	0	6	0	—
Total	515	29 (0.06)	175	17 (0.10)	> 0.05**

[1] In parentheses: number of individuals used in trials.

[2] In parentheses: proportion of pollinated flowers producing mature fruits.

[3] Pollinations conducted in natural population at El Sumidero, Chiapas, Mexico.

* Fisher's exact probability.

** Chi-square probability.

27 species Arroyo listed in that habitat/life form category as self-incompatible were *Erythrina* species. There are very few comparable studies on other genera of tropical woody Papilionoideae. With the information presently available, it is not known if *Erythrina* is an anomaly, or if self-compatibility is common in this group of plants. Because low fecundity and high rates of flower and fruit abortion are probably characteristic of these plants, greater caution is required in carrying out and interpreting self-incompatibility tests than has customarily been taken.

It is true that fruit set is frequently lower in self-matings than in outcrosses. This may be due not to genetic self-incompatibility, but rather to multiallelic inbreeding depression, expressed either in the progamic phase as failure of pollen tubes to reach the ovules (Mulcahy & Mulcahy, 1983) or as postzygotic abortion of young fruits.

Although *Erythrina* species are genetically self-compatible, the production of seed from selfed flowers in natural populations may be quite limited. A flowering tree visited by pollen-bearing birds will receive many geitonogamous pollinations (pollen from a different flower on the same individual) as well as xenogamous pollinations (pollen from a different individual). The reduced fruit production from self-pollinations, as well as the relatively poor viability of selfed seed (see section on F_1 viability below) suggests that progeny derived from selfed flowers are low in "quality" relative to progeny derived from outcrossed flowers. The selective abortion of low-quality selfed fruits, cited by Stephenson (1981), may be operative in *Erythrina*. Interfruit competition may be very intense under natural conditions, since such a small proportion of pollinated flowers develops into mature fruits. Therefore it is possible that most successful progeny are derived from outcrossing, and that the level of inbreeding in most *Erythrina* populations is quite low in spite of self-compatibility and a large proportion of geitonogamous pollinations. This is still speculative; the significance to mating success of mate competition among male parents has not been explored in *Erythrina*.

In regard to flower and fruit abortion, the attempts to increase mating success by eliminating the effects of competition and resource limitation in the experimental pollination trials were only partially successful. Certainly the fruit maturation rates of 25% or more obtained in some of the outcrossing trials represent an increase in fruit production over

TABLE 4. *Tests for autogamy and agamospermy in* Erythrina *at Pacific Tropical Botanical Garden.*

I. Test for autogamy

Species	Accession Number	Inflorescences Bagged	Flowers	Fruits	Seeds
E. abyssinica	770034001	3	90	0	0
E. berteroana	700044001	3	124	0	0
E. crista-galli	740283001	3	152	0	0
E. guatemalensis	720999001	2	165	1	2
E. guatemalensis	720999002	3	96	0	0
E. guatemalensis	750419001	3	148	5	8
E. humeana	740283001	4	156	0	0
E. macrophylla	750420001	4	86	0	0
E. salviiflora	721000002	2	63	0	0

II. Test for agamospermy (in individuals exhibiting autogamy)

Species	Accession Number	Inflorescences Treated	Flowers Emasculated	Fruits Set
E. guatemalensis	750419001	3	30	0
E. guatemalensis	720999001	3	66	0

the percentages found in natural populations. Usually the percentages of fruit maturation were much lower, however, and in all cases the majority of pollinated flowers were aborted early in development. The factors promoting flower and fruit abortion are several, including nutrition and resource limitation, competitive effects, possible damage to the flowers caused by emasculation, and factors such as adverse weather conditions, in addition to the factor under consideration here: the genetic compatibility of the female and male parents. Neither for the self-compatibility trials nor for the experimental hybridizations was it possible to sort out all of these variables.

Autogamy and Agamospermy. The results of the tests for autogamy and agamospermy are shown in Table 4. Autogamous fruits were produced only on two individuals of *Erythrina guatemalensis.* Significantly, these were rather "fecund" trees with relatively high mating success from controlled hand-pollinations. The autogamous fruits were produced only from the uppermost three fascicles of flowers on an inflorescence—the last flowers to bloom. They evidently were produced, in part, because of the occasional breakdown of protandry, which prevents autogamy on most flowers of *E. guatemalensis* and the other species that are adapted to hummingbird pollination (Neill, 1987).

Although autogamous fruits were produced in my limited trials only on *Erythrina guatemalensis,* I believe that occasional autogamy is widespread in the genus. Cultivated trees of many species produce some fruits spontaneously in the absence of evident pollen vectors.

The fact that autogamous fruits are produced only on the latest flowers of an inflorescence suggests that the breakdown of protandry may be an adaptive mechanism that allows some seed set in the absence of the appropriate avian pollen vectors. Each inflorescence, although it may produce 75 or more flowers, will mature only a few fruits, so fruit set on the lower, earlier-blooming flowers of the inflorescence must inhibit the formation of fruits on the upper, later-blooming portion. It is likely that autogamous fruits from the ultimate flowers of the inflorescence will be produced only if some allogamous fruits (from either xenogamous or geitonogamous pollinations) have not already been produced on the lower portion of the inflorescence.

The two *Erythrina guatemalensis* trees that produced autogamous fruits were tested for agamospermy (Table 4). No fruits were produced when stigmas were isolated from pollen deposition, so agamospermy is not indicated. Agamospermy is almost unknown in the Leguminosae (Arroyo, 1981) and it is unlikely to occur in *Erythrina.*

Hybridization Trials: Mating Success (Fruit Maturation). The complete results of the hybridization trials are listed in Appendix II. From 1,671 hybridization attempts in 155 hybrid combinations, 98 mature fruits were produced in 47 hybrid combinations, for an overall hybrid mating success of 6%, in 30% of the attempted combinations.

TABLE 5. *Proportion of hand-pollinated flowers producing mature fruit: all diploid* Erythrina *species.*

Pollination Treatment	Flowers Pollinated	Fruits Matured	Proportion Fruit Set
Selfed	515	29	5.6%
Intraspecific outcross	175	17	9.7%
Narrow hybridization (within section)	540	50	9.3%
Medium hybridization (between sections, within subgenus)	350	22	6.3%
Wide hybridization (between subgenera)	705	25	3.6%
Total	2,285	143	6.3%

Multiple comparison test for differences between treatments in proportion of fruit set

Self vs. outcross	N.S.[1]
Self vs. narrow hybrid	$P < 0.05$
Self vs. medium hybrid	N.S.
Self vs. wide hybrid	N.S.
Outcross vs. narrow hybrid	N.S.
Outcross vs. medium hybrid	N.S.
Outcross vs. wide hybrid	$P < 0.01$
Narrow hybrid vs. medium hybrid	N.S.
Narrow hybrid vs. wide hybrid	$P < 0.01$
Medium hybrid vs. wide hybrid	N.S.
Intraspecific vs. hybrids	N.S.
Outcross + narrow hybrids vs. self + medium + wide	$P < 0.01$

[1] N.S. = not significant ($P > 0.05$).

For the statistical analysis of mating success in selfs, intraspecific outcrosses, and hybridizations (Table 5), data from the diploid species only were included. The tetrapoloid *Erythrina amazonica* as male parent, after numerous pollination attempts with the diploids *E. guatemalensis* and *E. crista-galli* as female parents, produced one hybrid seed with each of the females. Neither of the seeds germinated, however, so there are no successful hybrids between *Erythrina* species of different ploidy levels. Since the results from *E. amazonica* are not germane to the hypotheses of the interfertility of diploid species and the formation of homogamic complexes, they were excluded from the statistical analysis.

The results for the diploid species in Table 5 indicate that the highest mating success was obtained with intraspecific outcrosses and "narrow" hybridizations (within sections). "Medium" hybridizations (intersectional, intrasubgeneric) and selfings were intermediate in mating success, and "wide" (intersubgeneric) hybrids were the least successful of the five treatment classes. A general trend, then, is evident: interspecific matings between closely related species (within sections) are just as likely to succeed as intraspecific matings. Mating success diminishes with increasing "taxonomic distance" between the parents (intersectional and intersubgeneric hybridizations). Mating success is also somewhat lower in selfings than either intraspecific outcrosses or hybridizations between closely related species.

This overall trend, shown by the percentages of fruit maturation in Table 5, is not a strong one; the differences between treatments are for the most part nonsignificant. The multiple comparison test revealed only three significant differences among the ten possible pairwise combinations. Fruit maturation in narrow hybridizations was significantly higher than in self-mating ($P < 0.05$). Intraspecific outcrosses and narrow hybridizations also had higher fruit maturation than wide hybridizations; in these comparisons the difference was highly significant ($P < 0.01$).

Because the pooled fruit maturation data for all species may obscure the heterogeneity in results among different species, it is instructive to examine the patterns of mating success in a few selected species. *Erythrina guatemalensis* as female parent accounted for 30% of all mature fruits in the pollination trials and 33% of all the hybrid fruits. Thirty-three hybrid fruits were produced from *E. guatemalensis* as female; of these, 30 (90%) were from a single genetic individual, a clone represented by one tree at each garden (PT 700018001, WA 74c1453). The pattern of mating success for *Erythrina guatemalensis* (Table 6) is very similar to the overall results for the combined species trials.

TABLE 6. *Proportion of hand-pollinated flowers producing mature fruit: female parent =* Erythrina guatemalensis*; male parents = diploid species.*

Pollination Treatment	Flowers Pollinated	Fruits Matured	Proportion Fruit Set
Selfed	33	3	9%
Intraspecific outcross	28	7	25%
Narrow hybridization (within section)	86	21	24%
Medium hybridization (between sections, within subgenus)	54	5	9%
Wide hybridization (between subgenera)	185	7	4%
Total	386	43	11%

Multiple comparison test for differences between treatments in proportion of fruit set

Self vs. outcross	N.S.
Self vs. narrow hybrid	N.S.
Self vs. medium hybrid	N.S.
Self vs. wide hybrid	N.S.
Outcross vs. narrow hybrid	N.S.
Outcross vs. medium hybrid	N.S.
Outcross vs. wide hybrid	$P < 0.01$
Narrow hybrid vs. medium hybrid	N.S.
Narrow hybrid vs. wide hybrid	$P < 0.05$
Medium hybrid vs. wide hybrid	N.S.
Outcross + narrow hybrid vs. self + medium + wide	$P < 0.01$

The *E. guatemalensis* trees were unusually fecund; fruit maturation was much higher than the overall average for intraspecific outcrosses (25%) and narrow hybridizations (24%). As in the combined species results, fruit maturation was significiantly higher in intraspecific outcrosses and narrow hybridizations than in wide hybridizations ($P < 0.01$ for both pairwise comparisons), and for narrow hybridizations vs. medium hybridizations the difference was marginally significant ($P < 0.05$).

The data set for *Erythrina crista-galli* as female parent (Table 7), although not so extensive, shows that the neat congruence of mating success and taxonomic distance evidenced by *E. guatemalensis* does not always apply. *Erthyrina crista-galli* as female, represented by one genetic individual at each of the two gardens, produced 16% of all the hybrid fruits in the trials, but it produced 49% of the "medium" and "wide" hybrid fruits. Fruit maturation was higher in the medium and wide hybridizations than in the few narrow hybridizations. (Only one species, *Erythrina falcata,* is in the same section with *E. crista-galli,* so the opportunities for narrow hybridization were limited.) There are no significant differences, however, in any of the pairwise comparisons between pollination treatments for *E. crista-galli*; the variances are large because the sample sizes are rather small.

For intersectional hybridizations (the "medium" and "wide" categories combined) mating success in *Erythrina crista-galli* as female parent was significantly higher than in *E. guatemalensis* (multiple comparison test for proportions, $P < 0.05$). This is illustrated by the results of attempted reciprocal hybridizations between these two species, which are in different subgenera. Sixty-four pollination attempts to produce the hybrid *E. guatemalensis* ♀ × *E. crista-galli* ♂ yielded a single fruit with two seeds, neither of which germinated. Only ten attempts at the reciprocal cross of *E. crista-galli* ♀ × *E. guatemalensis* ♂ yielded four fruits, 15 seeds, and eight vigorous F_1 plants. In all, *E. crista-galli* as female parent produced seeds from seven hybrid combinations with species in six sections and three subgenera. Five of these combinations in all three subgenera survived as healthy F_1 plants. *Erythrina crista-galli,* in short, was a singularly successful "wide hybridizer."

Summing up the contrasting results in fruit maturation for *Erythrina guatemalensis* and *E. crista-galli, E. guatemalensis* hybridized very readily with species in the same section, much less so with more distantly related species. *Erythrina crista-galli,* in contrast, hybridized with a number of species in different subgenera with apparently equal facility, regardless of the formal taxonomic relationships and presumed phylogenetic affinities between *E. crista-galli* and the male parents. These

TABLE 7. *Proportion of hand-pollinated flowers producing mature fruit: female parent =* Erythrina crista-galli; *male parents = diploid species.*

Pollination Treatment	Flowers Pollinated	Fruits Matured	Proportion Fruit Set
Selfed	27	7	26%
Narrow hybridization (within section)	22	2	9%
Medium hybridization (between sections, within subgenus)	69	11	16%
Wide hybridization (between subgenera)	64	10	16%
Total	182	30	16%

Multiple comparison test for differences between treatments in proportion of fruit set

Self vs. narrow hybrid	N.S.
Self vs. medium hybrid	N.S.
Self vs. wide hybrid	N.S.
Narrow hybrid vs. medium hybrid	N.S.
Narrow hybrid vs. wide hybrid	N.S.
Medium hybrid vs. wide hybrid	N.S.

TABLE 8. *Viability of hybrid* Erythrina: *proportions of seeds germinating and growing into healthy plants (at 6 months).*

Type of Hybrid Seed	Seeds Sown	Live Plants	Proportion Viability
Narrow F_1 hybrid	167	86	51%
Narrow F_2 hybrid (all within sect. *Erythrina*)	66	7	11%
Medium F_1 hybrid	62	16	26%
Wide F_1 hybrid	44	18	41%
Total	339	127	37%

Multiple comparison test for differences in viability between types of hybrid

F_1 narrow vs. F_2 narrow	$P < 0.01$
F_1 narrow vs. F_1 medium	$P < 0.01$
F_1 narrow vs. F_1 wide	N.S.
F_2 narrow vs. F_1 medium	N.S.
F_2 narrow vs. F_1 wide	$P < 0.01$
F_1 medium vs. F_1 wide	N.S.
All F_1 hybrids vs. F_2 narrow hybrids	$P < 0.01$

differences in mating success probably reflect individual variation rather than real and consistent interspecific differences in crossability.

F_1 Hybrid Viability. Viability of the F_1 hybrids was high and equal to or higher than normal viability of progeny within species. Overall, 143 (52%) of the 273 F_1 hybrid seeds germinated; 120 of these (44% of the total) survived as healthy F_1 plants. In other words, most of the F_1 seeds either germinated and grew vigorously or they did not germinate at all: the survival rate of those that germinated was 84%.

There were few instances of weakness in the hybrids. Two individuals completely lacked chloroplasts and died soon after germination: a narrow hybrid, *Erythrina macrophylla* × *E. berteroana*, and a wide hybrid, *E. crista-galli* × *E. speciosa*. In both cases, though, siblings from the same cross grew into healthy green plants. About 10 other hybrid plants in different combinations were chlorotic, with yellow-green foliage, and died within 1–2 months. Several others at first appeared chlorotic, but after several months they recovered the normal green color and grew vigorously.

The comparative viablity of narrow, medium, and wide hybrids is summarized in Table 8. Among the F_1 hybrids viability (defined as successful germination and survival of the plant for at least six months) was highest for narrow hybrids, intermediate for wide hybrids, and lowest for medium hybrids. The difference between viability of narrow and medium hybrids was statistically significant ($P < 0.01$), but between narrow and wide hybrids it was not.

Included in Table 8 is the viability data for the "narrow F_2" hybrid seed produced in 1984 from the two-year-old narrow F_1s within sect. *Erythrina*. Germination success of the F_2s was very low, an unexpected and anomalous result; the difference in viability between both the narrow F_1 hybrids (51%) and the wide F_1s (41%) vs. the narrow F_2s (11%) was highly significant (both comparisons, $P < 0.01$).

Viability data for the intraspecific and hybrid progeny of maternal *Erythrina guatemalensis* and *E. crista-galli*, respectively, are presented in Tables 9 and 10. The intraspecific progeny of these two species were grown for two purposes: to compare their viability with that of the hybrids from the same female parents, and to carry out a study of intraspecific variation of morphological traits among siblings. The second goal was thwarted, however, because of the poor germination of the intraspecific seeds. Although the seed lots were not large to begin with, viability of the seed derived from selfings was particularly low: all seven selfed

TABLE 9. *Viability of seed produced from* Erythrina guatemalensis *as female parent (intraspecific and hybrids). Proportion of seed germinating and growing into healthy plants (at 6 months).*

Paternity of Seed	Seeds Sown	Live Plants	Proportion Viability
Selfed	12	1	8%
Intraspecific outcross	14	4	29%
Narrow hybrid (within sect. *Erythrina*)	93	39	42%
Medium and wide hybrids	19	2	11%
Total	138	46	33%

Multiple comparison test for differences in viability between seed of different paternity; female parent = *Erythrina guatemalensis*

Self vs. outcross	N.S.
Self vs. narrow hybrid	$P < 0.05$
Self vs. medium & wide hybrid	N.S.
Outcross vs. narrow hybrid	N.S.
Outcross vs. medium & wide hybrid	N.S.
Narrow hybrid vs. medium & wide hybrid	$P < 0.01$
Self vs. all hybrids	$P < 0.01$
Outcross + narrow hybrid vs. self + medium + wide hybrids	$P < 0.01$

TABLE 10. *Viability of seed produced from* Erythrina crista-galli *as female parent (selfs and hybrids). Proportion of seeds germinating and growing into healthy plants (at 6 months).*

Paternity of Seed	Seeds Sown	Live Plants	Proportion Viability
Selfed	7	0	0%
Narrow hybrid	4	1	25%
Medium hybrid	33	7	21%
Wide hybrid	24	10	42%
Total	70	18	26%

Multiple comparison test for differences in viability between seed of different paternity; female parent = *Erythrina crista-galli*

Self vs. narrow hybrid	N.S.
Self vs. medium hybrid	$P < 0.01$
Self vs. wide hybrid	$P < 0.01$
Narrow hybrid vs. medium hybrid	N.S.
Narrow hybrid vs. wide hybrid	N.S.
Medium hybrid vs. wide hybrid	N.S.
Self vs. all hybrids	$P < 0.01$

seeds of *E. crista-galli* failed to germinate, as did all but one of 12 selfed seeds of *E. guatemalensis.* This could be an expression of inbreeding depression in the self-progeny, but this possibility must be corroborated with larger samples.

Among the hybrids derived from *Erythrina guatemalensis* and *E. crista-galli* females, the pattern of F_1 viability (Tables 9, 10) and its relationship to "taxonomic distance" between the parents was similar to the pattern of mating success discussed earlier (Tables 6, 7) for the same two species. Among the progeny of *E. guatemalensis*, viability of narrow hybrids was significantly higher than that of medium and wide hybrids. Among the progeny of *E. crista-galli,* by contrast, there was no correlation between F_1 hybrid viability and the degree of relatedness of the parentals.

A complete listing of the F_1 hybrid plants produced during 1982–1984 is contained in Tables 11–13. In all, there are 120 individuals in 33 hybrid combinations (21% of the 155 attempted combinations): 22 narrow hybrid combinations (34% of 65 attempted combinations); four medium hybrid combinations (15% of 27 attempts); and seven wide hybrid combinations (11% of 64 attempts). The number of individual F_1 hybrids for each combination ranges from one to nine.

Nineteen of the 22 narrow hybrid combinations are between species in sect. *Erythrina.* There is one narrow hybrid combination in each of sections *Cristae-galli, Chirocalyx,* and *Erythraster.* The medium and wide hybrids include species combinations in nine of the 26 sections of *Erythrina* and four of the five subgenera. In seven of the hybrid combinations, one parental species is native to the New World and the other is native to the Old World.

In summary, the viable F_1 hybrids obtained between the diploid species of *Erythrina* include representative crosses that bridge the entire range of taxonomic diversity and geographic distribution of the genus. Interspecific crossability appears to be largely a function of individual variation in fecundity of the female parent and only partially a function of taxonomic/phylogenetic distance between male and female parents. Given the results obtained in these experiments, it may be expected that with sufficient time, perseverance, and selection of compatible and fecund individual genotypes, any diploid *Erythrina* species could be crossed with any other to produce a viable F_1 hybrid.

Sexual Maturation and Fertility of F_1 Hybrids. Some F_1 hybrids not only were very rapid

TABLE 11. *Artificial* Erythrina *hybrids: narrow (intrasectional).*

Hybrid	Hybrid Number	Live Plants	Hybrid Accession Numbers*	Parental Accession Numbers*
Sect. *Cristae-galli*				
E. crista-galli × *E. falcata*	2×3-1	1	HO 84.284	PT 740283001 (F) PT 750086001 (M)
Sect. *Erythrina*				
E. americana × *E. berteroana*	25×53-1	1	PT 820420	WA 75c1171 (F) WA 74s864 (M)
E. berteroana × *E. guatemalensis*	53×43-1	6	HO 82.647 PT 820549	WA 78s564 (F) WA 74c1453 (M)
E. chiapasana × *E. berteroana*	36×53-1	8	HO 82.278 PT 820283	PT 721005001 (F) PT 700044002 (M)
E. goldmanii × *E. chiapasana*	29×36-1	1	WA 84c560	*Neill 5617* (F) *Neill 5497* (M)
E. guatemalensis × *E. berteroana*	43×53-1	2	HO 82.289	PT 700018001 (F) PT 700044001 (M)
E. guatemalensis × *E. berteroana*	43×53-3	6	HO 82.641 PT 820493	PT 750419001 (F) PT 730711001 (M)
E. guatemalensis × *E. berteroana*	43×53-4	1	HO 82.642	PT 720999001 (F) PT 700044001 (M)
E. guatemalensis × *E. chiapasana*	43×36-1	4	HO 82.283 PT 820254	PT 700018001 (F) PT 721005001 (M)
E. guatemalensis × *E. chiapasana*	43×36-2	5	HO 82.284 PT 820278	PT 700018001 (F) PT 730710001 (M)
E. guatemalensis × *E. folkersii*	43×31-1	2	HO 82.282	PT 700018001 (F) PT 700010001 (M)
E. guatemalensis × *E. macrophylla*	43×42-1	4	HO 82.285	PT 700018001 (F) PT 750420002 (M)
E. guatemalensis × *E. macrophylla*	43×42-3	2	PT 820276	PT 750420002 (M)
E. guatemalensis × *E. macrophylla*	43×42-4	2	HO 82.288	PT 750420002 (M)
E. guatemalensis × *E. salviiflora*	43×56-1	1	PT 820492	PT 750419001 (F) PT 721000002 (M)
E. guatemalensis × *E. standleyana*	43×23-3	2	HO 82.765	WA 74c1453 (F) WA 76s1056 (M)
E. guatemalensis × *E. tajumulcensis*	43×40-1	1	HO 82.335	WA 74c1453 (F) WA 74c1448 (M)
E. guatemalensis × *E. tajumulcensis*	43×40-4	2	HO 82.640	WA 74c1448 (M)
E. guatemalensis × *E. tajumulcensis*	43×40-5	5	PT 820546	WA 74c1448 (M)
E. guatemalensis × *E. tajumulcensis*	43×40-6	1	PT 820547	WA 74c1448 (M)
E. herbacea × *E. americana*	22×25-2	2	HO 82.759	WA 75c1103 (F) WA 75c1171 (M)
E. herbacea × *E. berteroana*	22×53-1	1	PT 820541	WA 75c1103 (F) WA 74s864 (M)
E. herbacea × *E. guatemalensis*	22×43-1	2	PT 820421	WA 75c1103 (F) WA 74c1453 (M)
E. macrophylla × *E. americana*	42×25-1	1	PT 820543	WA 75s1136 (F) WA 75c1171 (M)
E. macrophylla × *E. berteroana*	42×53-1	2	HO 82.280 PT 820253	PT 750420002 (F) PT 700044001 (M)
E. macrophylla × *E. berteroana*	42×53-2	2	HO 82.281	PT 700044001 (M)
E. macrophylla × *E. folkersii*	42×31-1	1	PT 820337	PT 750420002 (F) PT 700010001 (M)
E. macrophylla × *E. guatemalensis*	42×43-1	1	PT 820281	PT 750420002 (F) PT 700018001 (M)
E. macrophylla × *E. guatemalensis*	42×43-2	3	HO 82.763 PT 820544	WA 75s1136 (F) WA 74c1453 (M)

TABLE 11. *Continued.*

Hybrid	Hybrid Number	Live Plants	Hybrid Accession Numbers*	Parental Accession Numbers*
E. tajumulcensis × *E. guatemalensis*	40×43-1	4	HO 82.761 PT 820599	WA 74c1448 (F) WA 74c1453 (M)
	Sect. *Chirocalyx*			
E. abyssinica × *E. latissima*	95×94-1	1	HO 82.867	PT 770034001 (F) PT 750281004 (M)
	Sect. *Erythraster*			
E. perrieri × *E. variegata*	106×96-1	5	HO 82.768 PT 820550	WA 75s857 (F) WA 74s892 (M)
E. perrieri × *E. variegata*	106×96-2	3	HO 82.769 PT 820551	WA 74s892 (M) WA 74s892 (M)
E. perrieri × *E. variegata*	106×96-3	1	HO 82.770	WA 74s892 (M)

* HO = Ho'omaluhia Botanic Garden; PT = Pacific Tropical Botanical Garden; WA = Waimea Arboretum; F = female parent; M = male parent.

in growth rates, but they also produced flowers at an exceptionally early age. Many of the narrow hybrids between species in sect. *Erythrina* grew to be 4-m trees within two years after the seeds were sown, and most flowered within that time. Such sexual precocity is unknown in the parental species. Seeds from intraspecific matings were sown concurrently and in the same nursery with the hybrids; none grew as rapidly or flowered as early as most of the hybrids. None of the parental species, in cultivation, have been known to produce flowers in less than three years from seed.

An even more phenomenal case of precocious flowering was the intersectional (medium) hybrid *Erythrina crista-galli* × *E. fusca*. Two sibling individuals of this combination (PT 840231001 and -002) produced flowers when they were still small plants in nursery pots less than five months after the seeds were sown. The parentals are both large- to medium-sized trees and are not known to flower in the wild or in cultivation before at least several years of growth.

Twenty-five of the two-year-old F_1 hybrid plants flowered during February–March 1984. All were narrow hybrids within sect. *Erythrina*, and represented nine hybrid combinations. These are listed in Table 14 with the pollen fertility of each individual. Also included in Table 14 is the pollen fertility of each of the parental individuals from which these hybrids were derived.

With two exceptions, the pollen fertility of the F_1 hybrids was above 95%. The pollen fertility of the hybrids ($\bar{X} = 97.6\%$) was slightly but significantly higher ($P < 0.05$) than the fertility of the parentals ($\bar{X} = 95.0\%$). Eighteen of the 25 hybrid individuals had pollen fertilities higher than either of their parents. For this trait at least, the narrow hybrids in sect. *Erythrina* clearly exhibited interspecific heterosis.

Meiosis in pollen mother cells was examined in several of the F_1 hybrids in sect. *Erythrina*. An example is *Erythrina guatemalensis* × *E. macrophylla*, HO 82.288-A (Figs. 9, 10). Meiotic behavior in this hybrid can be compared with meiosis in its male parent *E. macrophylla*, PT 750420002 (Figs. 5, 6).

As in the parental species, meiosis in the hybrids was characterized by clumping of bivalents at late diakinesis and metaphase I and by "sticky" chromatin bridges and late disjunction of some bivalents at anaphase I. The normal meiotic process was, however, not disrupted. Nondisjunction or unequal assortment of chromosomes during meiosis I was not observed, and all cells examined at telophase I or subsequent stages had the expected number of 21 chromosomes. Meiotic behavior in the F_1 hybrids within sect. *Erythrina*, in short, was identical to the behavior described above for the parental species.

The only intersectional F_1 hybrid to flower by November 1984 was the five-month-old *Erythrina crista-galli* × *E. fusca*. Pollen fertility in this hybrid (PT 840231001) was 81%. This was lower than the pollen fertility of either parent (*E. crista-galli*, WA 74p840, 96.1%; *E. fusca*, WA 74s99, 96.3%) but probably not low enough to affect substantially fertility and mating success of the hybrid. Only limited material was available for analysis of meiosis in pollen mother cells of *E. crista-galli* × *E. fusca*. In some cells, several quadrivalents ap-

TABLE 12. *Artificial* Erythrina *hybrids: medium (between sections, within subgenera).*

Hybrid[1]	Hybrid Number	Live Plants	Hybrid Accession Numbers	Parental Accession Numbers
	Subg. *Duchassaingia*			
E. crista-galli (2) × *E. fusca* (1)	2×1-1	2	HO 84.234 PT 840232	PT 740283001 (F) PT 740230005 (M)
E. crista-galli (2) × *E. fusca* (1)	2×1-2	5	HO 84.235 PT 840231	WA 74p840 (F) WA 74s99 (M)
	Subg. *Erythrina*			
E. herbacea (12) × *E. humeana* (18)	22×73-1	2	HO 82.863 PT 820697	WA 76s187 (F) WA 74p1382 (M)
E. lysistemon (17) × *E. speciosa* (9)	72×16-1	1	HO 84.238	PT 750280003 (F) PT 730708001 (M)
E. lysistemon (17) × *E. speciosa* (9)	72×16-2	2	HO 84.243	PT 750280002 (F) PT 730708001 (M)
E. speciosa (9) × *E. lysistemon* (17)	16×72-1	1	HO 84.236	PT 730708003 (F) PT 750280003 (M)
E. speciosa (9) × *E. lysistemon* (17)	16×72-2	3	HO 84.237	PT 730742002 (F) PT 750280003 (M)

[1] Number in parentheses after each species denotes section (see Table 1).

peared to be formed at metaphase I (Fig. 11). In other cells, meiosis was normal with 21 bivalents at metaphase I. Without more thorough cytological analyses, it is not possible to state whether or not meiosis is significantly disrupted in this hybrid. Nondisjunction and unequal segregation of some chromosomes may contribute to the partial reduction in fertility of the pollen.

Fecundity of F_1 Hybrids. Fruit maturation from the controlled self-pollinations of the two-year-old F_1 hybrids in sect. *Erythrina* (Table 15) was very low, less than 3%, and nine of the 12 F_1s produced no fruits from controlled selfing. In common with the usual pattern of results in experimental pollinations of *Erythrina* parentals, much of the failure in fruit maturation was due to postzygotic abortion of young fruits, within one or two weeks after fertilization. Most of the F_1s did produce a few fruits spontaneously, on open-pollinated inflorescences. Animal pollen vectors were not present in the garden plots, and it is most likely that these open-pollinated fruits were produced by autogamy.

TABLE 13. *Artificial* Erythrina *hybrids: wide (intersubgeneric).*

Hybrid[1]	Hybrid Number	Live Plants	Hybrid Accession Numbers	Parental Accession Numbers
E. caffra (17) × *E. fusca* (1)	71×1-1	2	PT 820422	WA 74c1456 (F) WA 74s99 (M)
E. crista-galli (2) × *E. guatemalensis* (12)	2×43-3	8	HO 82.758 PT 820598	WA 74p840 (F) WA 74c1453 (M)
E. crista-galli (2) × *E. speciosa* (9)	2×16-1	1	HO 82.860	WA 740283001 (F) PT 730708001 (M)
E. crista-galli (2) × *E. variegata* (26)	2×96-2	1	HO 82.495	WA 74p840 (F) WA 76s996 (M)
E. guatemalensis (12) × *E. abyssinica* (25)	43×95-1	1	HO 84.287	PT 700018001 (F) PT 731006002 (M)
E. guatemalensis (12) × *E. senegalensis* (22)	43×79-2	1	HO 82.766	WA 74c1453 (F) WA 74s100 (M)
E. herbacea (12) × *E. fusca* (1)	22×1-1	4	HO 82.634 PT 820542	WA 75c1103 (F) WA 74s99 (M)

[1] Number in parentheses after each species denotes section (see Table 1).

TABLE 14. *Pollen fertility of artificial F_1 hybrids within sect.* Erythrina *and of their parents. At least 500 grains counted for all samples.*

I. Hybrids

Hybrid Combination	Accession Number	Percent Normal Grains
E. americana × *E. berteroana*	PT 820420001	99.4*
E. berteroana × *E. guatemalensis*	PT 820549001	96.7
E. berteroana × *E. guatemalensis*	HO 82.647-A	86.3
E. chiapasana × *E. berteroana*	HO 82.278-A	98.1
E. chiapasana × *E. berteroana*	HO 82.278-B	99.6*
E. chiapasana × *E. berteroana*	HO 82.278-C	99.6*
E. chiapasana × *E. berteroana*	HO 82.278-D	99.5*
E. guatemalensis × *E. berteroana*	PT 820493001	97.3*
E. guatemalensis × *E. berteroana*	PT 820493002	96.3
E. guatemalensis × *E. chiapasana*	HO 82.283-A	99.8*
E. guatemalensis × *E. chiapasana*	PT 820254002	96.6
E. guatemalensis × *E. chiapasana*	HO 82.284-A	98.6*
E. guatemalensis × *E. chiapasana*	HO 82.284-B	98.8*
E. guatemalensis × *E. chiapasana*	HO 82.284-E	99.1*
E. guatemalensis × *E. folkersii*	HO 82.282-A	99.4*
E. guatemalensis × *E. folkersii*	HO 82.282-B	98.4*
E. guatemalensis × *E. macrophylla*	HO 82.285-B	99.6*
E. guatemalensis × *E. macrophylla*	HO 82.288-A	97.8*
E. guatemalensis × *E. macrophylla*	PT 820276001	98.2*
E. guatemalensis × *E. standleyana*	HO 82.765-A	89.8
E. guatemalensis × *E. tajumulcensis*	PT 820547001	99.4*
E. macrophylla × *E. berteroana*	HO 82.281-A	98.8*
E. macrophylla × *E. berteroana*	HO 82.281-B	98.2*
E. macrophylla × *E. guatemalensis*	HO 82.763-A	96.4
E. macrophylla × *E. guatemalensis*	HO 82.763-B	98.6*

TABLE 14. *Continued.*

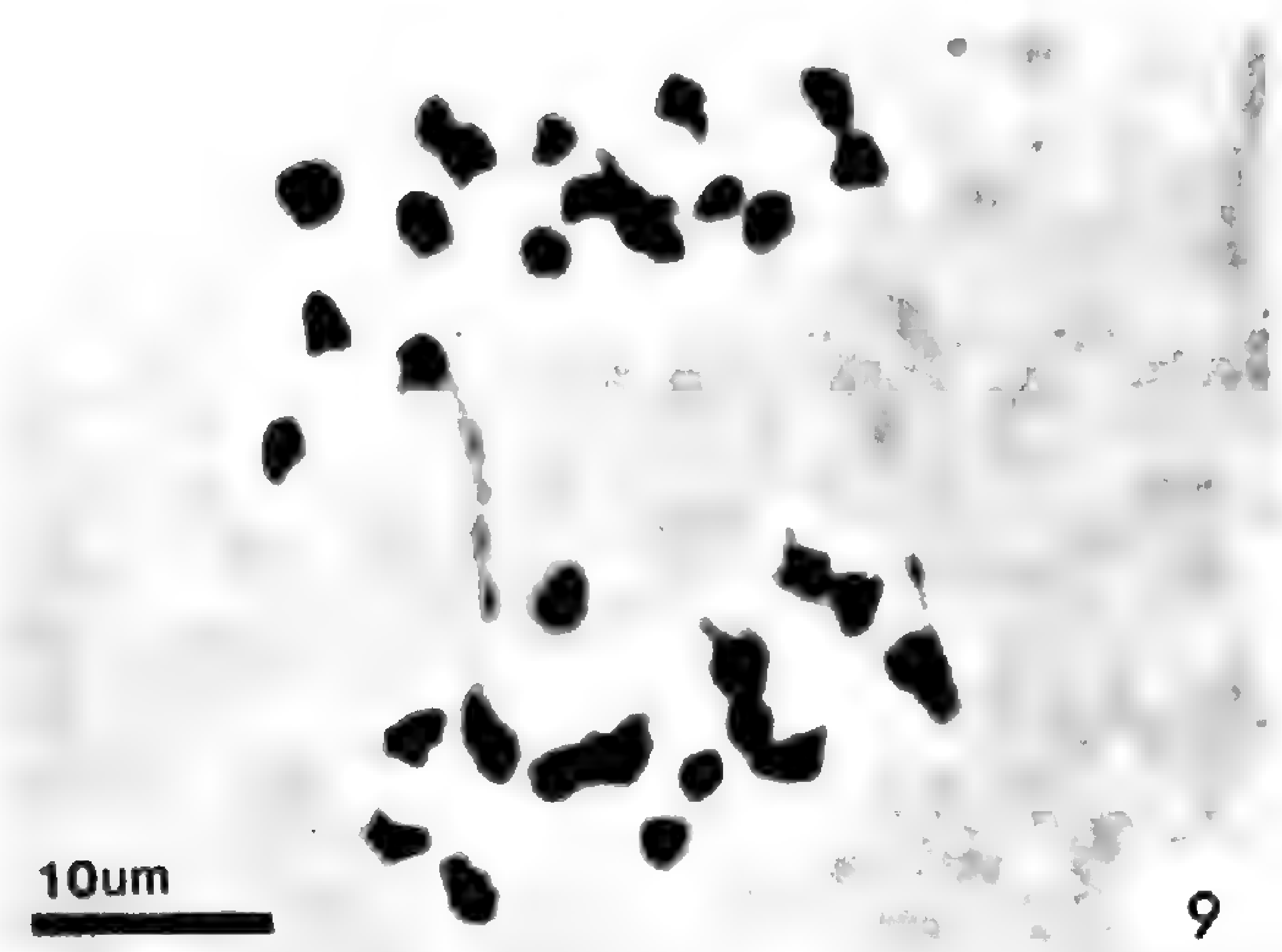
II. Parentals

Species	Accession Number	Percent Normal Grains
E. americana	WA 75c1171	97.3
E. berteroana	WA 74s864	96.6
E. berteroana	WA 78s564	97.2
E. berteroana	PT 700044001	96.4
E. berteroana	PT 700044002	98.1
E. berteroana	PT 730711001	97.4
E. chiapasana	PT 730710001	96.3
E. chiapasana	PT 721005001	94.4
E. folkersii	PT 700010001	85.3
E. guatemalensis	PT 70018001	97.7
E. guatemalensis	WA 74c1453	97.7
E. guatemalensis	PT 750419001	91.4
E. macrophylla	PT 750420002	94.4
E. macrophylla	WA 75s1136	96.9
E. standleyana	WA 75s1056	84.9
E. tajumulcensis	WA 74c1448	98.0

Hybrids: mean pollen fertility = 97.6% ± 3.0%.
Parentals: mean pollen fertility = 95.0% ± 4.1%.
Differences in pollen fertility, hybrids vs. parentals: $t = 2.28$; DF = 39; $P < 0.05$.
* Indicates hybrids with higher pollen fertility than either parent.

Also in Table 15 are comparisons of fruit maturation in the selfed F_1 hybrids vs. their parents. Several combinations of parental matings are included in the analyses. Fruit maturation was much lower in the selfed F_1s (3%) than in the original hybridizations which produced these F_1s (22%) ($P < 0.01$).

The second pairwise comparison of fruit maturation in Table 15, selfed F_1 hybrids vs. all of their parental hybrid combinations (including reciprocals), may be more biologically meaningful than the first comparison for the following reason: the female parents of the F_1 hybrids were very fecund, with higher than average fruit maturation. The male parents (pollen donors) of the F_1s generally had lower fruit maturation when employed as females in the hybridization trials; many of the reciprocal crosses produced no hybrid fruit at all. If it is assumed that fecundity (fruit maturation) is a quantitatively heritable trait, then an F_1 hybrid might be expected to be intermediate in fecundity between its two parents, providing there is no reduction in fruit maturation in the hybrid caused by incompatibilities between its constituent genomes. The proportion of fruit maturation expected in the F_1s, then, should approximate the proportion in all the parental hybrid combinations, including



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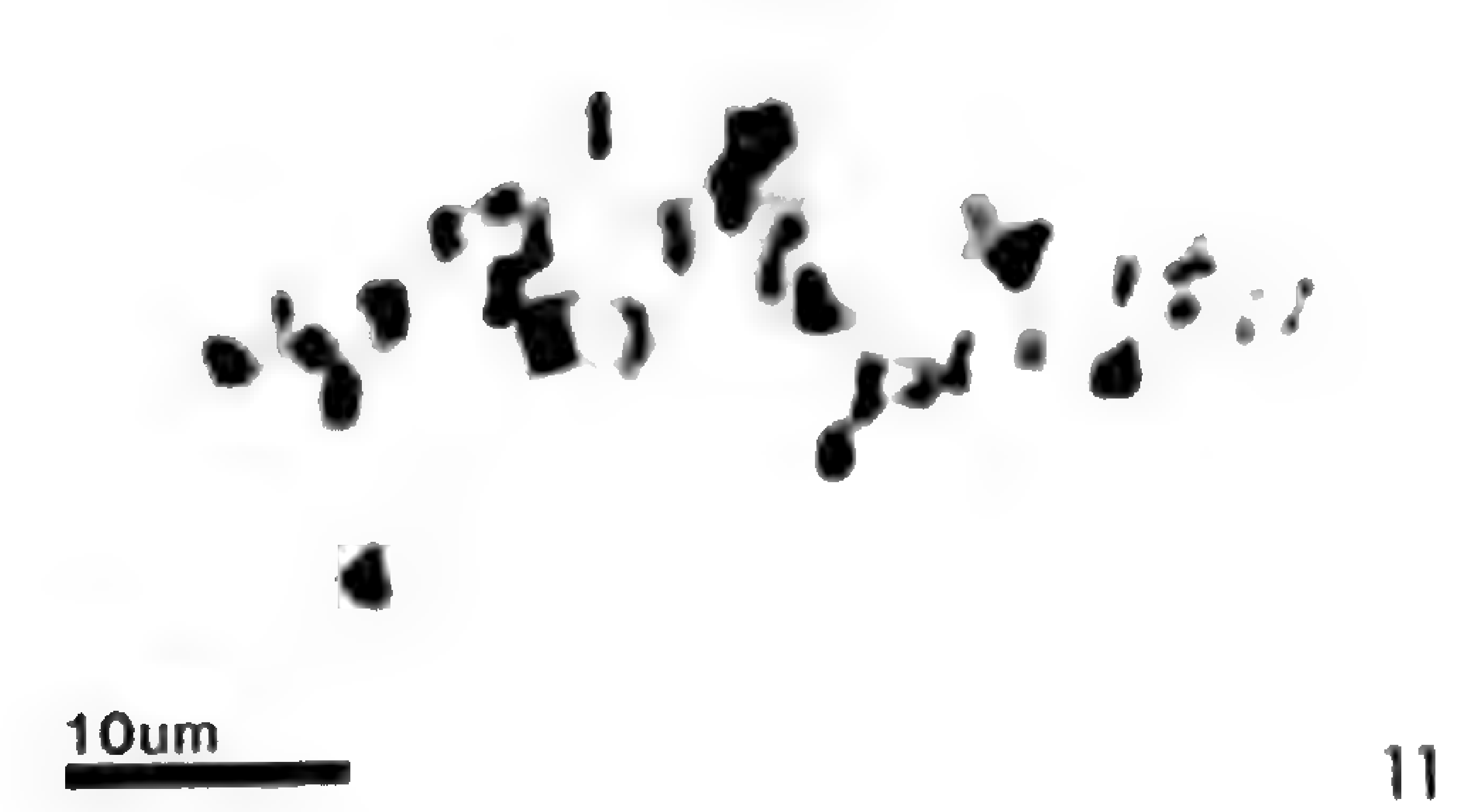

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FIGURES 9–11. *Meiosis in* Erythrina *hybrids (pollen mother cells)*.—9, *10. Late anaphase*, E. guatemalensis × E. macrophylla, *HO 82.288* (n = *21*). *Sticky chromatin bridges and late disjunction of some bivalents (compare with meiosis in male parent* E. macrophylla, *Figs. 5, 6*).—*11. Metaphase*, E. crista-galli × E. fusca, *PT 840231001* (n = *21*). *At least two quadrivalents are visible.*

the failed reciprocal hybridizations. By this measure, the second pairwise comparison in Table 15, fruit maturation in the F_1 hybrids, is still much lower than the 15% fruit maturation in the parental generation; the difference is highly significant ($P < 0.01$).

There are several possible reasons for the reduced fruit maturation in the F_1 hybrids in sect. *Erythrina*. The first is that the low fecundity is in fact a consequence of hybridity caused by genic incompatibility between the parental genomes. It is evidently not, however, a matter of "hybrid sterility" in the usual sense of the term, in which the microgametophytes (pollen) and/or megagametophytes (embryo sacs) borne on the F_1 sporophyte are abortive and nonfunctional (Grant, 1953; Stebbins, 1958). The pollen fertility of the F_1 hybrids, as discussed above, was exceptionally high; the pistil and ovules also appeared to develop normally in the hybrids. Much of the failure of fruit set in the selfed F_1s was at the postzygotic stage (abortion of young fruits). If the reduced fecundity was truly a consequence of hybridity and intergenomic incompatibility, it is probably best considered as a case of "hybrid breakdown" (Grant, 1953; Stebbins, 1958) expressed as low viability of the F_2 embryos.

There are other possible explanations for the low fecundity of the selfed F_1s that do not invoke hybrid breakdown or other effects of hybridity. The first is that it may be a consequence of self-mating, the opposite effect from the apparent heterosis evidenced by the exceptional vigor of the F_1 plants. Fruit set in the selfed F_1s was significantly lower than the one in the selfed parentals, which in turn were significantly lower in fruit set than the hybridizations. For both parental and F_1 selfings, the high incidence of fruit abortion may be an expression of inbreeding depression, a result of the homozygous pairing of deleterious recessive alleles in the genomes of the embryos. This possibility could be tested by controlled cross-pollinations between F_1s, a step that was not taken initially because the goal of the F_1 selfings was to produce F_2 plants with no more than two constituent genomes.

Another possible reason for the low fecundity in the F_1s may simply be the juvenility of the F_1 plants themselves. Although the F_1s were very vigorous and flowered precociously at two years of age, they were not yet full-sized trees. At their size, they might not be able to draw on sufficient resources for the full fruit crop of a larger adult.

In short, the variables accounting for reduced fecundity in the narrow F_1 hybrids still need to be sorted out. This should be possible once the F_1 trees attain their full adult size and several categories of matings within and between individuals are carried out.

Viability of F_2 Hybrids. The viability of the F_2 hybrid seed, obtained from selfed and open-pollinated F_1 plants in sect. *Erythrina* (Table 16), was

TABLE 15. *Fruit and seed maturation from controlled self-pollinations of narrow F_1 hybrids in sect.* Erythrina.

Hybrid Combination	Accession Number	Flowers Pollinated	Mature Fruits	Total Number of Seeds
E. berteroana × *E. guatemalensis*	HO 82.674-A	18	0	0
E. guatemalensis × *E. berteroana*	PT 820493002	13	0	0
E. guatemalensis × *E. chiapasana*	HO 82.284-A	32	3	7
E. guatemalensis × *E. chiapasana*	HO 82.284-B	6	0	0
E. guatemalensis × *E. chiapasana*	HO 82.283-A	38	0	0
E. guatemalensis × *E. chiapasana*	PT 820254002	7	2	3
E. guatemalensis × *E. chiapasana*	PT 820278002	10	0	0
E. guatemalensis × *E. macrophylla*	HO 82.288-A	27	0	0
E. guatemalensis × *E. macrophylla*	HO 82.285-B	16	0	0
E. guatemalensis × *E. tajumulcensis*	HO 820547001	20	1	1
E. macrophylla × *E. berteroana*	HO 82.281-B	23	0	0
E. macrophylla × *E. guatemalensis*	HO 82.763-A	15	0	0
Total selfed F_1 hybrids		225	6 (3%)	11
Parental hybridizations		51	21 (22%)	
All parental hybrid combinations (including reciprocals)		171	25 (15%)	
Selfed parentals (sect. *Erythrina*)		144	12 (8%)	

Multiple comparison test for differences in fruit maturation

Selfed F_1s vs. parental hybridizations	$P < 0.01$
Selfed F_1s vs. all parental hybrid combinations	$P < 0.01$
Selfed F_1s vs. selfed parentals	$P < 0.05$
Parental hybridizations vs. selfed parentals	$P < 0.01$
All parental hybrid combinations vs. selfed parentals	N.S.

significantly lower than viability of the F_1 hybrids. This was shown in Table 8, where the F_2s were compared with all the narrow F_1 hybrids; the difference was highly significant ($P < 0.01$). In Table 16 the viability of the F_2 seed is compared specifically with that of their own parents, i.e., with the F_1 seed lots producing the parents of the F_2s. The viability of the F_2s (13%) was significantly lower ($P < 0.01$) than that of their F_1 parent generation (61% viability).

In Table 16 the viability of the F_2 seed and of their F_1 parents is also compared with seed from intraspecific matings in *Erythrina guatemalensis* (including seed from selfings and intraspecific outcrosses, the only intraspecific viability data available for sect. *Erythrina*). The F_1 hybrid seed was significantly higher in viability than the intraspecific seed ($P < 0.05$). The viability of the intraspecific seed (19%) was somewhat higher than that of the F_2 seed, but the difference was nonsignificant.

In summary, the viability of F_1 hybrid seed was significantly higher than F_2 seed derived from selfed F_1 matings and higher than seed derived from intraspecific matings. If the very high F_1 viability is truly an expression of interspecific heterosis, this hybrid advantage is not retained in the F_2 generation, when the F_2s are derived from selfed F_1 hybrids.

It is possible to interpret the reduction in F_2 viability with respect to F_1 viability as "hybrid breakdown." However, with the data presently available, the reduced viability of the F_2s derived from selfed F_1s could also be interpreted as an expression of inbreeding depression. It could also be interpreted simply as an absence of the heterotic advantage possessed by the F_1s, since the viability of the F_2s was not significantly lower than that of the intraspecific progeny. These three alternatives cannot be differentiated with the presently available information. Additional progeny trials of F_1, F_2, and intraspecific seed lots are needed to test the possibility that hybrid breakdown may be expressed in the F_2 generation of *Erythrina* hybrids.

In any case, the lowered average viability of the F_2s was a function only of poor germination of the seed. The seeds that did germinate produced healthy plants with normal growth and vigor at six months of age. There were no indications of chlorosis or other debilities in the F_2 plants.

Studies of Previously Synthesized Hybrids. Nine artificially produced *Erythrina* hybrids, all between

TABLE 16. *Viability of F_2 hybrids within sect.* Erythrina.

F_2 Hybrid Combination	Accession Number	Female Parent (F_1 Hybrid)	Paternity	Seeds Sown	Live F_2 Plants
E. guatemalensis × *E. berteroana*	HO 84.288	HO 82.641-A	Open	9	0
E. guatemalensis × *E. chiapasana*	PT 840234 PT 840235	PT 820254002	Self	3	0
E. guatemalensis × *E. chiapasana*	HO 84.289	HO 82.284-A	Self	7	1
E. guatemalensis × *E. macrophylla*	HO 84.290	HO 82.288-A	Open	5	1
E. guatemalensis × *E. tajumulcensis*	PT 840243	PT 820547001	Self	1	0
E. herbacea × *E. guatemalensis*	PT 840241	PT 820421001	Open	5	0
E. macrophylla × *E. berteroana*	HO 84.245	HO 82.281-A	Open	4	1
E. macrophylla × *E. berteroana*	HO 84.291	HO 82.281-B	Open	4	4
E. macrophylla × *E. guatemalensis*	HO 84.244 HO 84.292 PT 840242	HO 82.763-B	Open	18	1
Total F_2 hybrids in sect. *Erythrina*				56	7 (13%)
F_1 hybrid parents of F_2s				28	17 (61%)
Intraspecific progeny, *Erythrina guatemalensis*				26	5 (19%)

Multiple comparison test for differences in viability of seed

F_2 hybrids vs. their F_1 hybrid parents	$P < 0.01$
F_2 hybrids vs. intraspecific *E. guatemalensis*	N.S.
F_1 hybrids vs. intraspecific *E. guatemalensis*	$P < 0.01$

species of different sections, have been reported prior to this study (Table 17). Krukoff & Barneby (1974) described most of these; in the same paper they described some putative natural hybrids between sympatric Mesoamerican and African species. The parentage of only two of the artificial hybrids is known for certain; both of these F_1s are "wide" intersubgeneric hybrids and are reported to be fertile.

The oldest and best-known *Erythrina* hybrid is *E.* ×*bidwillii* Lindley, synthesized from *E. herbacea* (sect. *Erythrina*) ♀ and *E. crista-galli* (sect. *Cristae-galli*) ♂ in Australia in the 1840s and since spread around the world as a cultivar by propagation of cuttings. Krukoff & Barneby (1974) reported *E.* ×*bidwillii* to produce viable seed and also that "no Mendelian segregation of phenetic characters is observed in the F_1 or subsequent generations." They further claimed that this hybrid had naturalized in Fiji and was therefore a stabilized "neospecies."

I examined *E.* ×*bidwillii* in cultivation at Foster Garden, Honolulu (FG 64.2035). Meiosis in pollen mother cells was normal with 21 bivalents at metaphase I. Pollen fertility was 63%, comparable to Graham & Tomb's (1974) report of 76% normal pollen for this hybrid. I attempted to produce an F_2 generation by controlled self-pollination of 60 flowers over a period of several weeks. Young fruits were obtained but they invariably aborted before two weeks of development. I have not seen mature spontaneously produced fruits on any cultivated plants or herbarium specimens of *E.* ×*bidwillii*, so the reports of its viable seed production are questionable.

I made limited attempts (12 trial pollinations) to backcross *E.* ×*bidwillii* to one of its parents, *E. crista-galli*. The pollinations all failed, but given the reasonably high pollen fertility of *E.* ×*bidwillii*, it is likely that with perseverance some backcross progeny could be obtained.

The other previously reported hybrid of known parentage is *Erythrina* ×*resuparcellii* Srivastava (a *nomen nudum*, not validly published), a hybrid between the perennial herb *E. resupinata* (sect. *Suberosae*) ♀ and *E. variegata* (sect. *Erythraster*) ♂ (Jalil et al., 1982). The F_1 is a branched shrub, and in other morphological traits is also intermediate between the two parents. The flowers, however, resemble those of the female parent much more closely than those of the male. This hybrid was not available to me, but Jalil et al. (1982) reported that it had normal meiosis in pollen mother cells with 21_{II} at metaphase I, pollen fertility of 62%, and viable seed.

Erythrina ×*sykesii* Barneby & Krukoff was the only other hybrid among those listed in Table 17 available to me for experimental studies. This

TABLE 17. *Previous reports of artificial* Erythrina *hybrids.*[1]

1. *Erythrina* ×*bidwillii* Lindley, Bot. Reg. 33: pl. 9. 1849.
   E. herbacea ♀ (12) × *E. crista-galli* ♂ (2)
2. *Erythrina* ×*bellangeri* Focke, Die Pflanzen-mischlinge. 110. 1881.
   ? *E. crista-galli* ♀ (2) × *E. herbacea* ♂ (12)
3. *Erythrina* ×*crassifolia* Koorders ex Backer, Schoolflora voor Java 1: 360. 1911.
   ? *E. subumbrans* (6) × *E. variegata* (26)
   ? *E. fusca* (1) × *E. variegata* (26)
4. *Erythrina* ×*fluminensis* Barneby & Krukoff, Lloydia 37: 446. 1974.
   ? *E. speciosa* (9) × *E.* sp. (subg. *Micropteryx*)
5. *Erythrina* ×*hennesyae* Barneby & Krukoff, Lloydia 37: 448. 1974.
   ? *E. humeana* (18) × *E. lysistemon* (17)
6. *Erythrina* ×*orba* Barneby & Krukoff, Lloydia 37: 449. 1974.
   E. lysistemon (17) × *E. speciosa* (9)
7. *Erythrina* ×*sykesii* Barneby & Krukoff, Lloydia 37: 447. 1974.
   ? *E. americana* (12) × *E. lysistemon* (17)
   ? *E. speciosa* (9) × *E. lysistemon* (17)
8. *Erythrina* ×*vlissingensis* Waby ex Barneby & Krukoff, Lloydia 37: 446. 1974.
   ? *E. fusca* (1) × *E. variegata* (26)
   ? *E. fusca* (1) × *E. suberosa* (4)
9. *Erythrina* ×*resuparcellii* Srivastava, Allertonia 3: 19. 1982. *nomen nudum.*
   E. resupinata ♀ (4) × *E. variegata* ♂ (26)

[1] Known or presumed parental species combinations are listed below each hybrid binomial; question mark preceding hybrid combination indicates uncertain parentage. Numbers in parentheses following species refer to sections to which species belong (Table 1).

hybrid was reputedly produced under cultivation in Australia in the 19th century, but its parentage is unknown. Krukoff & Barneby (1974) believed the parents to be *E. lysistemon* (sect. *Caffrae*) and *E. americana* (syn. *E. coralloides*) (sect. *Erythrina*). Based on study of floral and leaf morphology, I believe instead that the parents are *E. lysistemon* and *E. speciosa* (sect. *Stenotropis*). Since I have obtained both reciprocal hybrids of *E. speciosa* × *E. lysistemon* (Table 12), these F_1s can be compared with *E.* ×*sykesii* when they come into flower.

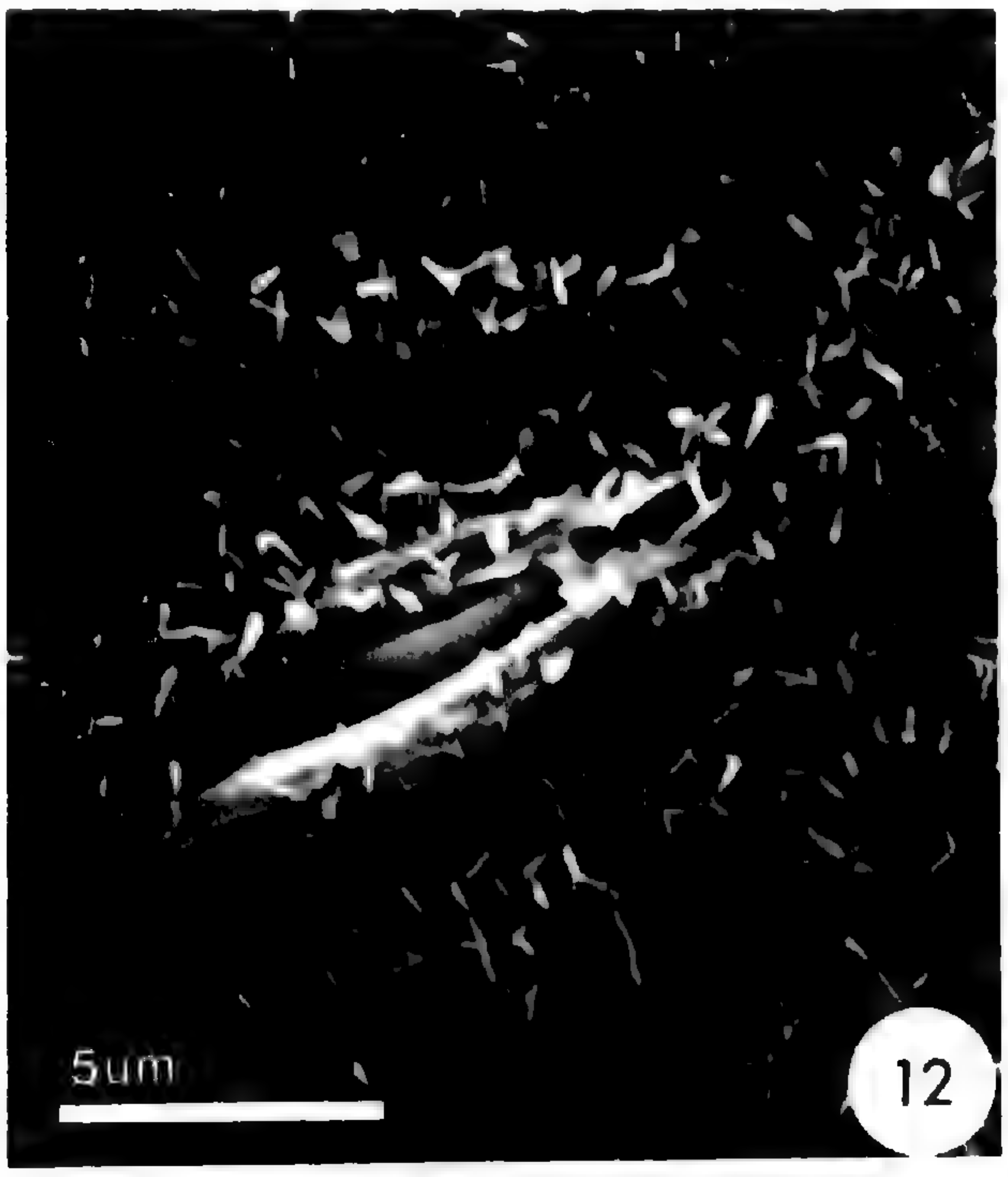
I examined cytologically several individual ramets of *E.* ×*sykesii* (WA 76p864, WA 75s1706, Foster Garden FL.669) and attempted to produce F_2 plants by controlled self-pollination. Meiosis in PMCs was apparently normal, with 21 bivalents at metaphase I. Pollen fertility was 81–84%, which agreed closely with results reported earlier for the same taxon by Graham & Tomb (1974). However, no mature fruits were obtained from 65 attempts at selfing. Young fruits with partially developed seeds were produced in abundance as with *E.* ×*bidwillii*, but these always aborted within two to three weeks following pollination.

Erythrina ×*bidwillii*, *E.* ×*resuparcellii*, and *E.* ×*sykesii* are the only intersectional or intersubgeneric hybrids that have been tested for fecundity at this time. An F_2 generation was reportedly obtained from *E.* ×*resuparcellii* (Jalil et al., 1982), but the other two may be incapable of producing F_2 progeny, at least from selfing of the F_1. Zygotes, embryos, and young fruits are formed, but the fruits abort before maturity. These "wide" hybrids, then, may be subject to hybrid breakdown expressed as inviability of the F_2 hybrid embryos borne on the F_1 hybrid sporophyte. As discussed in the previous section, the cause of mating failure in the F_1 hybrids is subject to different interpretations. Whether or not F_2 hybrid breakdown is a general phenomenon in *Erythrina* remains to be investigated.

CONCLUSIONS: EXPERIMENTAL HYBRIDIZATIONS AND SELF-COMPATIBILITY TRIALS

From the information presented in this section, a series of generalizations regarding breeding systems and species relationships in *Erythrina* can be outlined:

1. Even under the most carefully controlled conditions, mating success (proportion of pollinated flowers producing mature fruits) is low in all *Erythrina* species. This is true even when the effects of "resource competition" are eliminated by removing most flowers from an inflorescence as well as all of the spontaneously produced fruits on the tree, and pollinating only a few selected flowers per inflorescence. Mating failure results partly from prefertilization abortion of pollinated flowers, but also to a large extent from postfertilization abortion of young fruits.



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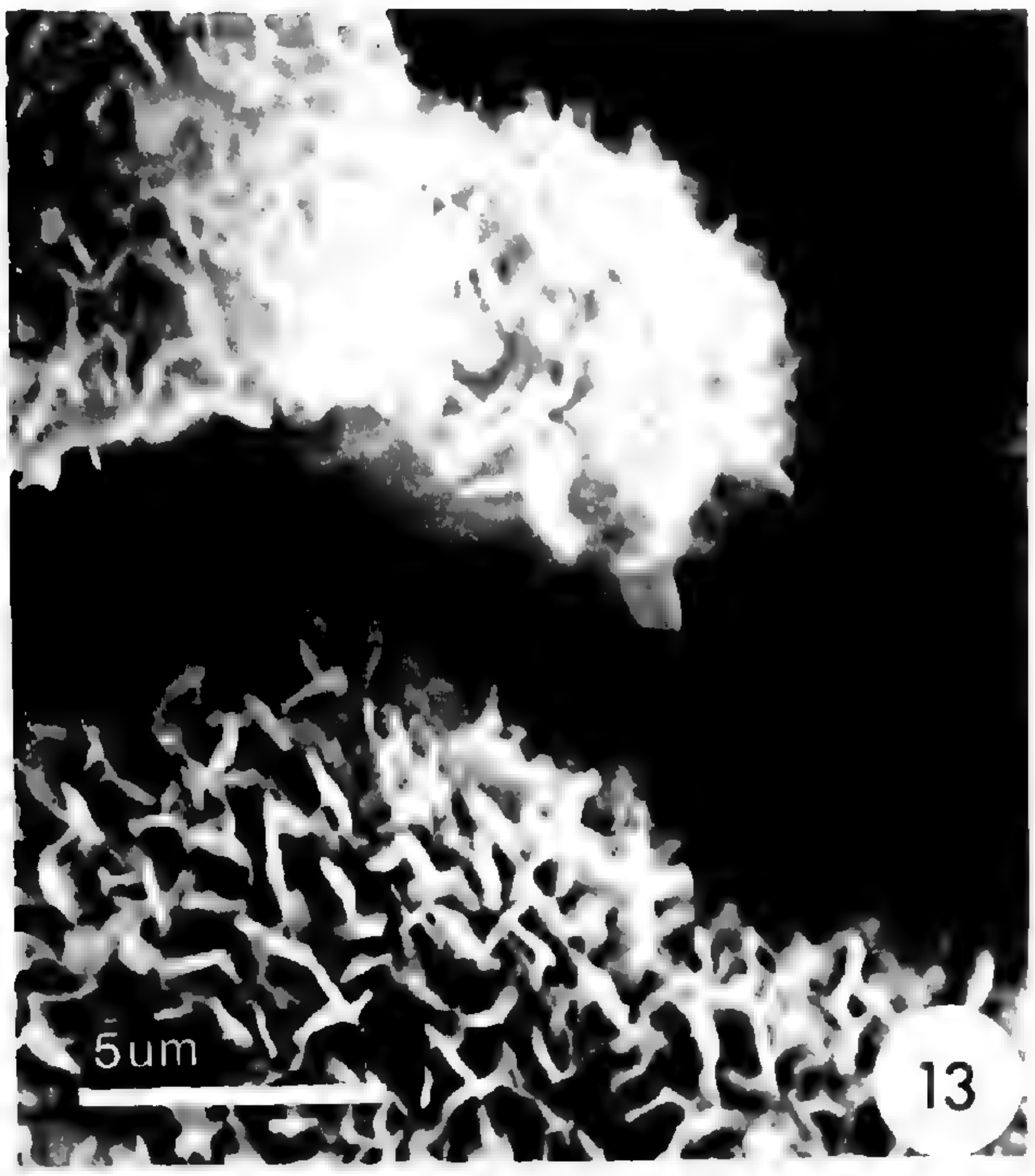

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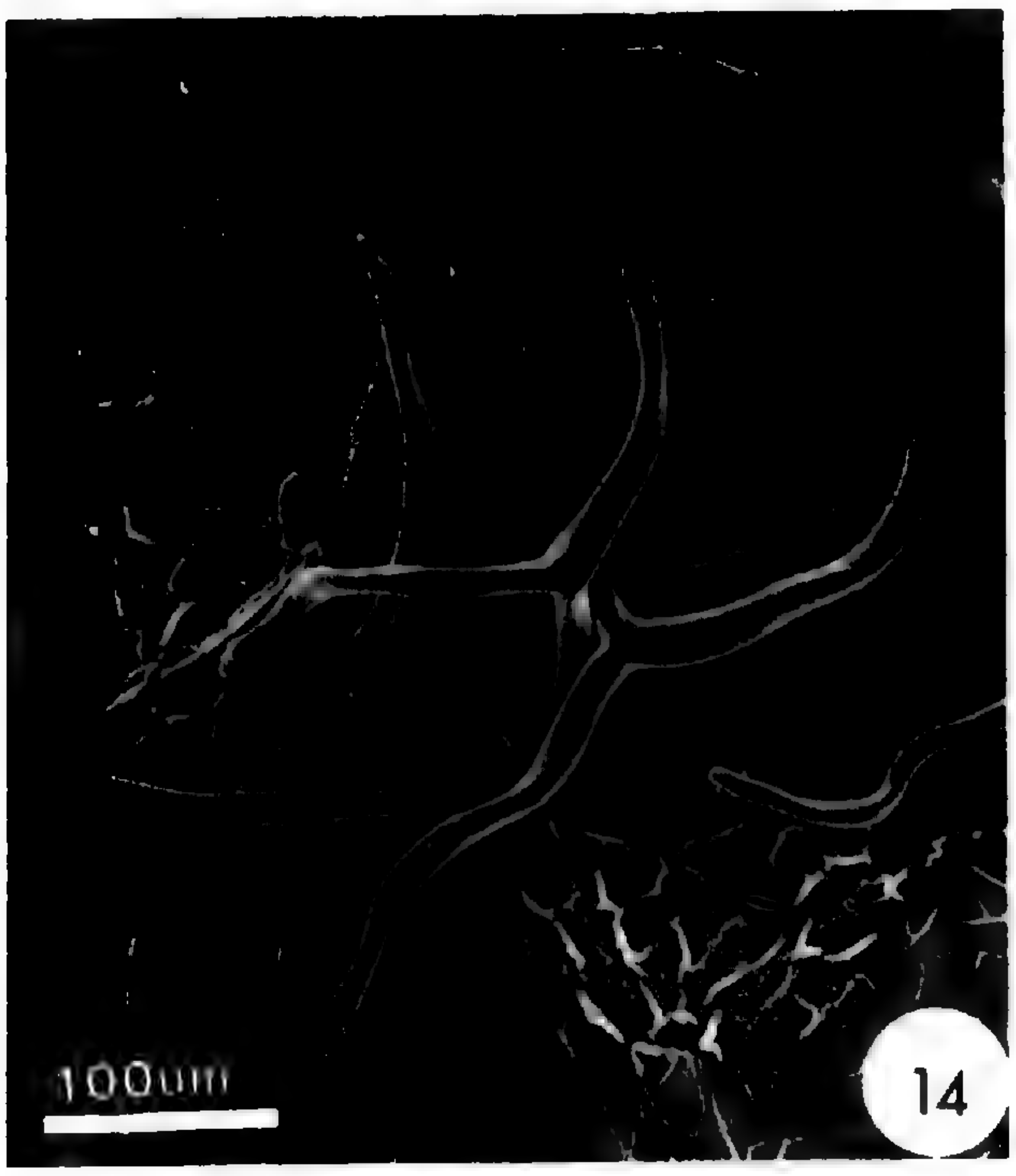

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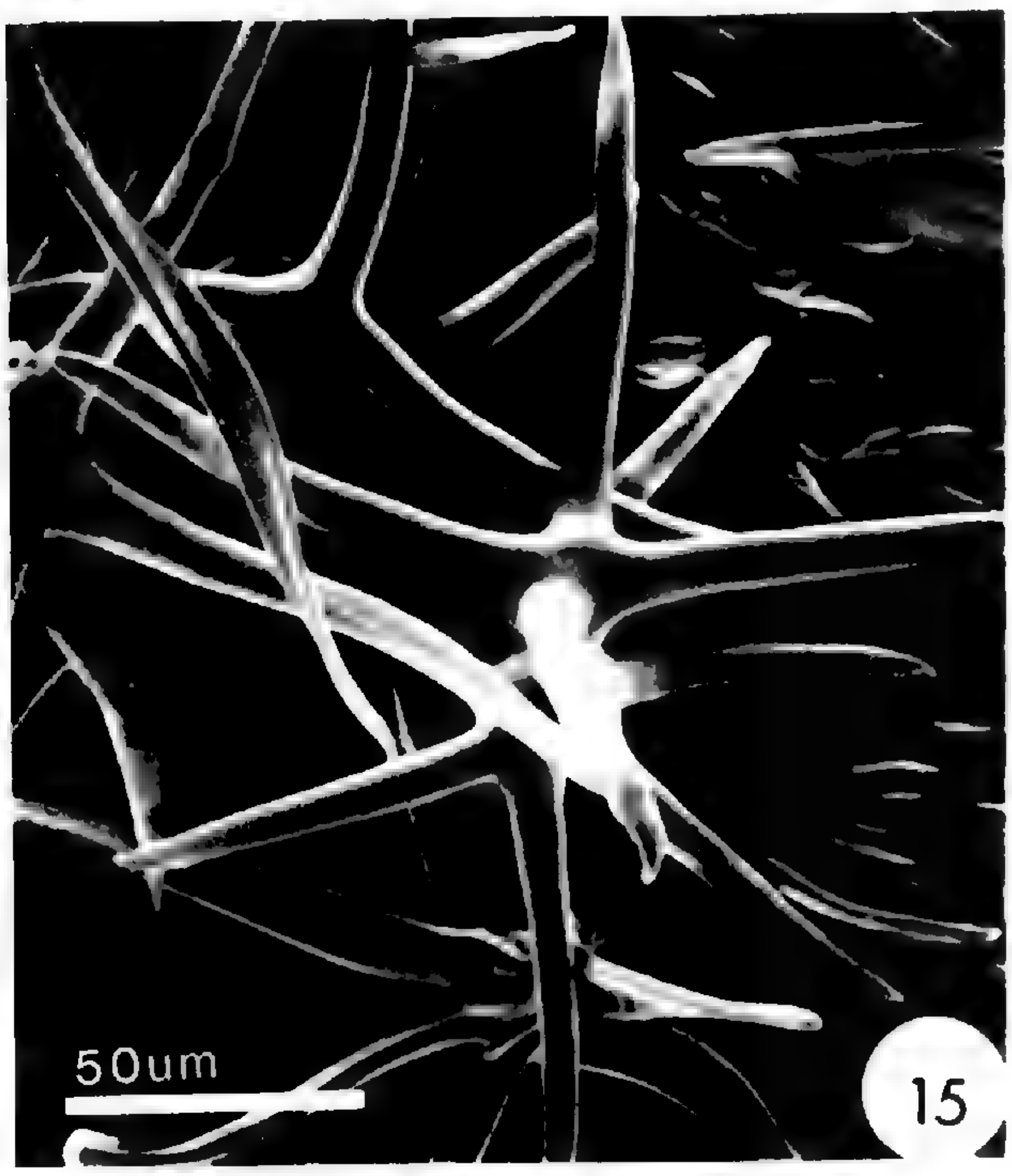

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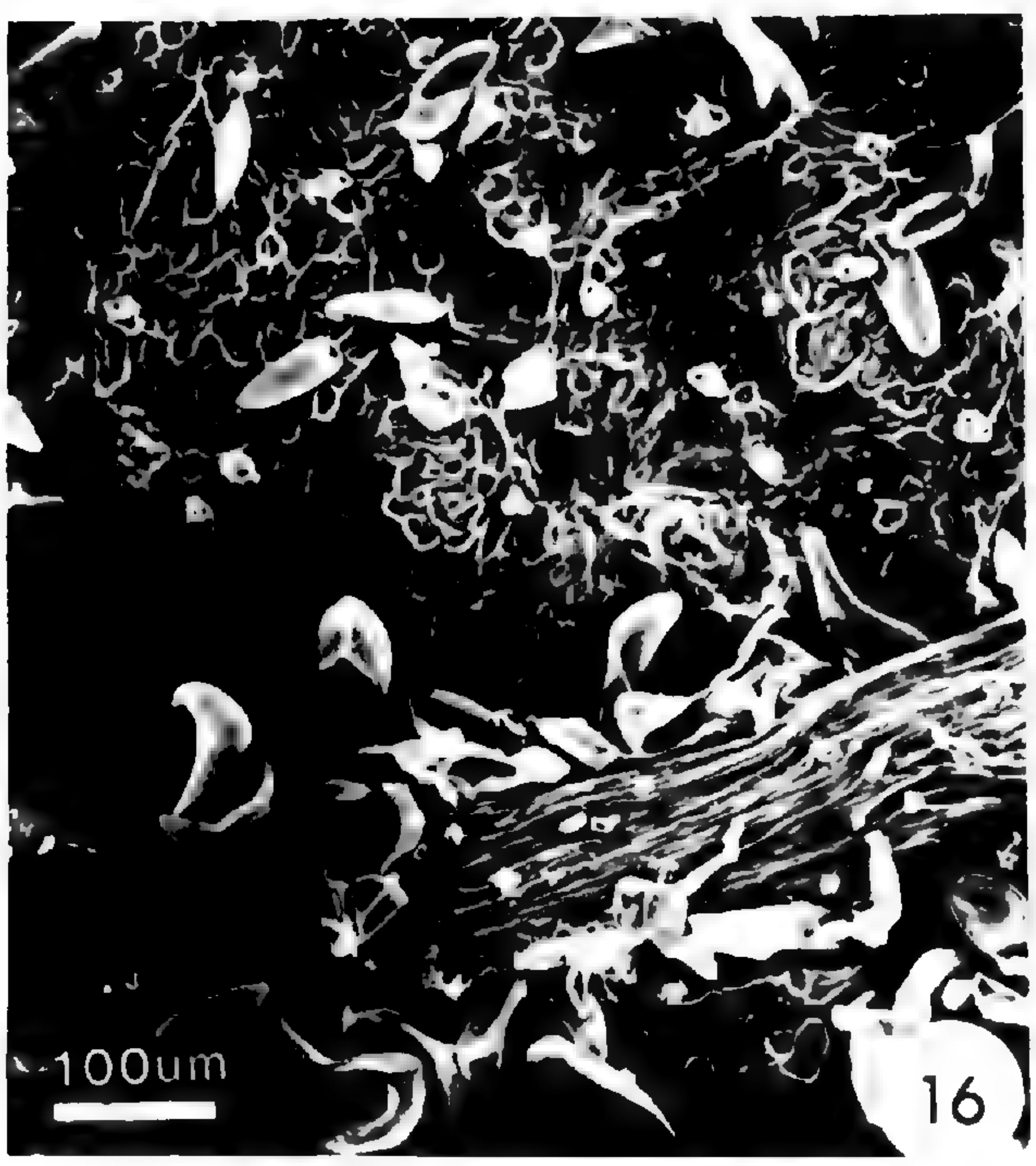

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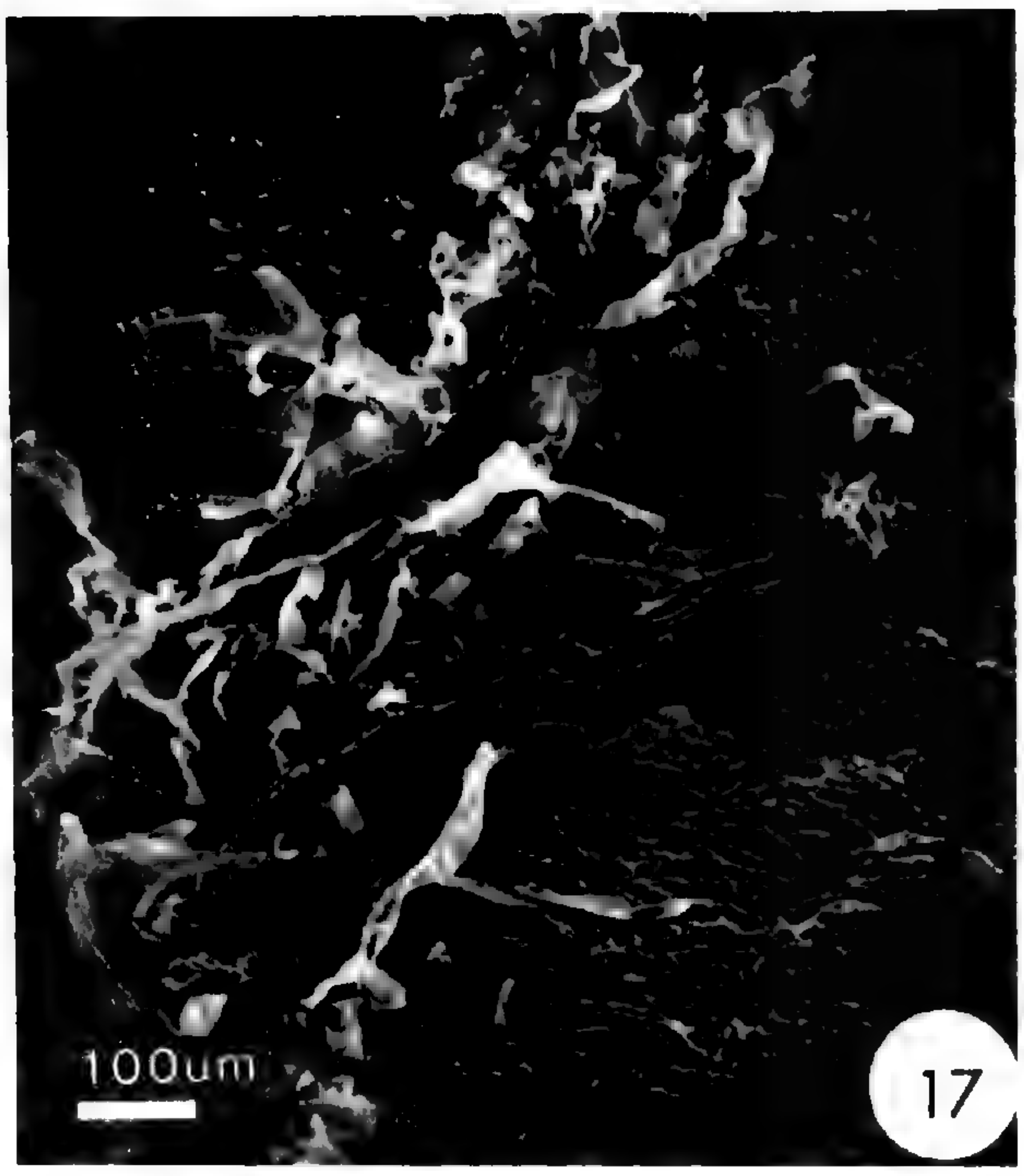

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2. Gametophytic or sporophytic self-incompatibility systems of the "classical" model, mediated by inhibition of pollen tubes in the style or stigma and governed by a single-locus, multiallelic S-gene, are evidently not present in any of the *Erythrina* species examined. Self-incompatibility in this strict sense is probably absent from the entire genus. There is considerable individual variation in fecundity, and some individuals may be cryptically female-sterile, but if an individual produces seed from outcrossing it will also produce some seed from self-mating. For some individuals and some populations, mating success is lower in selfing than in outcrosses, but much of the mating failure is expressed postzygotically by abortion of young fruits. This is probably an expression of inbreeding depression, the consequence of increased homozygosity for any number of deleterious recessive alleles, rather than the action of a specific S-allele. Inbreeding depression may also be expressed in the progamic stage as inhibition of pollen tubes.

3. Spatial separation of anthers and stigma in some *Erythrina* species, and protandry in other species, limits autogamous pollinations. For the protandrous species at least, this mechanism is not absolutely effective; autogamous fruits are occasionally produced. Autogamy occurs only with the ultimate flowers on an inflorescence and may be an adaptive feature of the breeding system to produce some seed as a "last resort" if no "high-quality" (i.e., outbred) seed was produced on earlier flowers of the inflorescence.

4. The hybridization trials indicate that matings between closely related species (within sections) are just as likely to produce viable progeny as are matings within species. Mating success is usually higher, in fact, in interspecific hybridizations within sections than in self-mating. At increasing taxonomic distance between parental species, there is a general trend to lower mating success in the hybridization trials. This trend is not universally applicable, however. Viable F_1 hybrids have been produced between the most distantly related groups of species in the genus—between species of different subgenera indigenous to different continents. It is probable that viable F_1 hybrids can be obtained between any two diploid species in the genus *Erythrina*.

5. F_1 hybrids between the closely related species in sect. *Erythrina* exhibit interspecific heterosis by several measures: viability of the F_1 seed is higher, and the F_1 plants are more vigorous, sexually precocious, and have higher pollen fertility than the parental species. Pollen fertility is somewhat lower in hybrids between more distantly related species, but these hybrids are generally comparable in viability and vigor with the parental species.

6. A reduction in fecundity is exhibited by the F_1 hybrids, at least when the F_1s are selfed. This lowered mating success is not due to "hybrid sterility" per se, since the gametes produced by the F_1 hybrid function normally. Mating failure is expressed postzygotically by abortion of young fruits and evidently is a consequence of inviability of the F_2 hybrid embryo. An alternative explanation may be that mating failure in the selfed F_1s is a consequence of inbreeding depression.

These experiments support the first two hypotheses presented in the introduction: 1) the species in sect. *Erythrina* can hybridize freely with each other, and there are no internal qualitative or quanitative postmating isolating barriers between the species; and 2) hybridization between more widely divergent species is also possible; there is generally a quantitative reduction in mating success in the wider hybridizations, but this probably does not constitute an absolute barrier to the formation of F_1 hybrids. The only major unanswered question regarding interspecific compatibility among diploid *Erythrina* is the possibility of hybrid breakdown in the F_2 and subsequent generations. F_2 breakdown, if it exists, does not form an absolute isolating barrier within sect. *Erythrina*, but it may form an absolute barrier in hybridizations between more widely divergent species.

SECTION 5. INHERITANCE OF PHENETIC TRAITS IN INTERSPECIFIC HYBRIDS

The fact that plant species with large morphological discontinuities can be hybridized, and that large hybrid progenies can be grown together in a common garden, has allowed for analyses of the genetic basis of these phenetic differences (review in Gottlieb, 1984). A thorough genetic analysis, of course, requires at least the study of segregating

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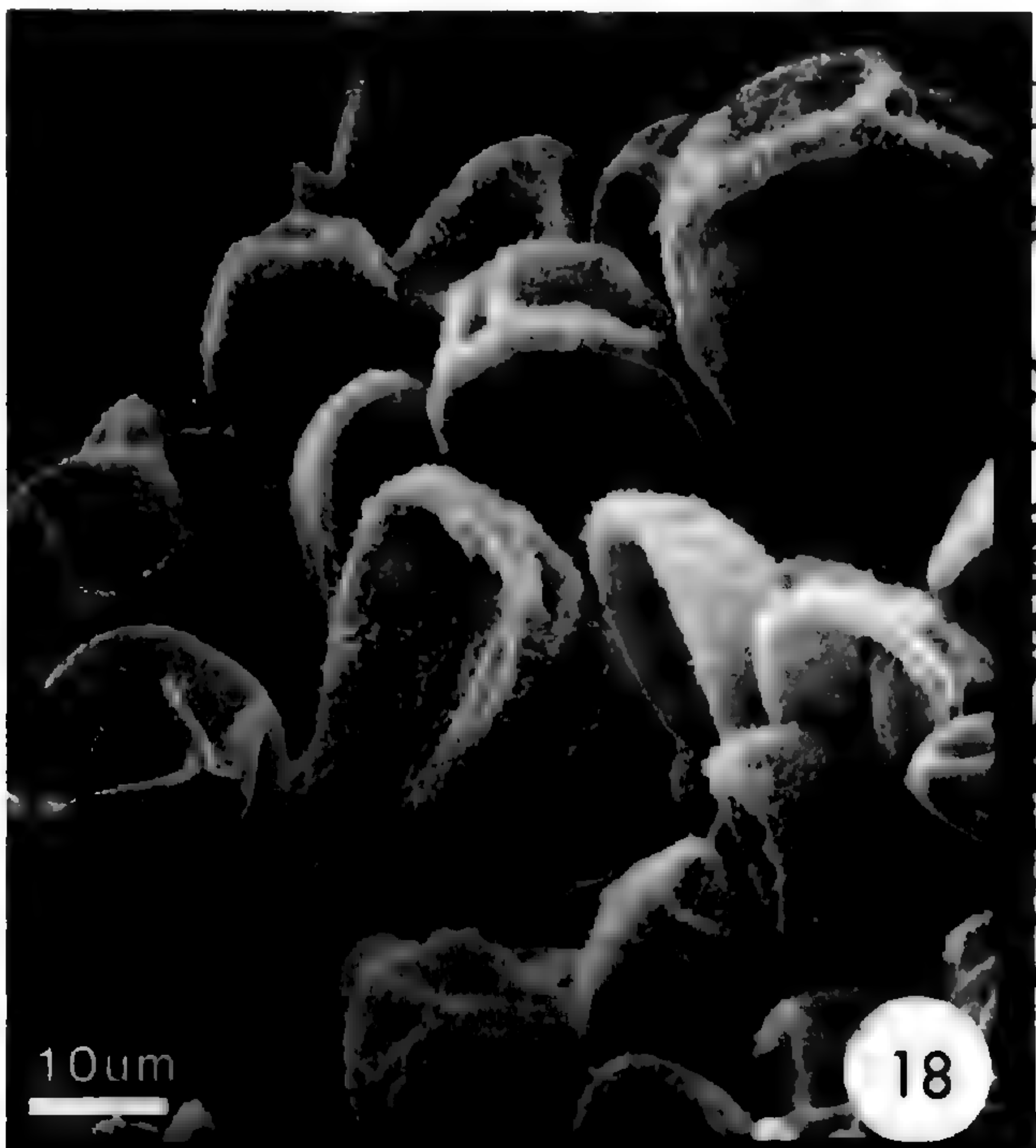
FIGURES 12–17. *SEM images of abaxial leaf surface of* Erythrina.—*12. Epicuticular wax platelets,* E. suberosa, *WA 45s960.*—*13. Epicuticular wax platelets,* E. berteroana, *PT 700044001.*—*14. Two-armed hairs,* E. chiapasana, *WA 74s876.*—*15. Dendritic hairs,* E. perrieri, *WA 74s876.*—*16. Balloonlike hairs,* E. arborescens, *WA 78s225.*—*17. Ribbonlike hairs,* E. leptorhiza, Neill 5646.



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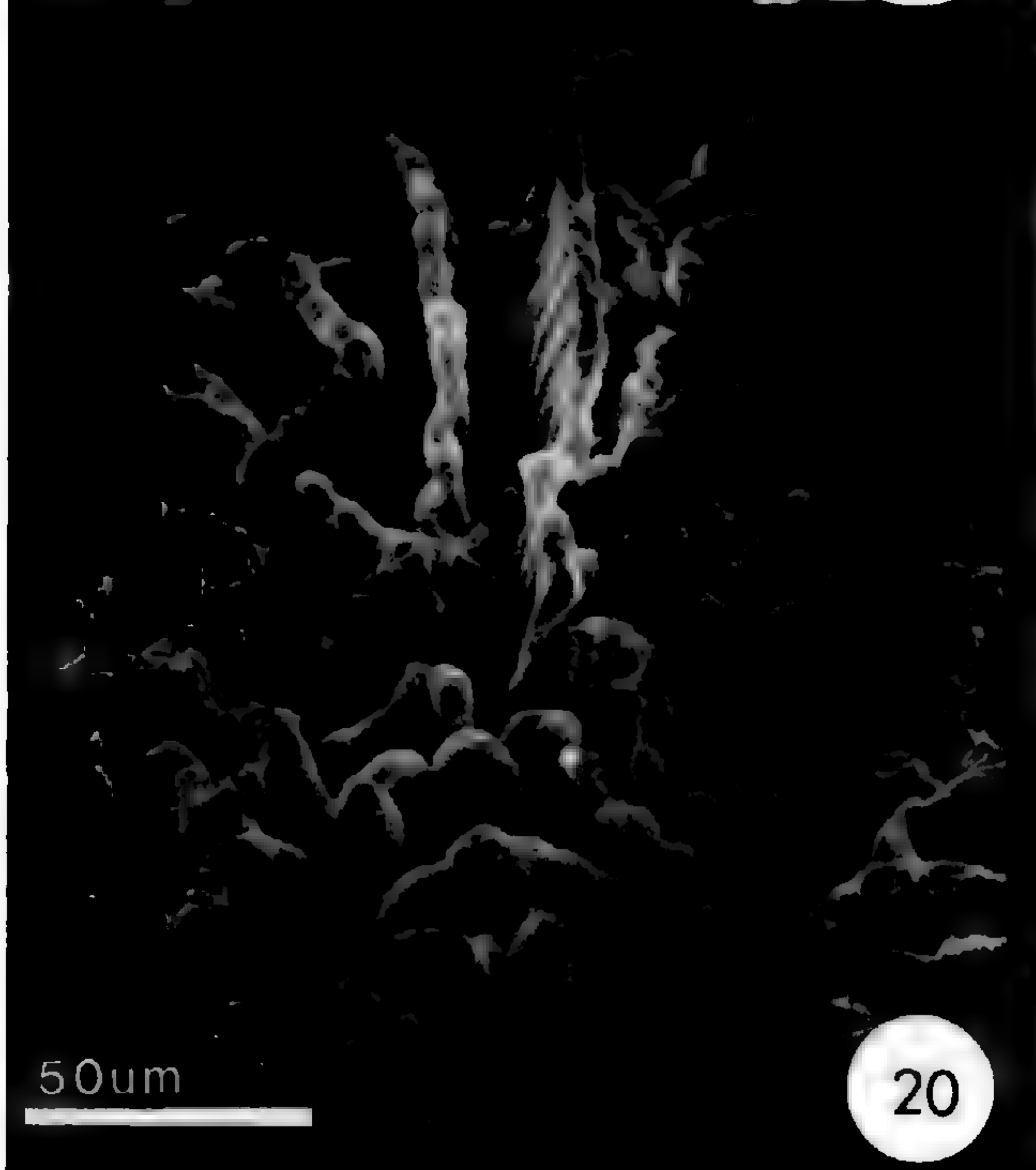

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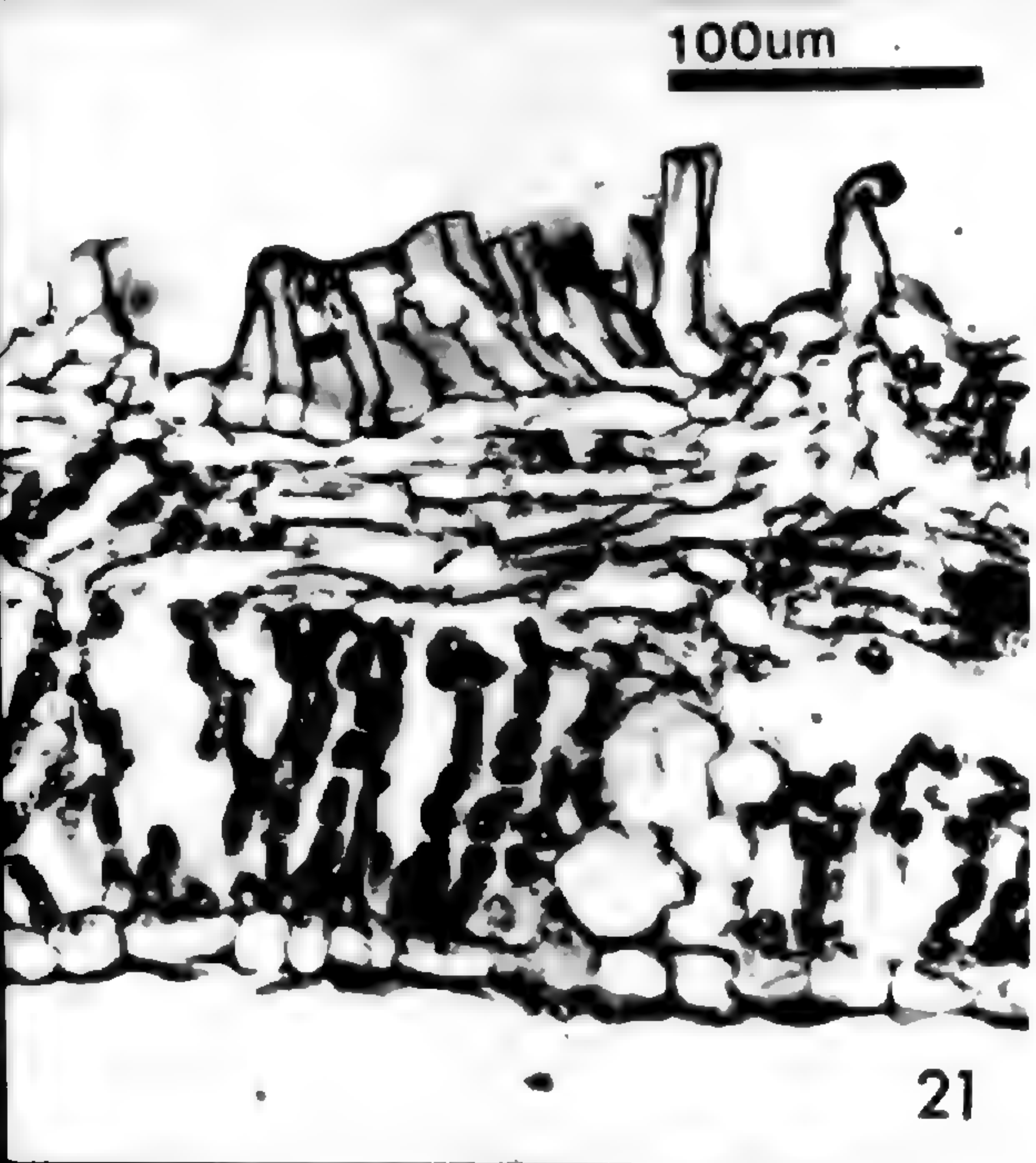

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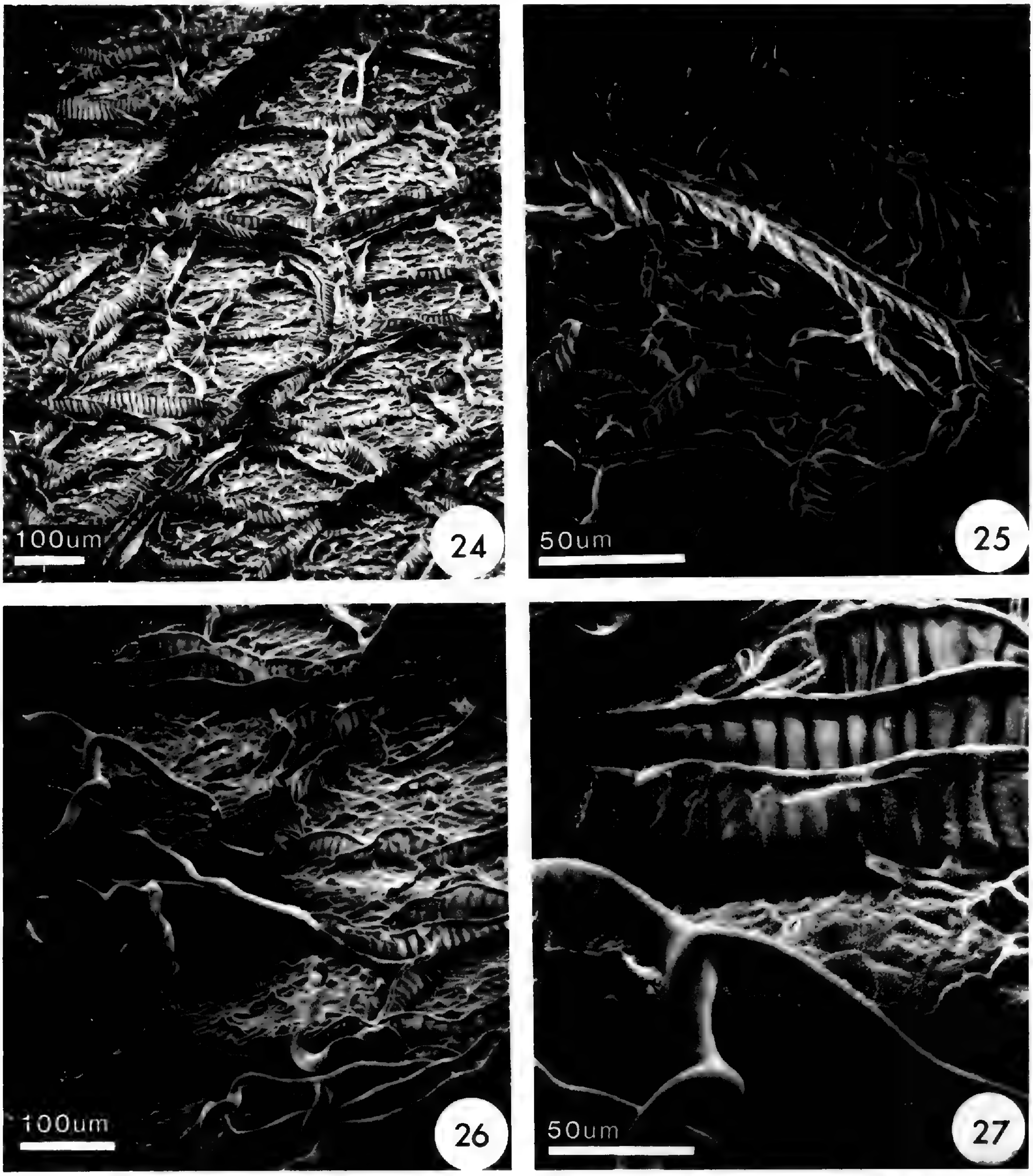

FIGURES 24–27. *SEM images, abaxial leaf surfaces of* Erythrina. *All images at 60° tilt.—24, 25. Lamellae,* E. stricta, *WA 74s897.—26, 27. Lamellae and two-armed hairs,* E. suberosa, *WA 75s960.*

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FIGURES 18 23. *Epidermal features of abaxial leaf surfaces of* Erythrina. *18, 20, 22.—SEM images. 19, 21, 23.—Anatomical sections.—18. Papillae,* E. guatemalensis, *PT 750419001.—19. Papillae,* E. folkersii, *PT 700010001.—20. Lamellae,* E. salviiflora, *PT 721346001.—21. Lamellae,* E. suberosa, *WA 75s960.—22. Glandular hair,* E. salviiflora, *PT 721346001.—23. "Glandular" hair, papillae, and lamellae,* E. berteroana, *WA 74s864.*

TABLE 18. *Comparison of leaf epidermal characters in* Erythrina *hybrids and parents.*

	Female Parent	F_1 Hybrid	Male Parent
	E. chiapasana PT 721005001	HO 82.278	*E. berteroana* PT 700044002
Figures	28–30	31–33	34–36
Hairs	dense covering of two-armed hairs	sparse two-armed hairs	hairs absent
Epidermal sculpturing	low ridges around stomata; no lamellae	open, irregular network of discontinuous lamellae; uneven in height, less than 15 μm tall	dense network of discontinuous lamellae, up to 40 μm tall
Epicuticular wax	wax absent	wax present	wax present
	E. guatemalensis PT 700018001	HO 82.289	*E. berteroana* PT 700044001
Figures	37–39	40 42	43–45
Hairs	hairs absent	hairs absent	hairs absent
Epidermal sculpturing	dense papillae, to 40 μm tall	sparse covering of papillae and 2–6-celled lamellae; short, less than 25 μm tall	dense network of discontinuous lamellae, to 40 μm tall
Epicuticular wax	wax present	wax present	wax present
	E. guatemalensis PT 700018001	HO 82.283	*E. chiapasana* PT 721005001
Figures	46, 47	48, 49	50, 51
Hairs	hairs absent	sparse scattering of two-armed hairs	dense covering of two-armed hairs
Epidermal sculpturing	dense papillae to 40 μm tall	incipient papillae: low crescent-shaped ridges outlining anticlinal walls of epidermal cells	low ridges around stomata: no papillae
Epicuticular wax	wax present	wax present	wax absent
	E. guatemalensis PT 700018001	HO 82.647	*E. abyssinica* PT 731006002
Figures	52–54	55–57	58–60
Hairs	hairs absent	sparse covering of two-armed hairs	dense covering of two-armed hairs
Epidermal sculpturing	dense papillae to 40 μm tall	low epidermal ridges, less than 10 μm tall	low epidermal ridges, less than 10 μm tall
Epicuticular wax	wax present	wax present	wax present
	E. guatemalensis WA 74c1453	HO 82.766	*E. senegalensis* WA 745100
Figures	61–63	64–66	67–69
Hairs	hairs absent	sparse scattering of balloonlike hairs, up to 50 μm × 100 μm in size	sparse scattering of balloonlike hairs, up to 50 μm × 100 μm in size
Epidermal sculpturing	dense papillae, to 40 μm tall	low, crescent-shaped epidermal ridges, less than 5 μm tall	low stellate papillae, less than 10 μm tall

TABLE 18. *Continued.*

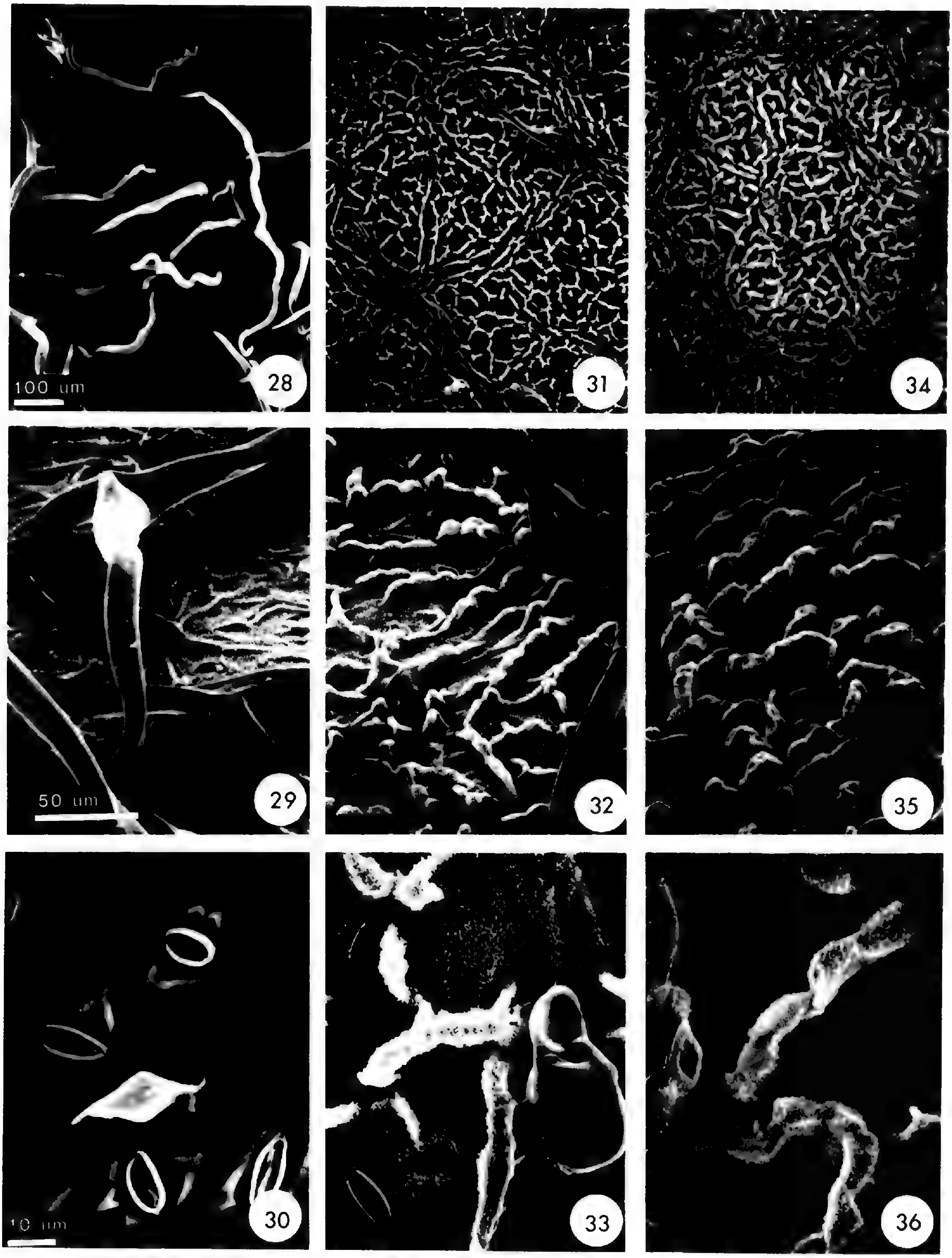
	Female Parent	F_1 Hybrid	Male Parent
Epicuticular wax	wax present	wax present	wax absent
	E. lysistemon PT 75028003	HO 84.238	*E. speciosa* PT 730708001
Figures	70, 71	72, 73	74, 75
Hairs	hairs absent	sparse scattering of two-armed hairs	sparse scattering of two-armed hairs
Epidermal sculpturing	low papillae, less than 10 μm tall	low epidermal ridges, less than 5 μm tall	low epidermal ridges, less than 5 μm tall
Epicuticular wax	wax present	wax present	wax present
	E. crista-galli WA 74p840	(4 individuals)	*E. guatemalensis* WA 74c1453
Figures	76, 82	78–81, 84–87	77, 83
Hairs	hairs absent	hairs absent	hairs absent
Epidermal sculpturing	low, discontinuous lamellae, less than 10 μm tall, forming reticulate pattern	variable: papillae or discontinuous lamellae, to 15 μm tall	dense papillae, to 40 μm tall
Epicuticular wax	wax absent	wax present in all	wax present
	E. crista-galli WA 74p840	PT 840231 HO 84.235 (3 individuals)	*E. fusca* PT 74s99
Figures	88, 94	90–92, 96–98	89, 95
Hairs	hairs absent	hairs absent	hairs absent
Epidermal sculpturing	low discontinuous lamellae, less than 10 μm tall, forming reticulate pattern	variable: scattered low papillae, 3–4-celled lamellae or nearly flat	irregular convoluted surface with deep cavities, knobs, and protrusions
Epicuticular wax	wax absent	wax present in all	wax absent

progeny in the F_2 generation. In the absence of large F_2 families, however, preliminary characterization of the inheritance of morphological characters can be obtained from F_1 hybrids.

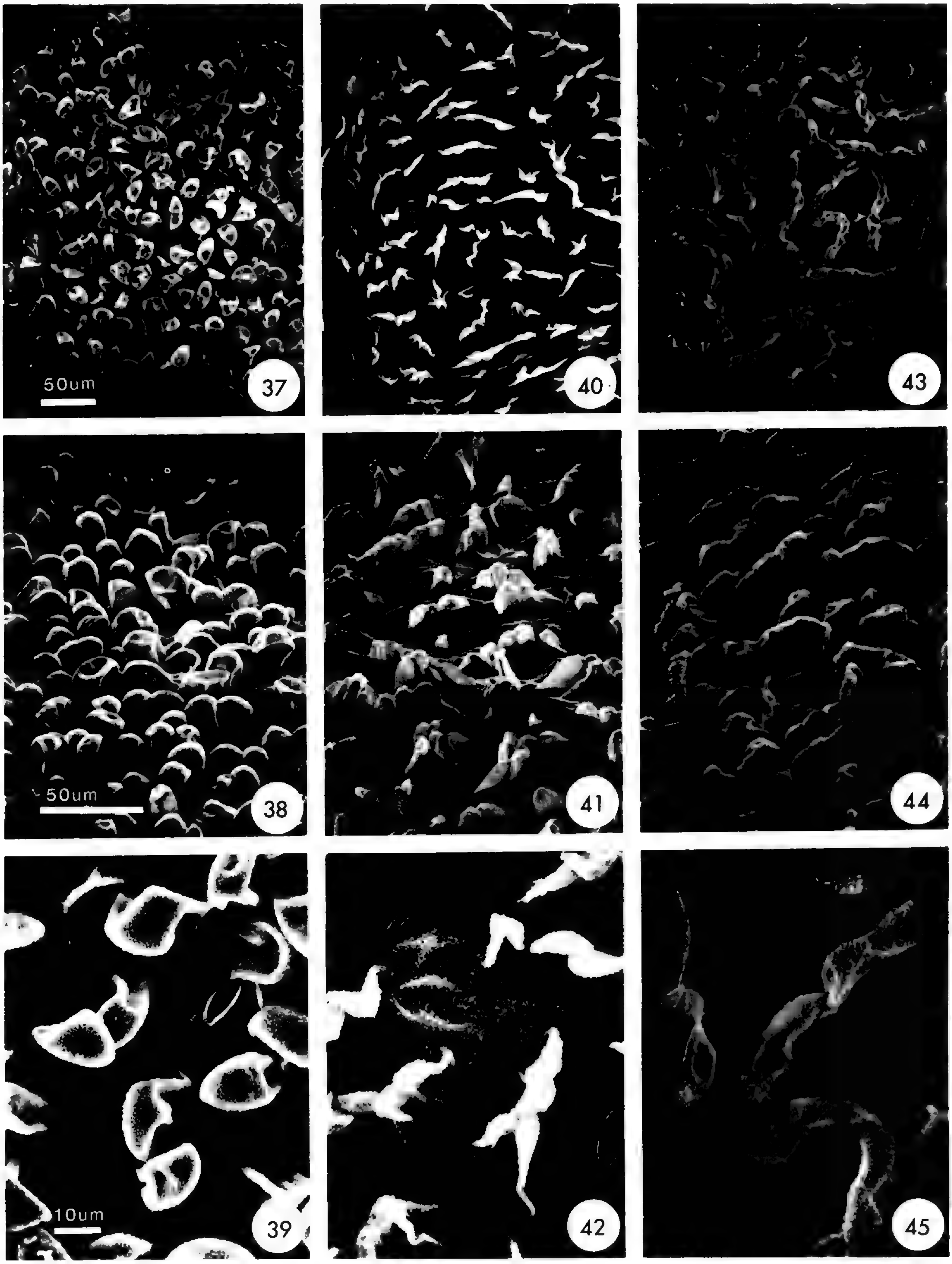
A study of the inheritance of phenetic traits in artificially produced hybrids serves several purposes beyond that of genetic analysis. Firstly, it allows for confirmation of hybridity in the hybrid progeny. In any experimental hybridization, there exists the possibility that the cross may be spurious; the progeny could result from contamination of self-pollen on the stigma, or from agamospermy. However, if the progeny possess a character present in the male parent but absent in the female, their hybrid nature is reasonably confirmed.

A second purpose for studying the inheritance of morphological traits in artificial hybrids is to generate information on the patterns of variation to be expected when hybridization occurs in nature. If, as Raven (1980) and Grant (1981) have suggested, there is a great deal of hybridization in flowering plants that passes undetected as such, then study of the products of artificial hybridization may help in the discovery and confirmation of hybrids in natural populations. This method was used effectively, for example, by Nobs (1963) in his biosystematic study of *Ceanothus*. Some of the artificial F_2 hybrid segregates of *Ceanothus* closely resembled stabilized populations with restricted ranges recognized as species. Nobs used this evidence to support his hypothesis that these species were of hybrid origin and were derived from pairs of extant, more wide-ranging species.

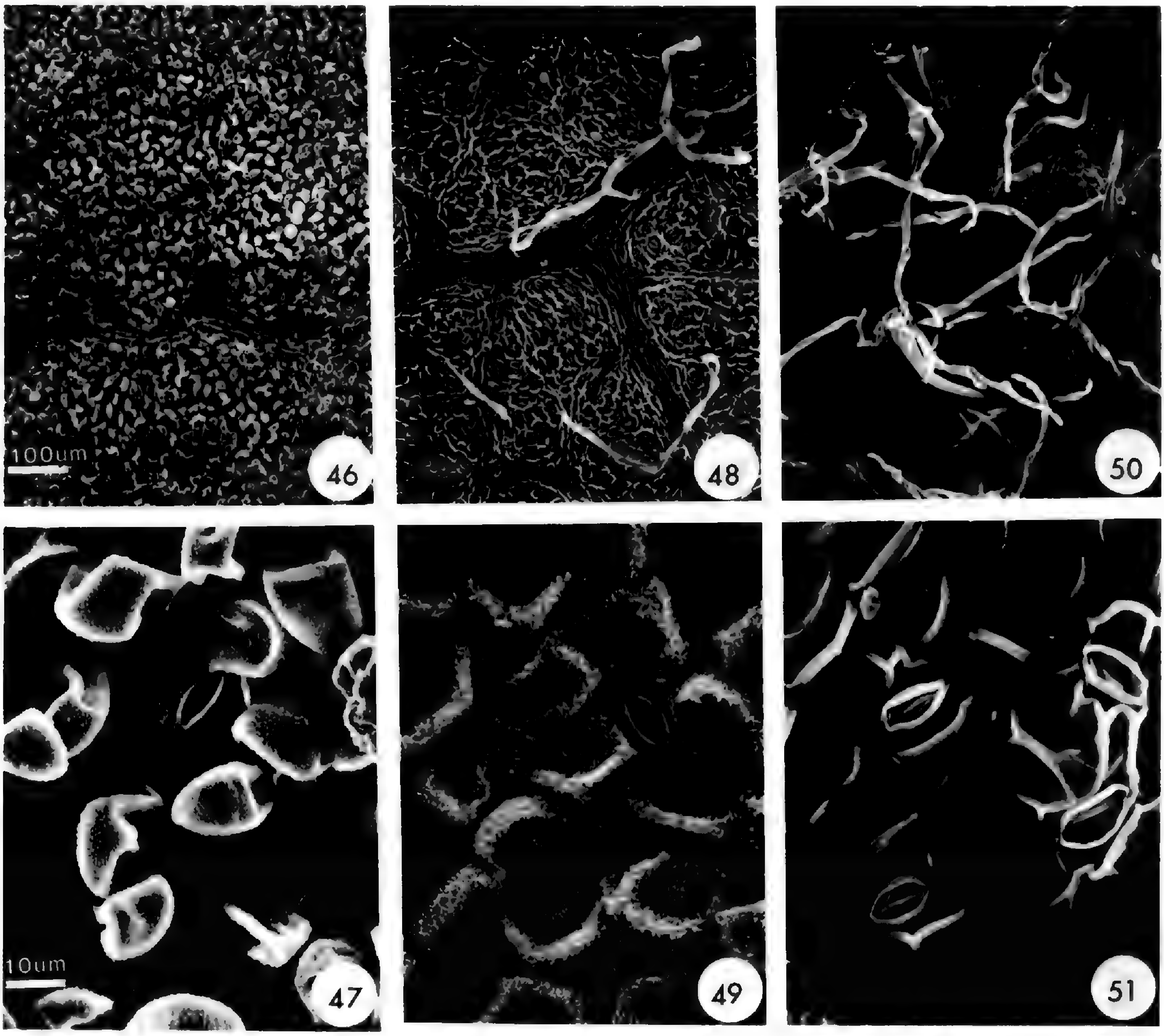
A similar study, combining artificial hybridization and analysis of natural hybridization, conducted by Gillett & Lim (1970) on *Bidens* in



FIGURES 28–36. *SEM images, abaxial leaf surfaces of* Erythrina chiapasana × E. berteroana *and parents. Each horizontal row at equal magnification. 29, 32, 35 at 60° tilt.—28–30.* E. chiapasana, *PT 721005001, female parent.—31–33.* E. chiapasana × E. berteroana, *HO 82.278.—34–36.* E. berteroana, *PT 700044002, male parent.*



FIGURES 37–45. *SEM images, abaxial leaf surfaces of* Erythrina guatemalensis × E. berteroana *and parents. Each horizontal row at equal magnification. 38, 41, 45 at 60° tilt.—37–39.* E. guatemalensis, *PT 700018001, female parent.—40–42.* E. guatemalensis × E. berteroana, *HO 82.289.—43–45.* E. berteroana, *PT 700044001, male parent.*



FIGURES 46–51. *SEM images, abaxial leaf surfaces of* Erythrina guatemalensis × E. chiapasana *and parents. Each horizontal row at equal magnification.—46, 47.* E. guatemalensis, *PT 700018001, female parent.—48, 49.* E. guatemalensis × E. chiapasana, *HO 82.283.—50, 51.* E. chiapasana, *PT 721005001, male parent.*

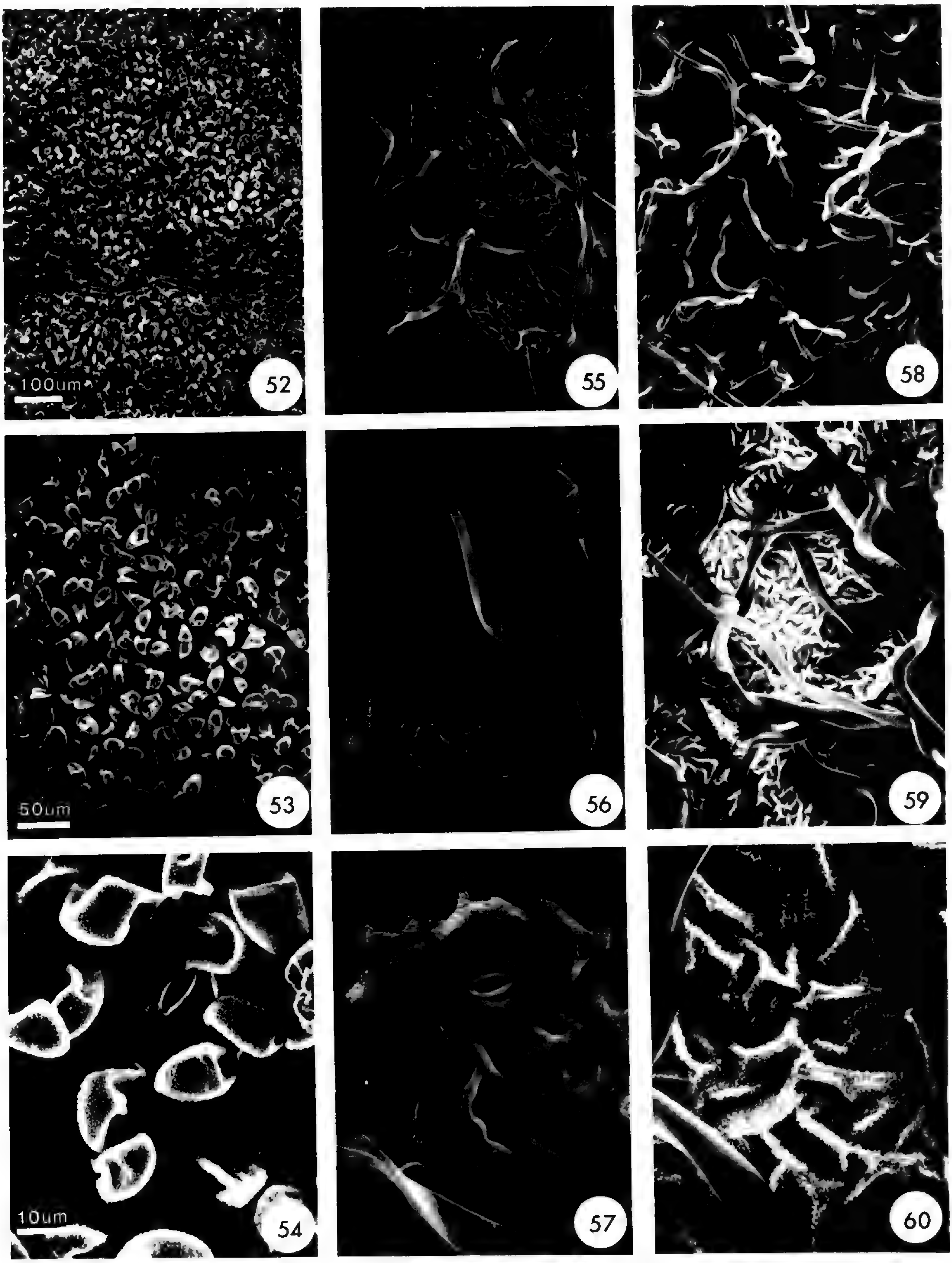
Hawaii, has been questioned by Ganders & Nagata (1984). They showed that some of the putative natural hybrids were merely intraspecific variants, and Ganders & Nagata concluded that adaptive divergence was more important than hybridization in the evolution of *Bidens* in the Hawaiian Islands. Although all of the 17 Hawaiian *Bidens* species are in fact interfertile, natural hybridization is rare because they are mostly allopatric. Evidently Gillett & Lim used too few characters and ignored intrapopulation variation. An important caveat is to avoid a too facile interpretation of hybridization results when applying them to the study of processes in nature.

In this research, two sets of phenetic traits were examined in the *Erythrina* hybrids and their parent species: 1) features of the epidermis of abaxial leaf surfaces, and 2) morphology and color of the flowers.

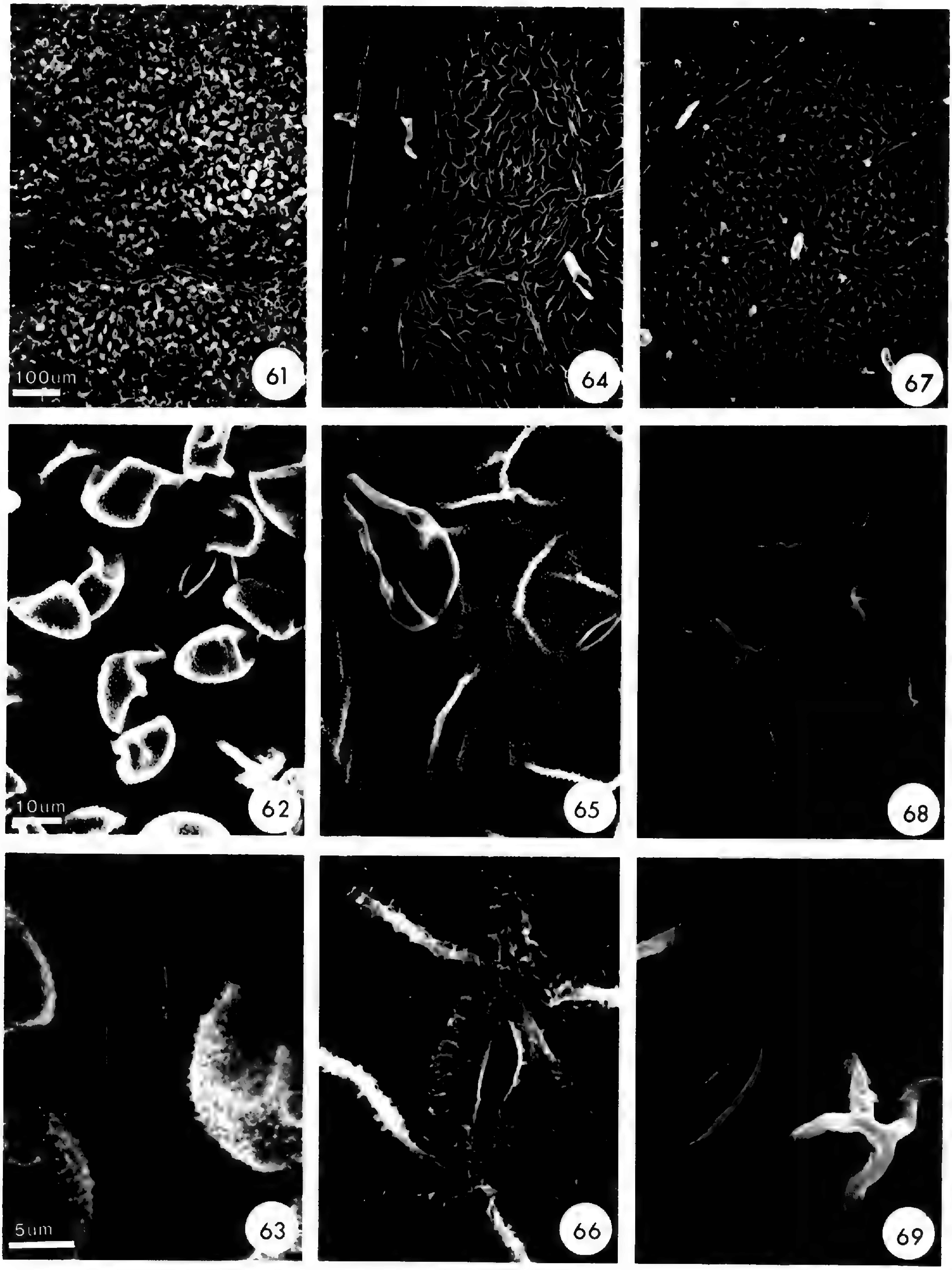
EPIDERMAL FEATURES OF *ERYTHRINA* LEAVES

Characters of the leaf are second only to those of flowers in their use and value in taxonomic studies (Stace, 1984). Studies of the inheritance of leaf surface characters in interspecific hybrids have recently been carried out in *Aloe* and *Gasteria* (Liliaceae) (Cutler, 1972), in *Ilex* (Baas, 1978), and in *Quercus* (Cottam et al., 1982).

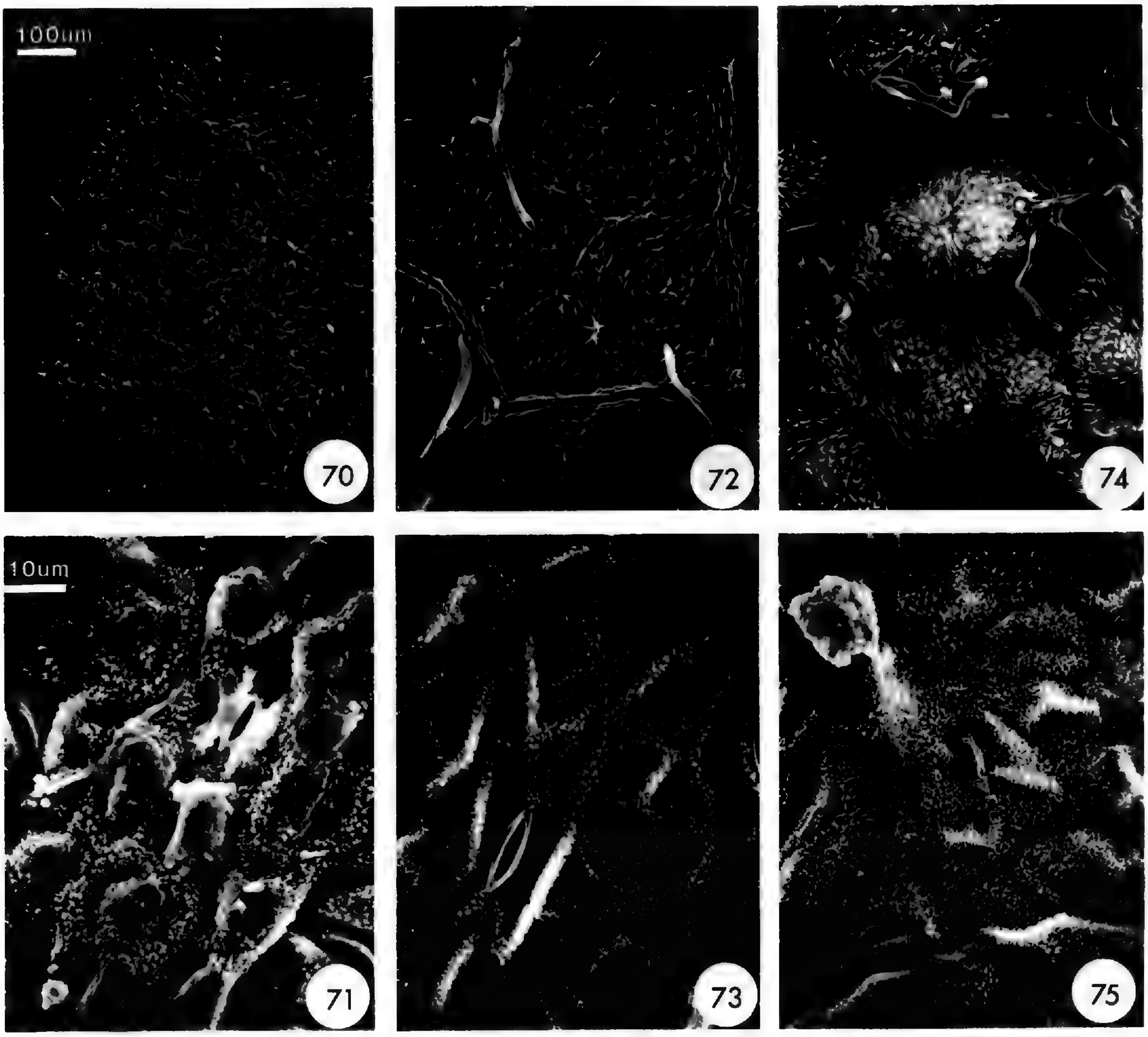
Erythrina species possess a wide variety of leaf surface characters. These have figured prominently in the taxonomic delimitation of the species (Krukoff, 1939a, b; Krukoff & Barneby, 1974). In these previous works the surface characters



FIGURES 52–60. *SEM images, abaxial leaf surfaces of* Erythrina guatemalensis × E. abyssinica *and parents. Each horizontal row at equal magnification.—52–54.* E. guatemalensis, *PT 700018001, female parent.—55–57.* E. guatemalensis × E. abyssinica, *HO 82.647.—58–60.* E. abyssinica, *PT 731006002, male parent.*



FIGURES 61–69. *SEM images, abaxial leaf surfaces of* Erythrina guatemalensis × E. senegalensis *and parents. Each horizontal row at equal magnification.—61–63.* E. guatemalensis, *WA 74c1453, female parent.—64–66.* E. guatemalensis × E. senegalensis, *HO 82.766.—67–69.* E. senegalensis, *WA 74s100, male parent.*



FIGURES 70–75. *SEM images, abaxial leaf surfaces of* Erythrina lysistemon × E. speciosa *and parents. Each horizontal row at equal magnification.—70, 71.* E. lysistemon, *PT 750280003, female parent.—72, 73.* E. lysistemon × E. speciosa, *HO 84.283.—74, 75.* E. speciosa, *PT 730708001, male parent.*

were not studied with high magnification or anatomical sectioning, however, and the structure of some of the surface characters was misinterpreted. This is discussed below in the description of epidermal characters. Leaf epidermal features of a few species of *Erythrina* have also been surveyed using scanning electron microscopy (Ayensu, 1977).

Materials and Methods

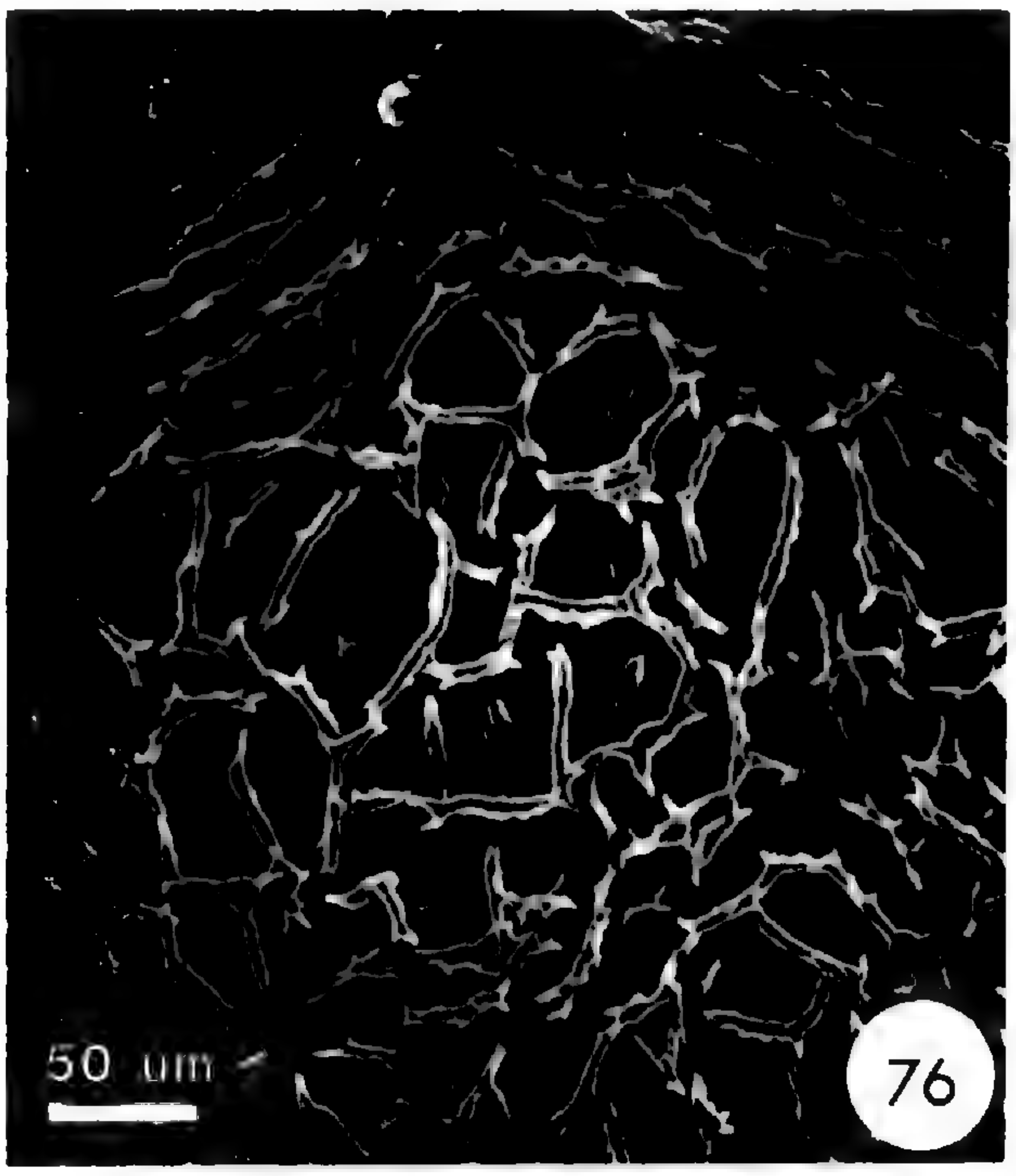
In this study, only the abaxial surfaces of leaves were examined. All samples were obtained from mature, fully expanded leaves, which were pressed and dried as in preparation of herbarium specimens. The specimens were gold-coated with a Polaron E5000 sputter-coater and observed with an Hitachi 450-S scanning electron microscope. For a few selected species, anatomical sections of paraffin-embedded leaves were prepared by Dr. Hiroshi Tobe of Chiba University, Japan.

Results

Survey of Leaf Epidermal Features in Erythrina

Epicuticular Wax. Platelets of epicuticular wax cover the abaxial leaf surfaces of many *Erythrina* species. The wax gives a whitish, glaucous appearance to the leaf observed without magnification. The platelets are 1–3 μm in size, are oriented randomly on the leaf surface, and vary in density (Figs. 12, 13). Epicuticular wax is consistently present in some species, but in others its presence or absence is variable even among individuals of a single population.

Multicellular Branched Hairs. Several types of



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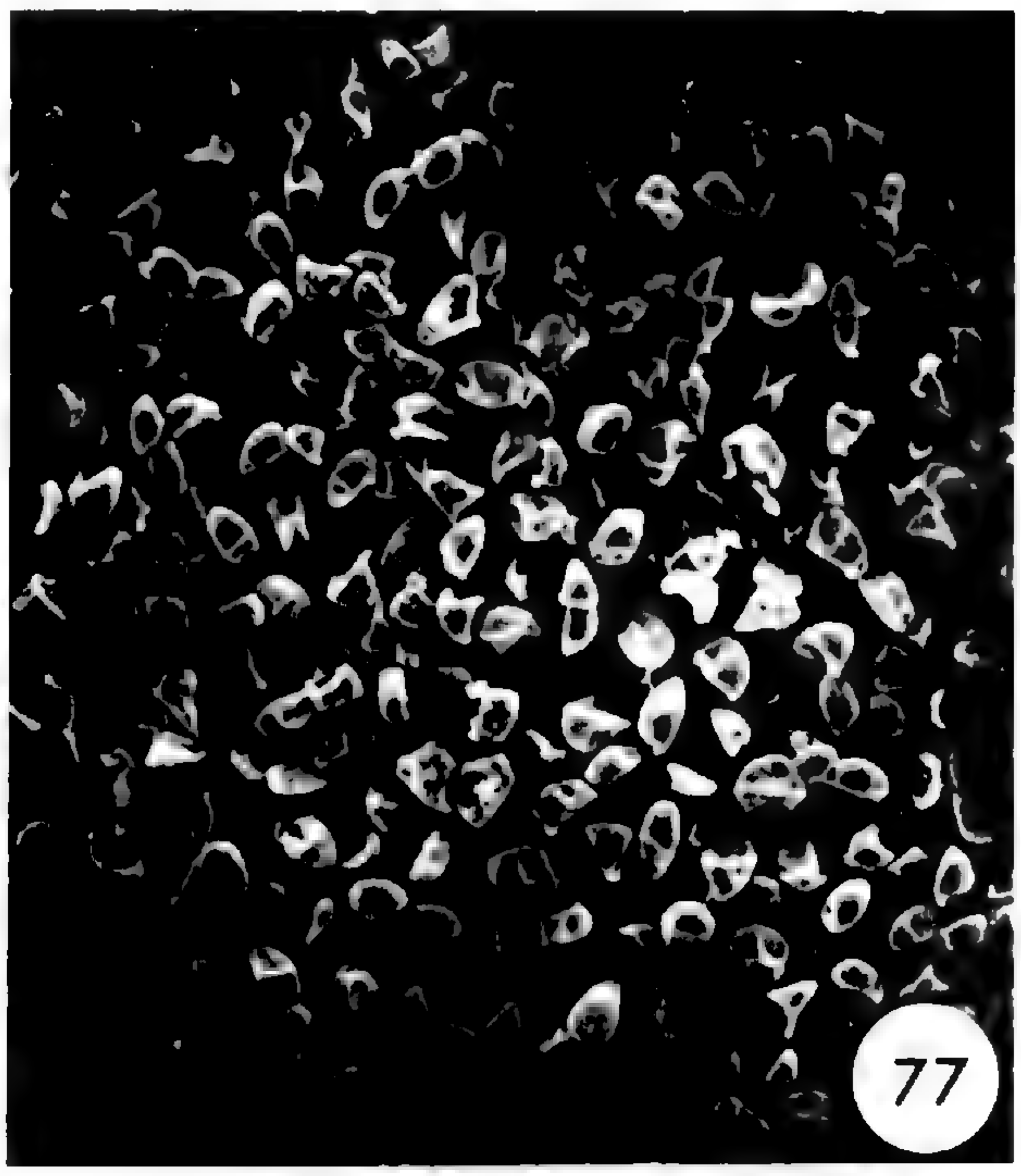

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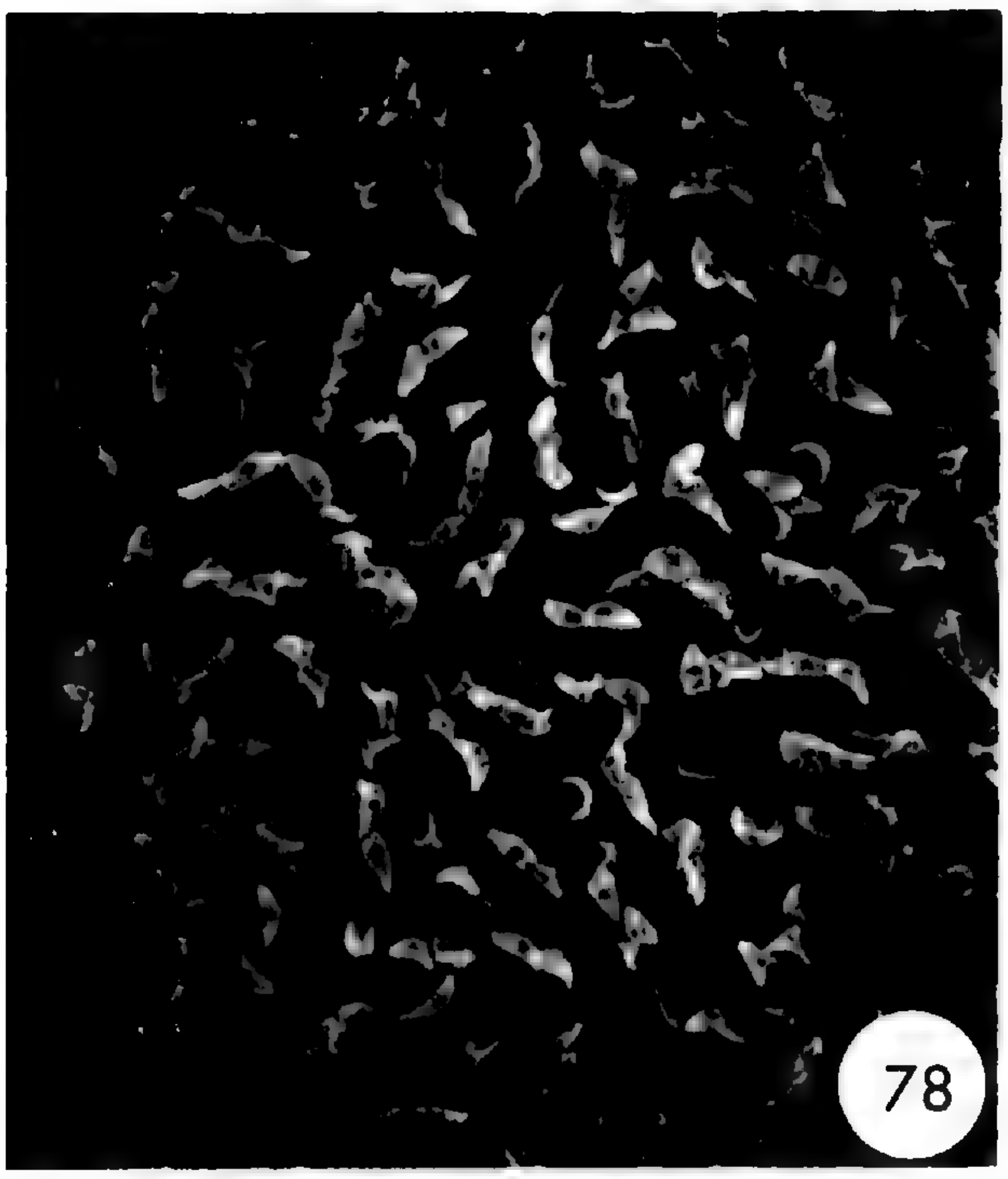

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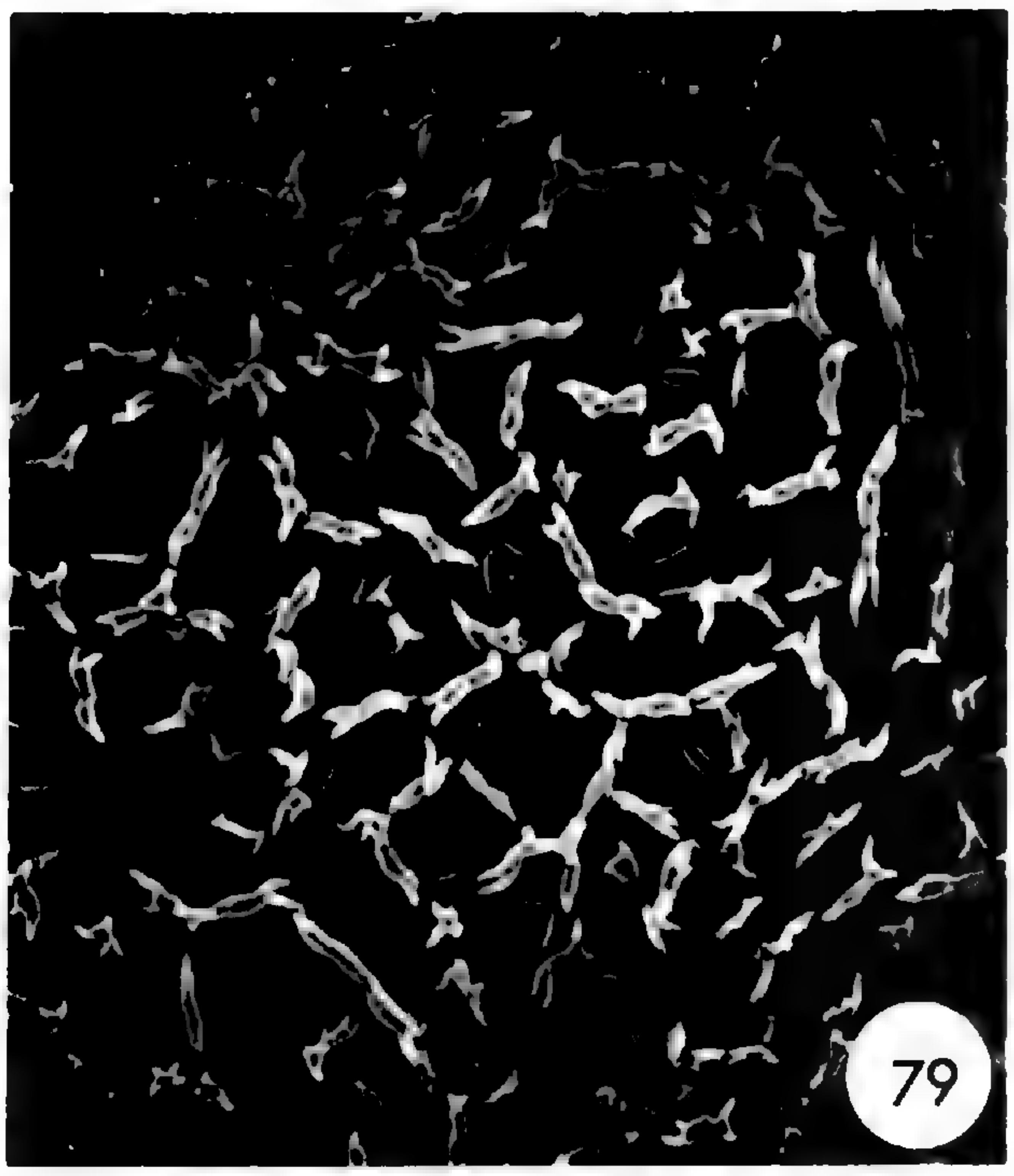

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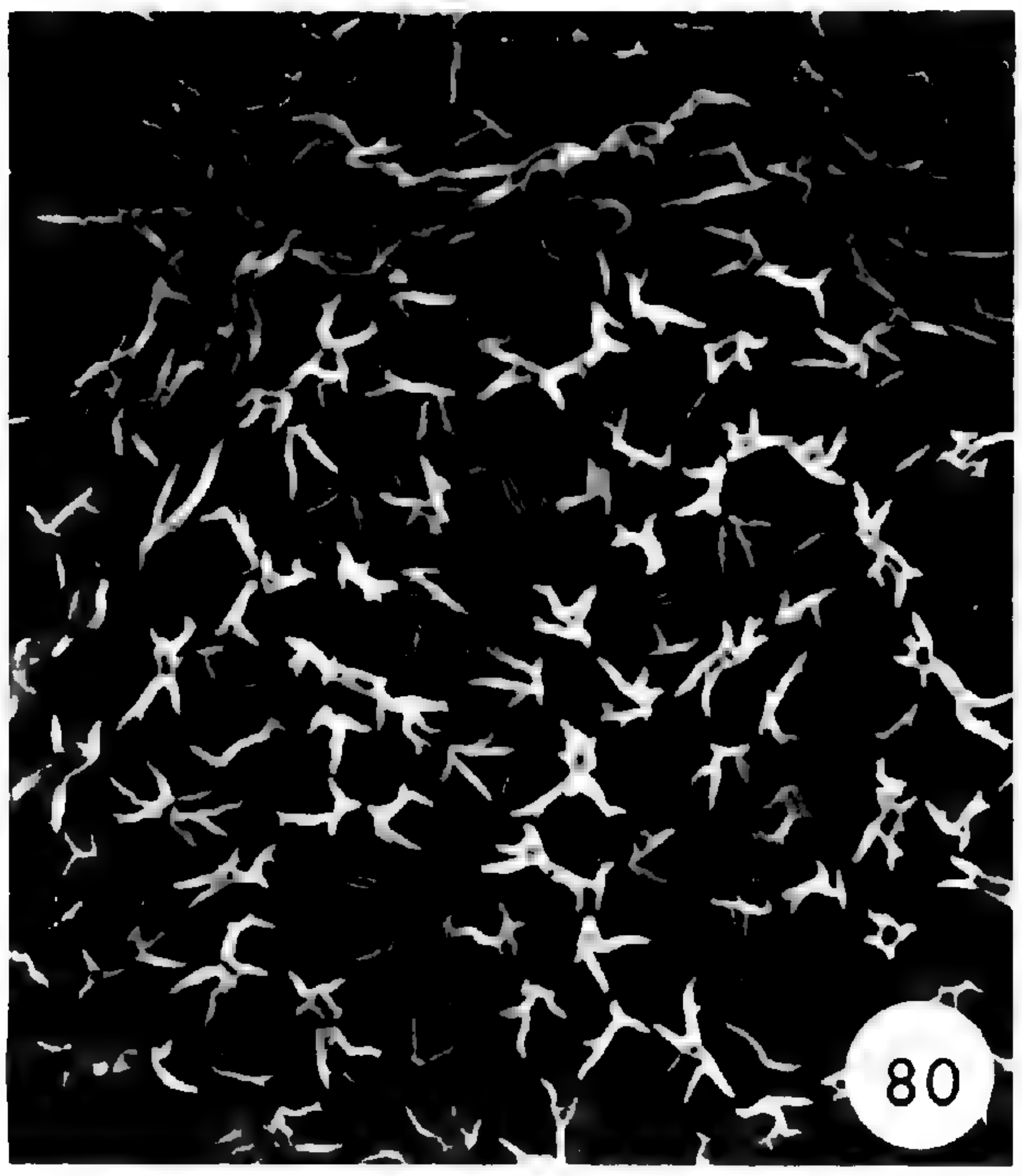

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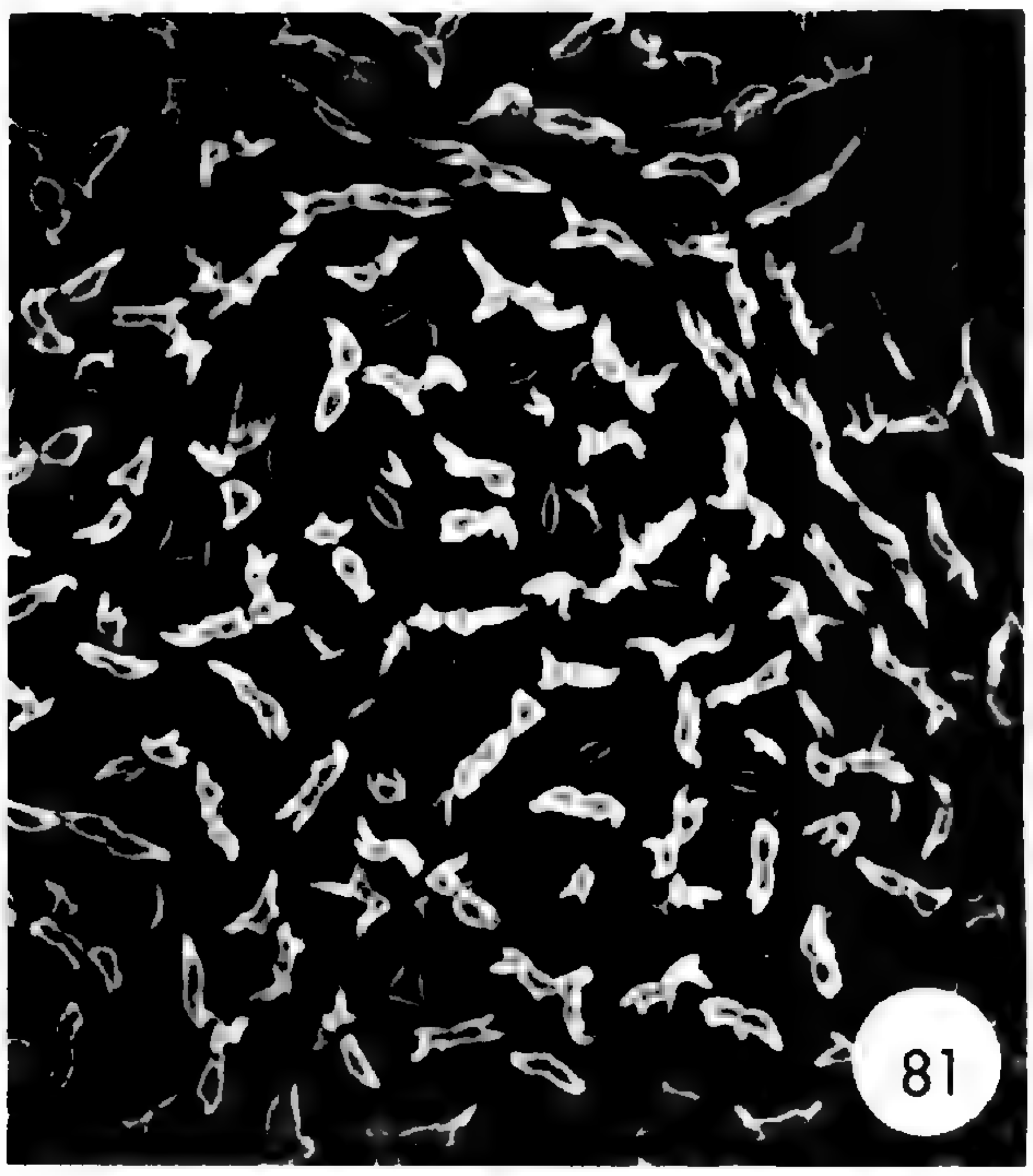

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hair occur on the abaxial leaf surfaces of *Erythrina* species. The most common, and the only type found in sect. *Erythrina,* is a multicellular, two-armed hair (Fig. 14). This consists of several short basal cells, one or two longer cells forming the stalk, and one cell forming each of the arms, which may be 1,000 μm or more in length. Two-armed hairs are present on the young leaves of most species in sect. *Erythrina* and in species of other sections as well, but in many species they are deciduous and are absent from fully expanded leaves. In the other species, the hairs are retained on mature leaves and form a dense tomentum.

Multiple-branched, dendritic hairs (Fig. 15) are restricted to sect. *Erythraster.* They occur in all species of that section and are found on calyces, inflorescence branches, and on leaves. Each branch of the dendritic hair is 50–100 μm long and is formed by a single cell. The dendritic hair has about 8–12 branches and extends up to 300 μm above the surface of the epidermis.

"Glandular" Hairs. Multicellular, uniseriate hairs occur sporadically on leaf surfaces of many *Erythrina* species (Figs. 22, 23). They appear to be glandular, but what substance these hairs secrete, if any, is not known. They are squat, rounded hairs about 50 μm long and comprised of five or six cells. Observed with a microscope, they glisten with a translucent amber color.

Unicellular Hairs. The most common type of multicellular hair in *Erythrina* is formed by a rounded or elliptic, thin-walled cell which loses its cytoplasm and collapses at leaf maturity or upon drying (Fig. 16). These I refer to as "balloonlike" hairs. They occur in several sections of *Erythrina.* Long, flat, ribbonlike hairs 500 μm or more in length are found particularly along the principal veins of the leaf in some species (Fig. 17). This type of hair is predominant in the Mexican sects. *Breviflorae* and *Leptorhizae.*

Epidermal Sculpturing: Papillae and Lamellae. The remaining types of *Erythrina* trichomes are considered separately from hairs because they are more integrally a part of the foliar epidermis. These are papillae and lamellae, which I refer to collectively as "epidermal sculpturing."

Papillae are single-celled, fingerlike trichomes. Each papilla is formed by the protrusion of an epidermal cell above the leaf surface. Papillae are up to 40 μm tall and 15 μm in diameter (Figs. 18, 19). Papillae and the epidermal surface between them are usually covered with epicuticular wax platelets. Under low magnification, a leaf surface with papillae appears covered with whitish granules. Krukoff (Krukoff & Barneby, 1974) termed such leaf surfaces "farinose-ceriferous" or "granular-ceriferous," but the "granules" he described are wax-covered papillate cells, not individual particles of wax.

Papillae similar to the ones found in *Erythrina* occur on leaf surfaces in many groups of plants, but the structures I have termed "lamellae" have not to my knowledge been reported from leaf epidermis of any angiosperm besides *Erythrina.* Lamellae, like papillae, are formed by protrusions of epidermal cells, but in lamellae the cells are joined edge-to-edge to form continuous "walls" one cell thick that stand above the surface of the leaf (Figs. 20, 21). Leaf surfaces with lamellae are also usually covered with epicuticular wax.

Lamellae occur in several species of sect. *Erythrina.* In these species the lamellae are discontinuous; each lamella is composed of several to twenty cells standing edge-to-edge. The lamellae form a dense, discontinuous network with a characteristic pattern when observed at low magnification (Fig. 34). Krukoff (Krukoff & Barneby, 1974) referred to leaves with wax-covered lamellae as "reticulately ceriferous."

A unique pattern of lamellae occurs only in the Asian sect. *Suberosae* (Figs. 24–27). The lamellae are tall (50 μm) and continuous. Parallel rows of several lamellae, each leaning at a different angle with respect to the leaf surface (Fig. 25), are joined to form an open network of interconnected polygons (Fig. 24). Shorter lamellae extend into the center of the polygons. The distribution of the polygons is associated with the vascular tissue of the leaf. *Erythrina suberosa* (Figs. 26, 27) has both polygon-forming lamellae and two-branched hairs.

Trichome characters are generally quite constant within a species and are useful taxonomic markers, often allowing species identification from

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FIGURES 76–81. *SEM images, abaxial leaf surfaces of* E. crista-galli × E. guatemalensis *and parents. All photos at equal magnification.—76.* E. crista-galli, *WA 74p840, female parent.—77.* E. guatemalensis, *WA 74c1453, male parent.—78–81.* E. crista-galli × E. guatemalensis, *four F_1 siblings, PT 820548 and WA 82.278.*

sterile material. In contrast, presence or absence of epicuticular wax is variable within populations and is not a useful marker. As will be seen in the discussion of the hybrids below, epicuticular wax is evidently a simply inherited trait. Krukoff (Krukoff & Barneby, 1973) separated the Mexican species *Erythrina americana* Miller and *E. coralloides* A. DC. (sect. *Erythrina*) solely on the basis of presence or absence of epicuticular wax. This trait is variable and is not well correlated with geographic distribution. For this and other reasons, *Erythrina coralloides* is here considered a synonym of *E. americana.*

Inheritance of Leaf-Surface Characters in Interspecific Hybrids

Each of the six plates comprising Figures 28–75 illustrates the leaf surface features of a single F_1 hybrid and its two parents. On each plate, the female parent is illustrated on the left, the male parent on the right, and the hybrid in the center. Each horizontal row of photographs is a comparison of the three individuals at equal magnification (indicated by the bar in the left-hand photograph). Table 18 summarizes the features present in the parents and hybrids.

Four of the six hybrids illustrated were derived from the same genetic individual as female parent, *Erythrina guatemalensis* PT 700018001 and WA 74c1453. It is particularly instructive to note the pattern of inheritance in the hybrids produced from the combination of this genome with those of four different species: *E. berteroana*, *E. chiapasana*, *E. abyssinica*, and *E. senegalensis.*

Erythrina guatemalensis has well-developed papillae on the abaxial leaf surface, each composed of a single epidermal cell; the male parent *E. berteroana* has well-developed lamellae, each composed of about 4–5 cells forming a "wall-like" structure. The F_1 hybrid has lamellae intermediate in length between the two parents, composed of 2–3 cells, but these are lower in stature and less developed than the epidermal sculpturing of either parent (Figs. 37–45).

Erythrina guatemalensis lacks hairs on mature leaf surfaces. The male parents *E. chiapasana* and *E. abyssinica* have dense covering of two-armed hairs. The hybrids derived from these males with *E. guatemalensis* as female also possess two-armed hairs, but at a much lower density than in the male parents (Figs. 46–51, 52–60). *Erythrina senegalensis* has scattered balloonlike hairs, and these are also inherited in the F_1 hybrid *E. guatemalensis* × *E. senegalensis* (Figs. 61–69). The male parents *E. chiapasana* and *E. senegalensis* lack epicuticular wax; this trait is present in the female *E. guatemalensis* and in the hybrids. (Other individuals of *E. chiapasana* than the one used in this cross do have epicuticular wax.)

Similar patterns of inheritance are exhibited by the other F_1 hybrids, for example, *Erythrina chiapasana* × *E. berteroana* (Figs. 28–36). The female parent *E. chiapasana* has a dense covering of hairs and lacks lamellae and epicuticular wax. The male parent *E. berteroana* lacks hair but possesses lamellae and wax. The F_1 hybrid has scattered hairs, lamellae reduced in stature, and epicuticular wax.

In the interspecific hybridization that produced *Erythrina lysistemon* × *E. speciosa*, the male parent possesses two-armed hairs, which are lacking in the female parent; hairs are present in the F_1 hybrid, but again, at a rather lower density than in the male parent (Figs. 70–75).

These results demonstrate that it is possible to confirm hybridity in the progeny by examination of leaf epidermal characters. Many of the hybrids possess characters present in the male parent but absent in the female parent. There is no evidence

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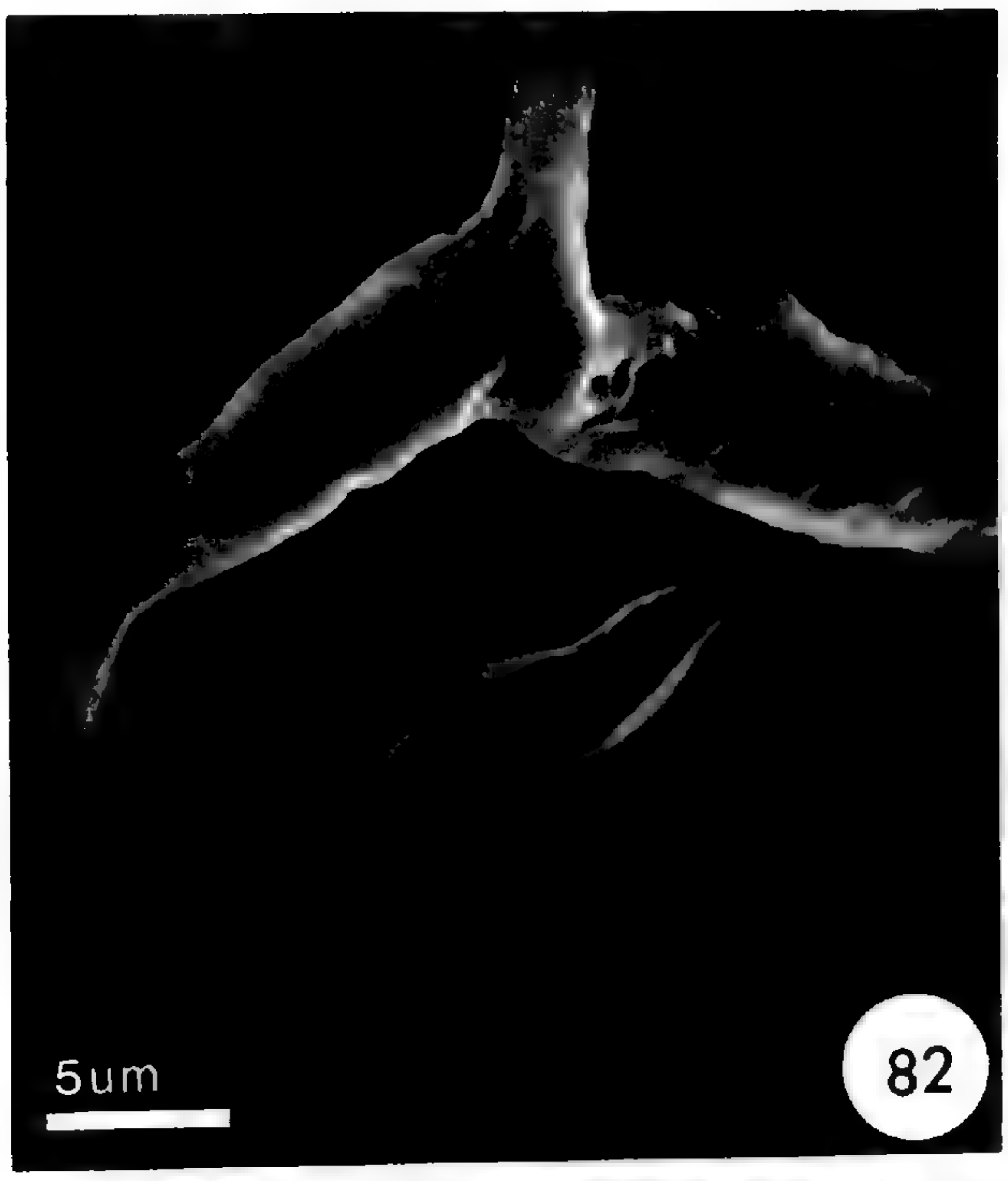
FIGURES 82–87. *SEM images, abaxial leaf surfaces of* E. crista-galli × E. guatemalensis *and parents. All photos at equal magnification.—82.* E. crista-galli, *WA 74p840, female parent.—83.* E. guatemalensis, *WA 74c1453, male parent.—84–87.* E. crista-galli × E. guatemalensis, *four F_1 siblings, PT 820548 and WA 82.278.*

FIGURES 88–93. *SEM images, abaxial leaf surfaces of* Erythrina crista-galli × E. fusca *and parents, and* E. dominguezii. *All photos at equal magnification.—88.* E. crista-galli, *WA 74p840, female parent.—89.* E. fusca, *WA 74s99, male parent.—90–92.* E. crista-galli × E. fusca, *three F_1 siblings, PT 840231 and HO 84.235.—93.* E. dominguezii, *PT 740234001.*

FIGURES 94–99. *SEM images, abaxial leaf surfaces of* Erythrina crista-galli × E. fusca *and parents, and* E. dominguezii. *All photos at equal magnification.—94.* E. crista-galli, *WA 74p840, female parent.—95.* E. fusca, *WA 74s99, male parent.—96–98.* E. crista-galli × E. fusca, *three F_1 siblings, PT 840231 and HO 84.235.—99.* E. dominguezii, *PT 740234001.*



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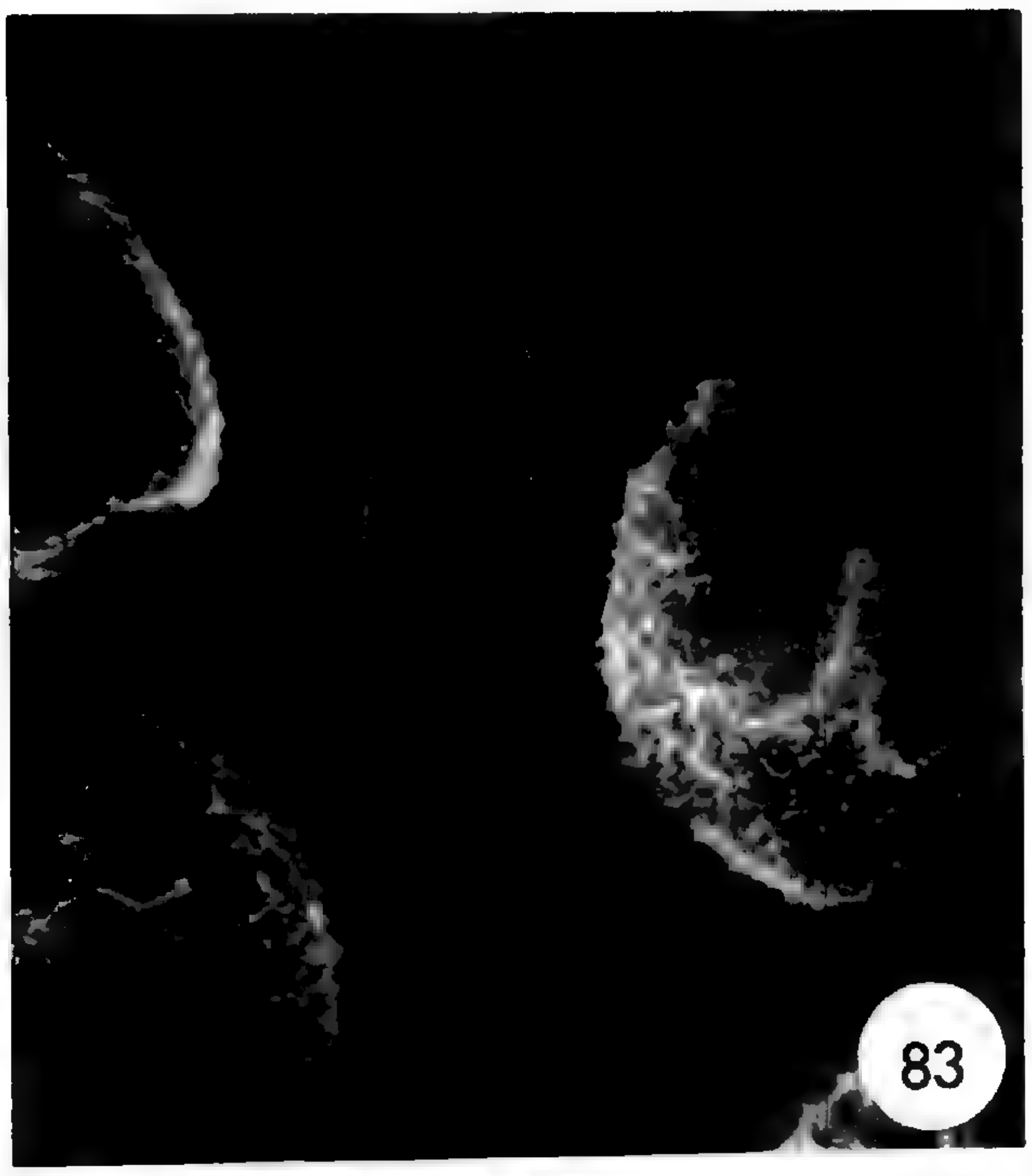

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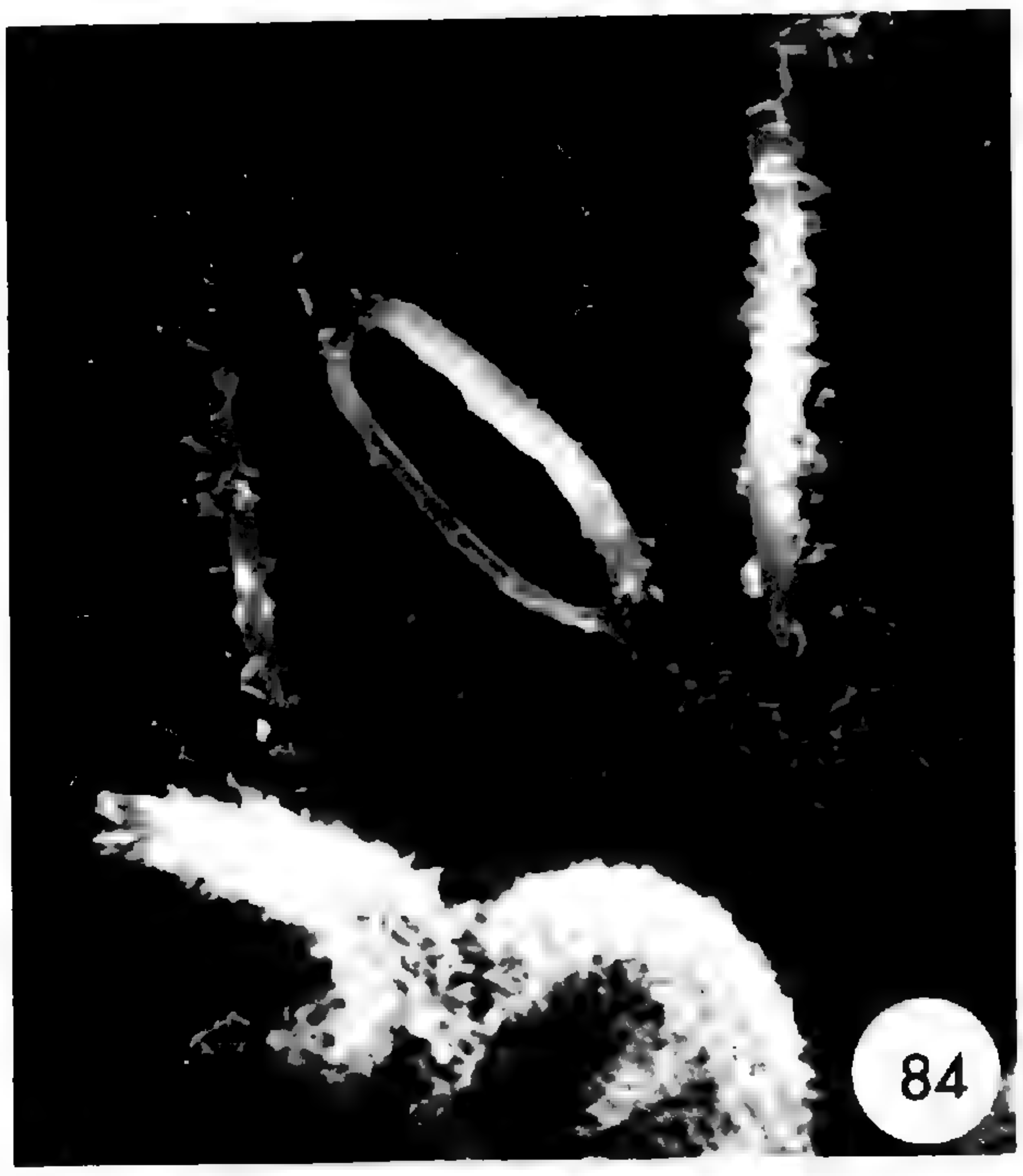

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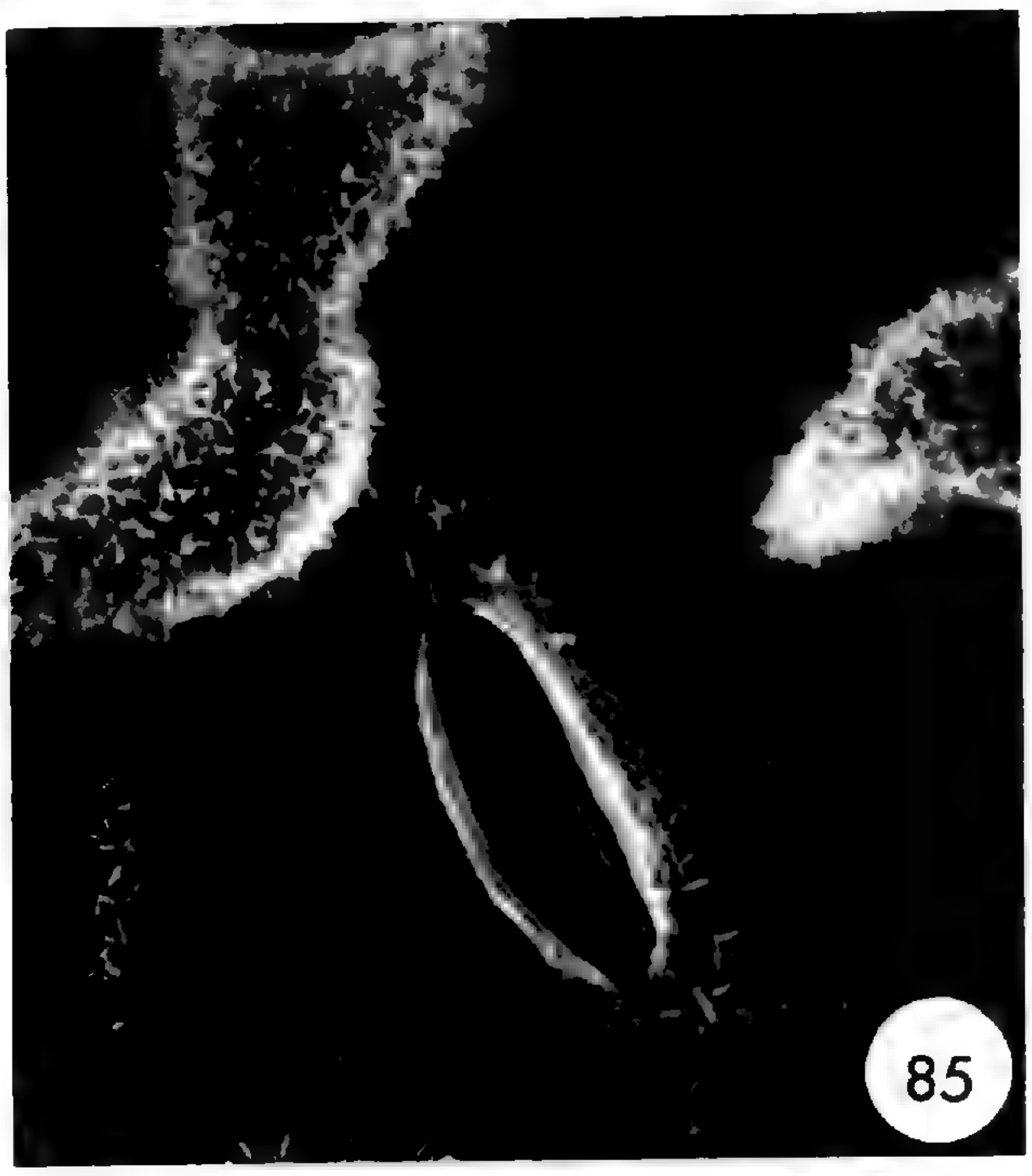

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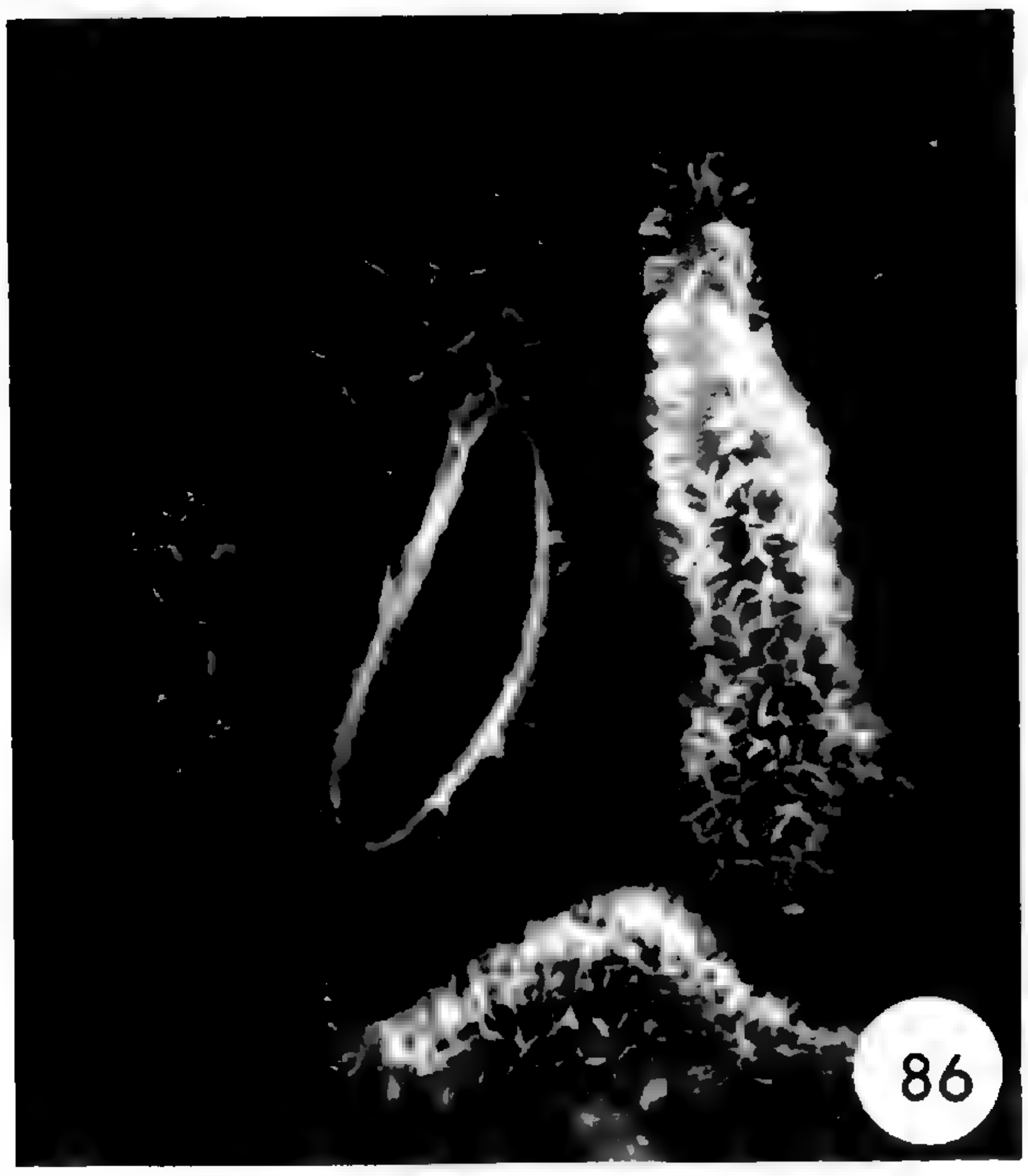

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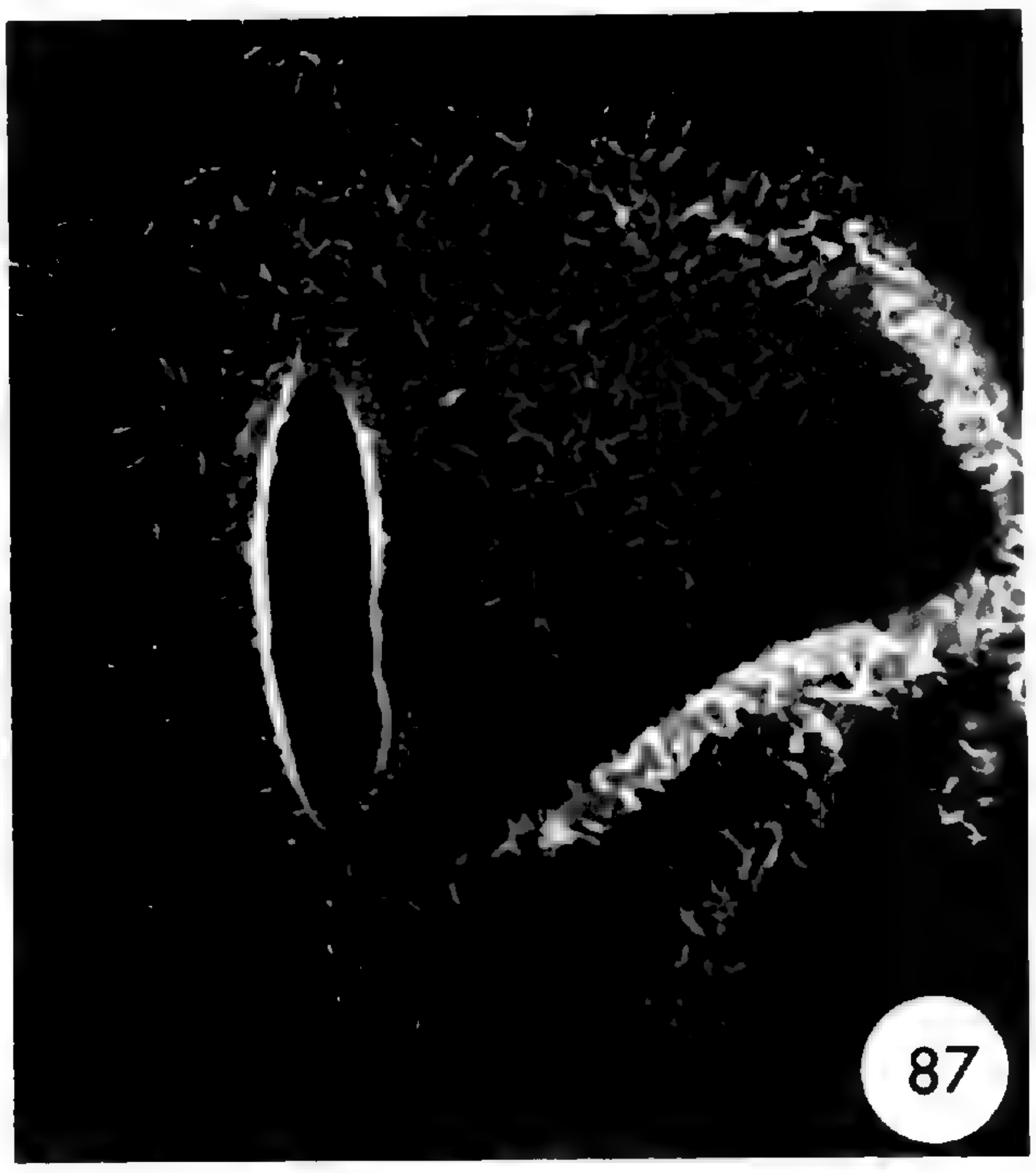

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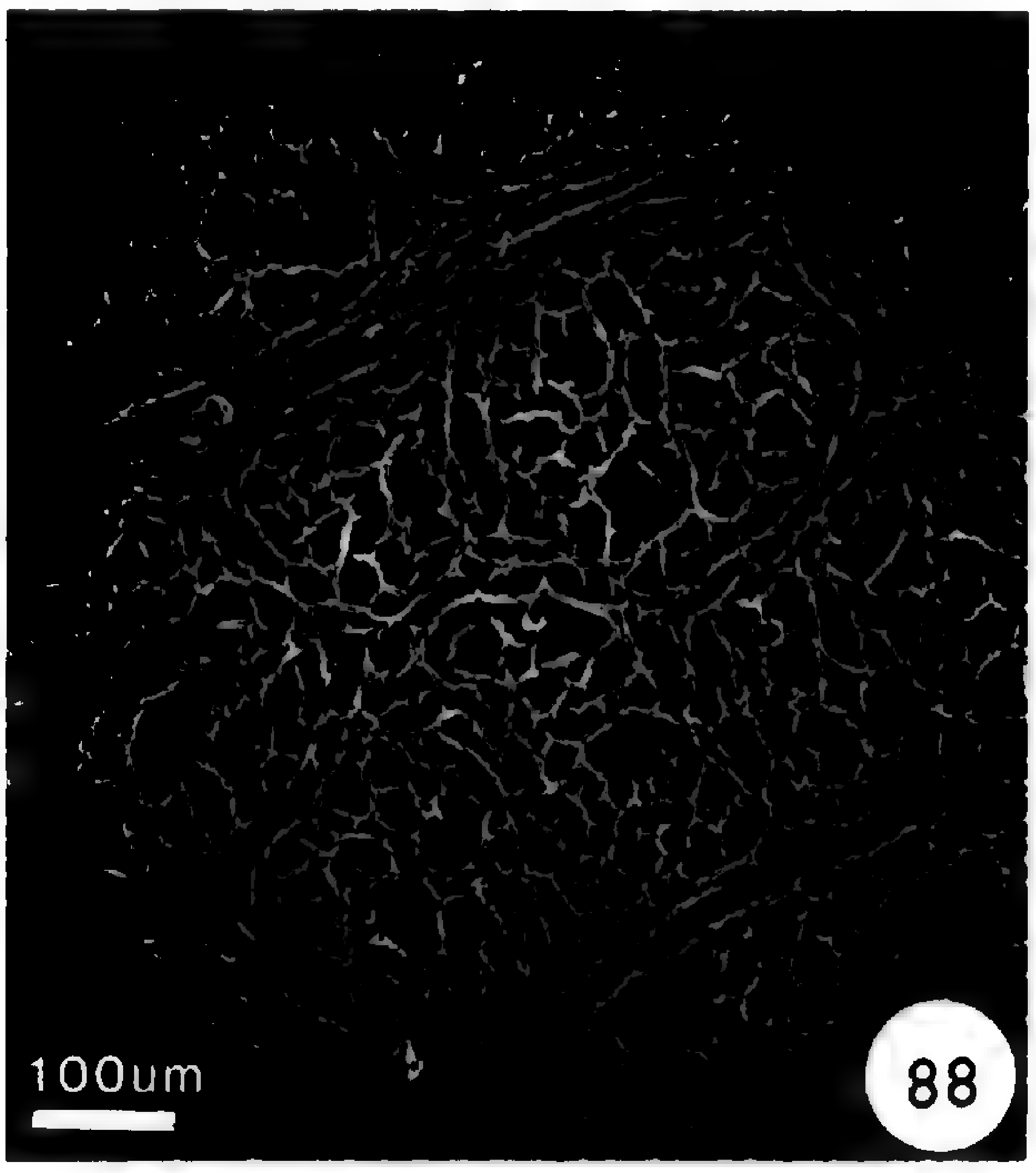

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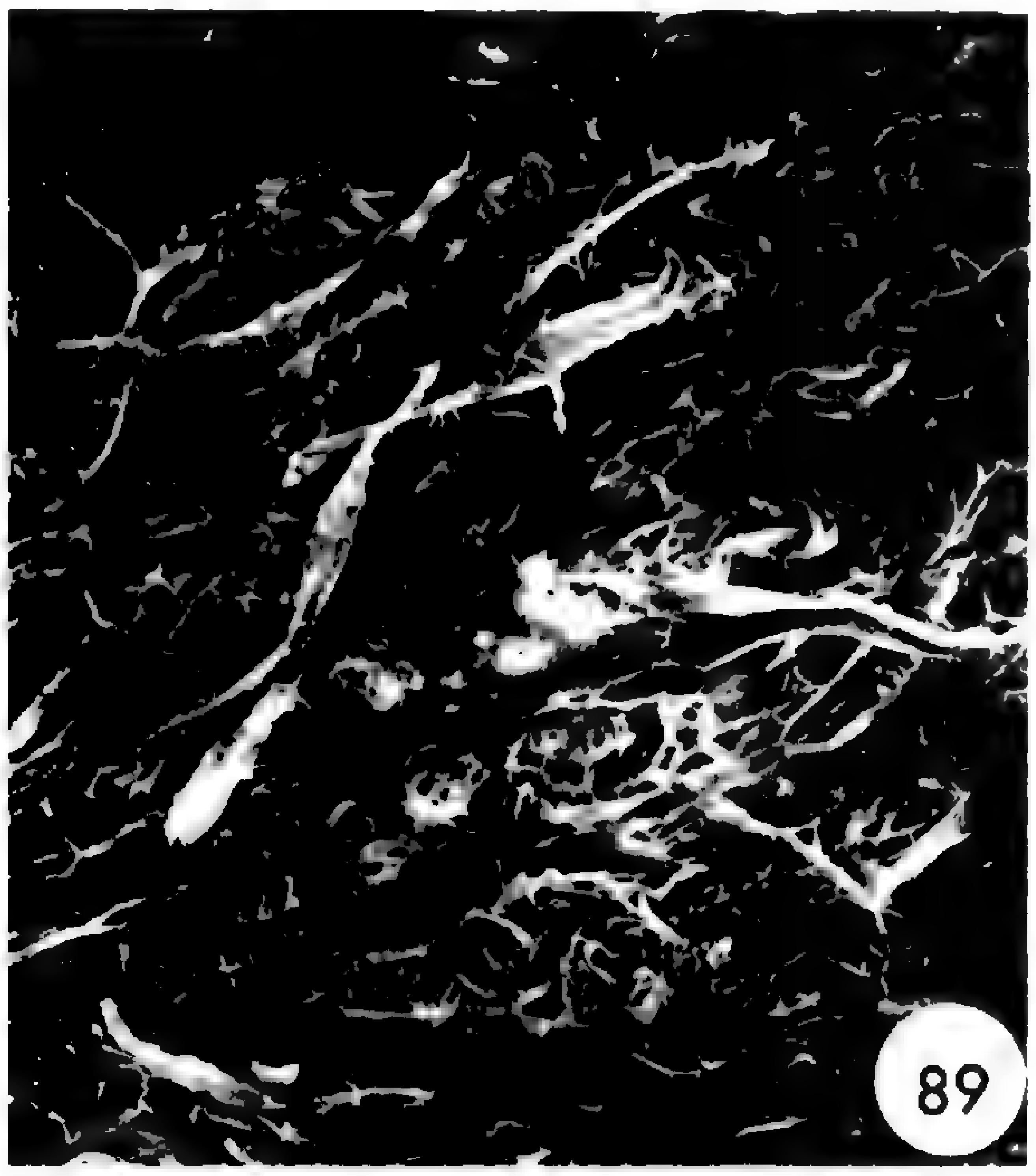

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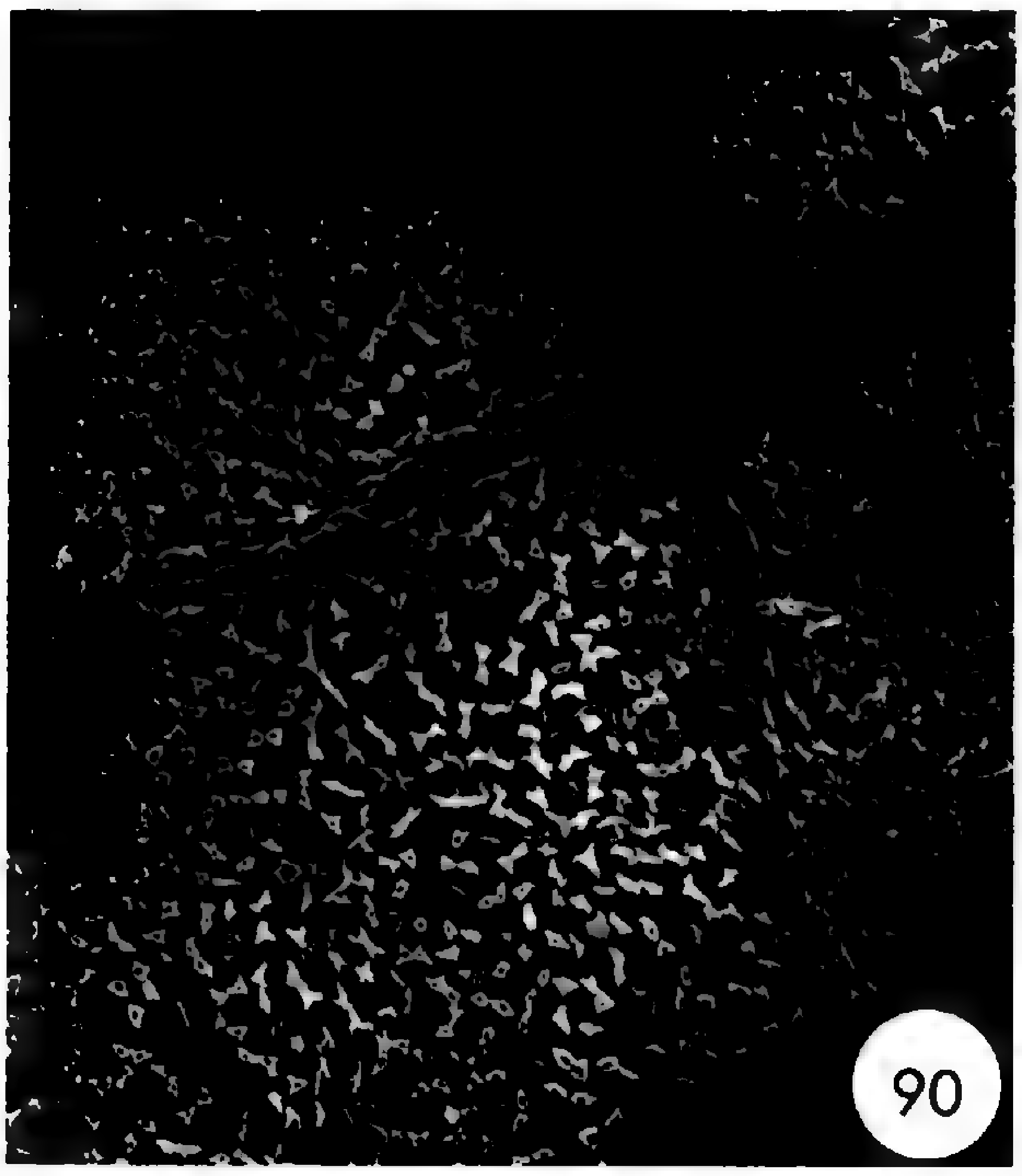

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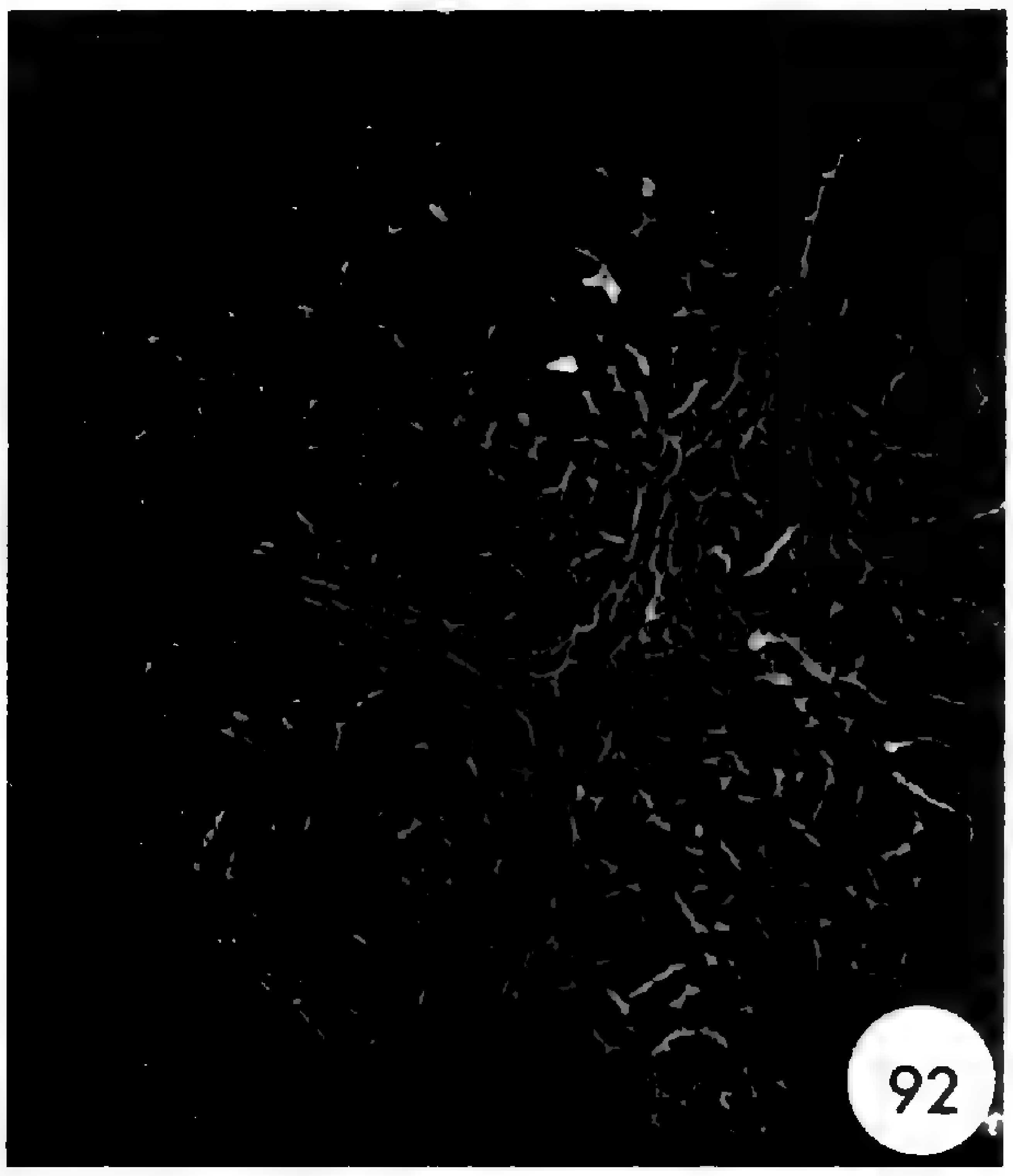

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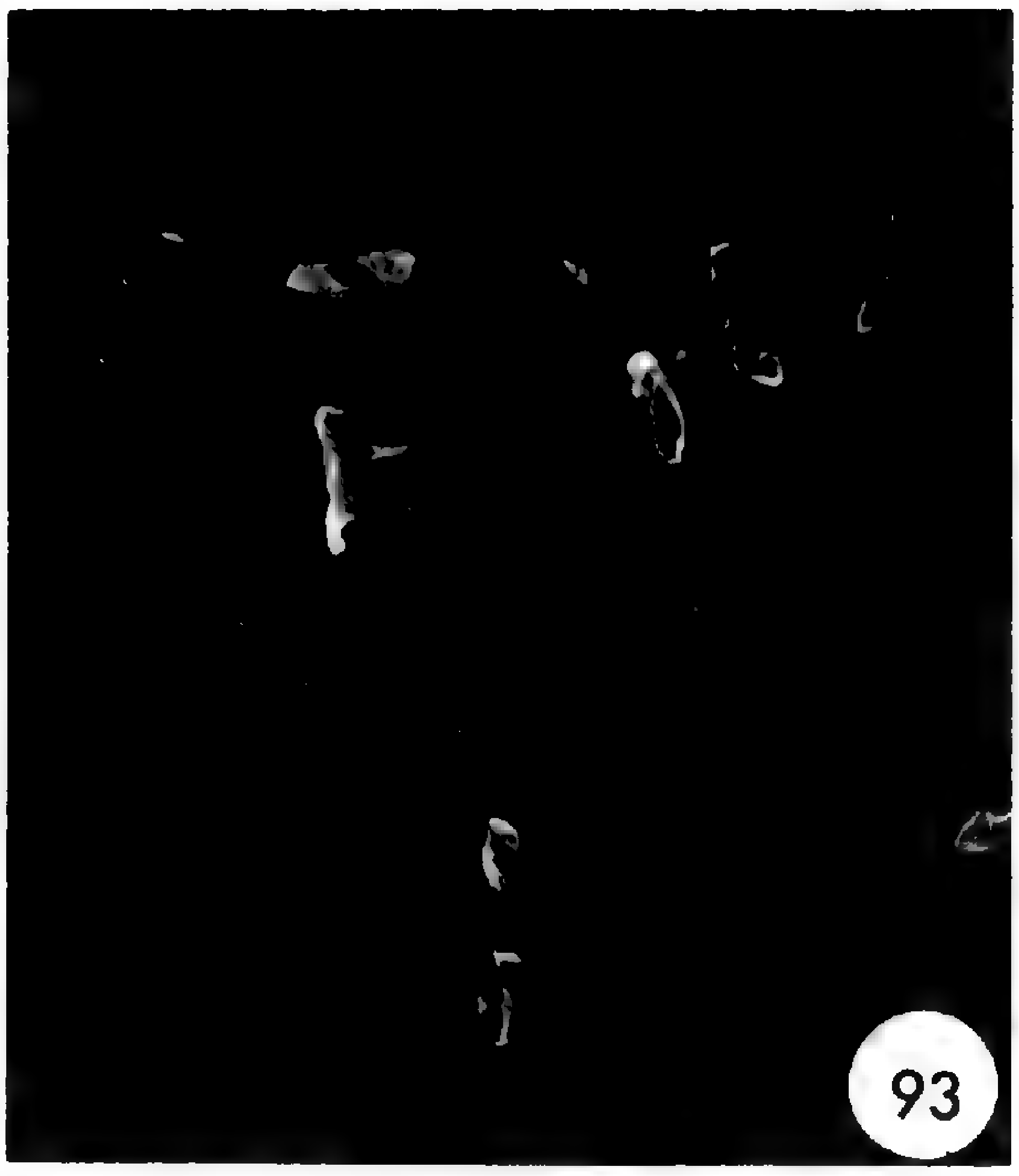

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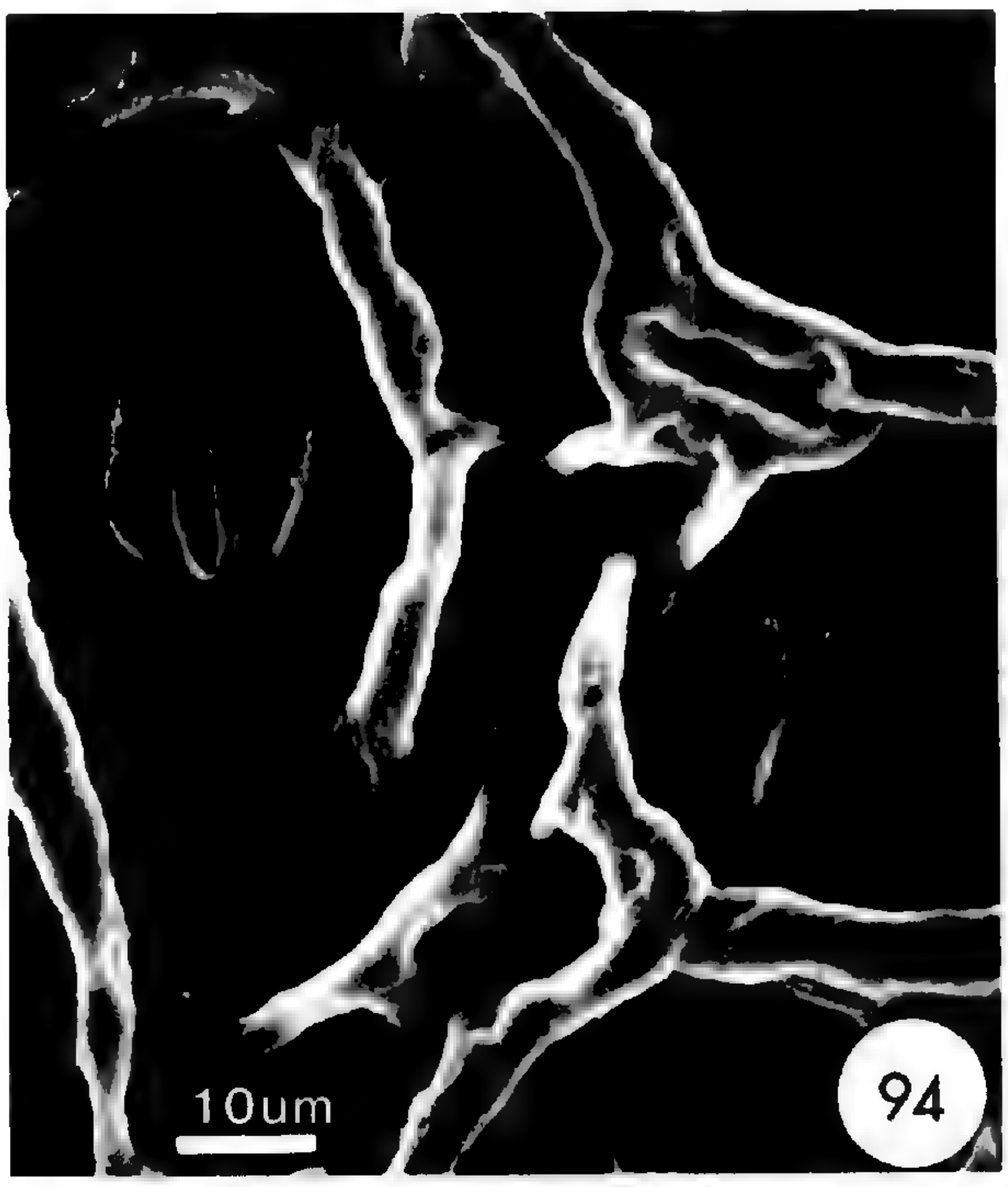

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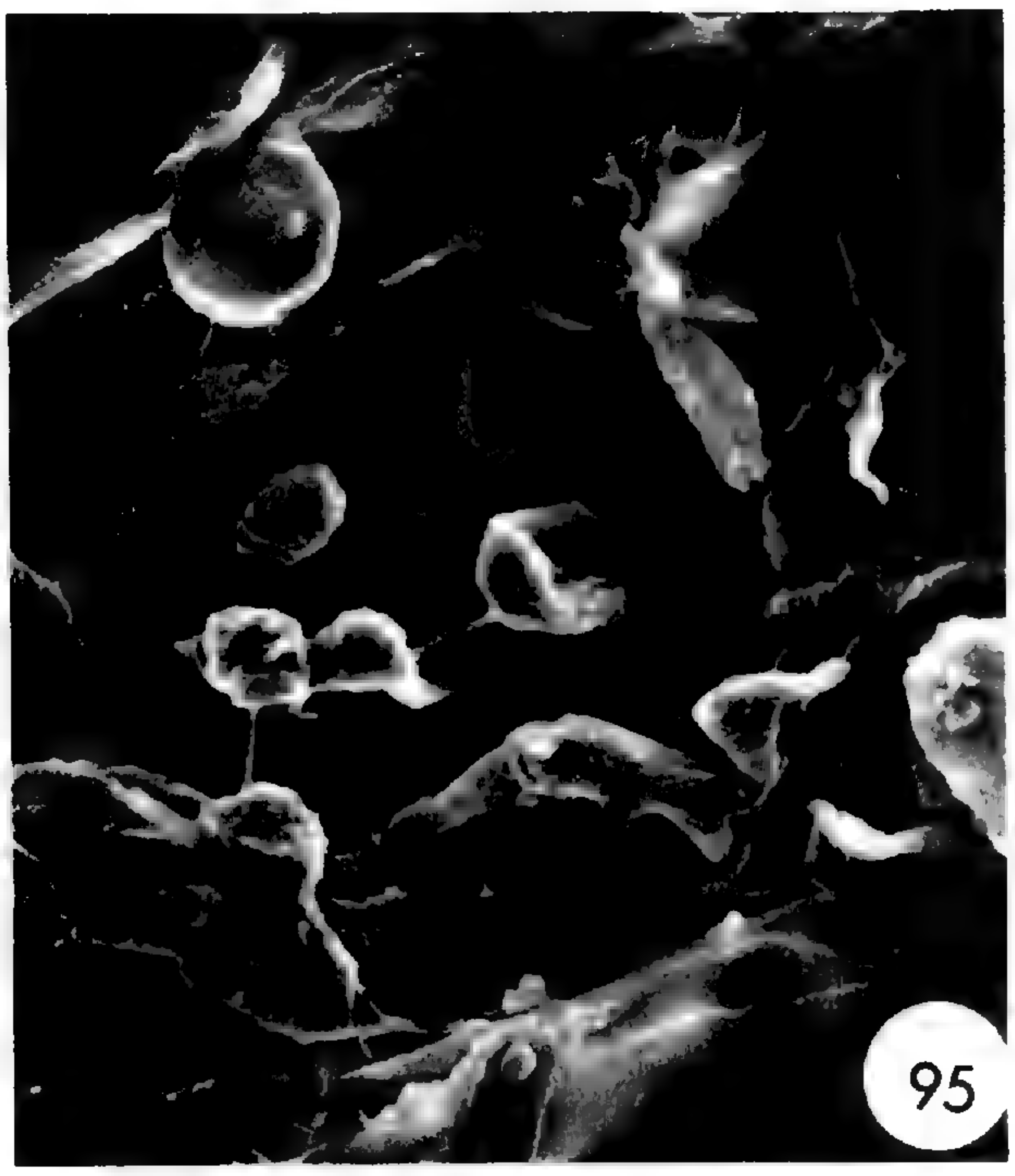

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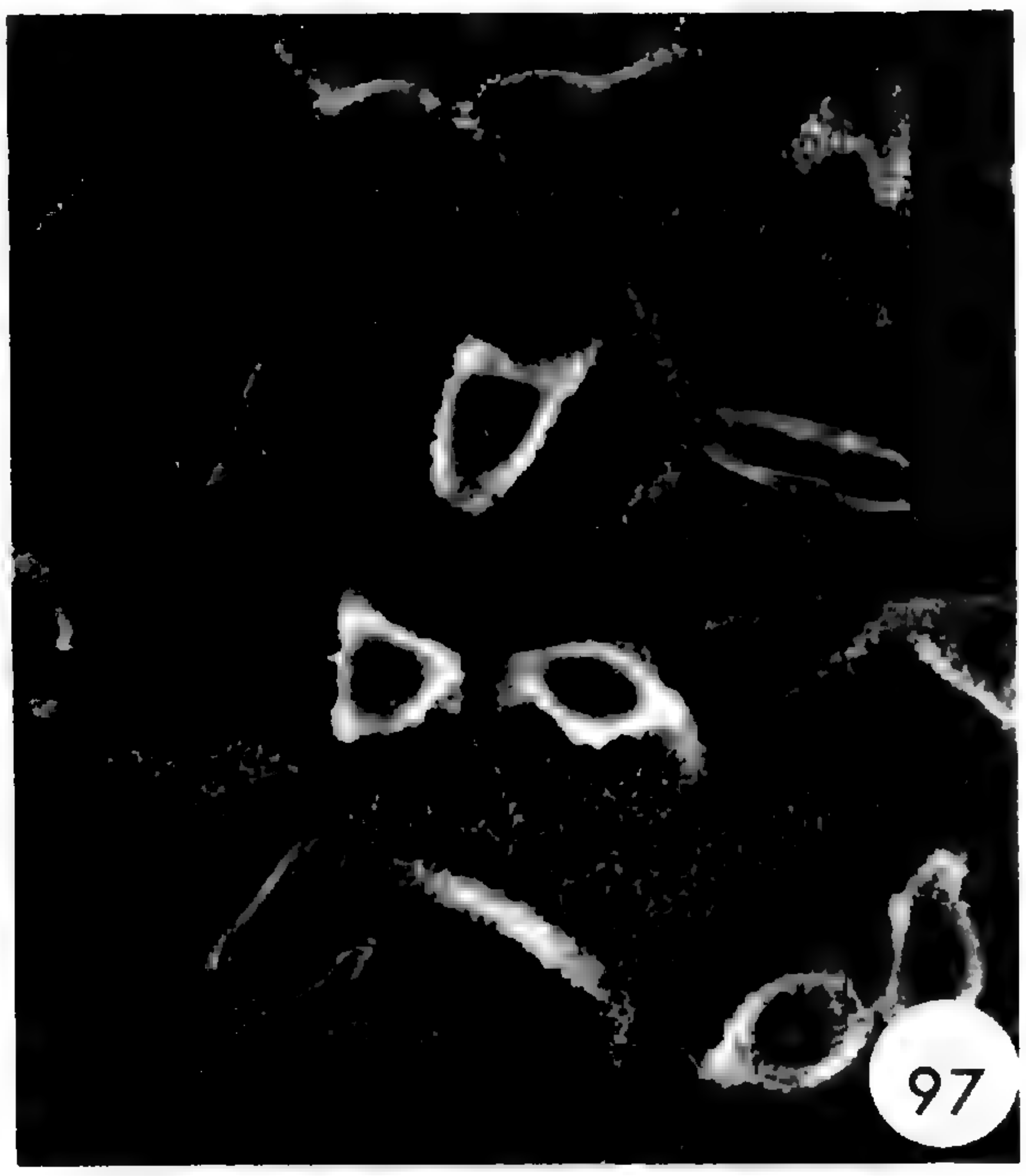

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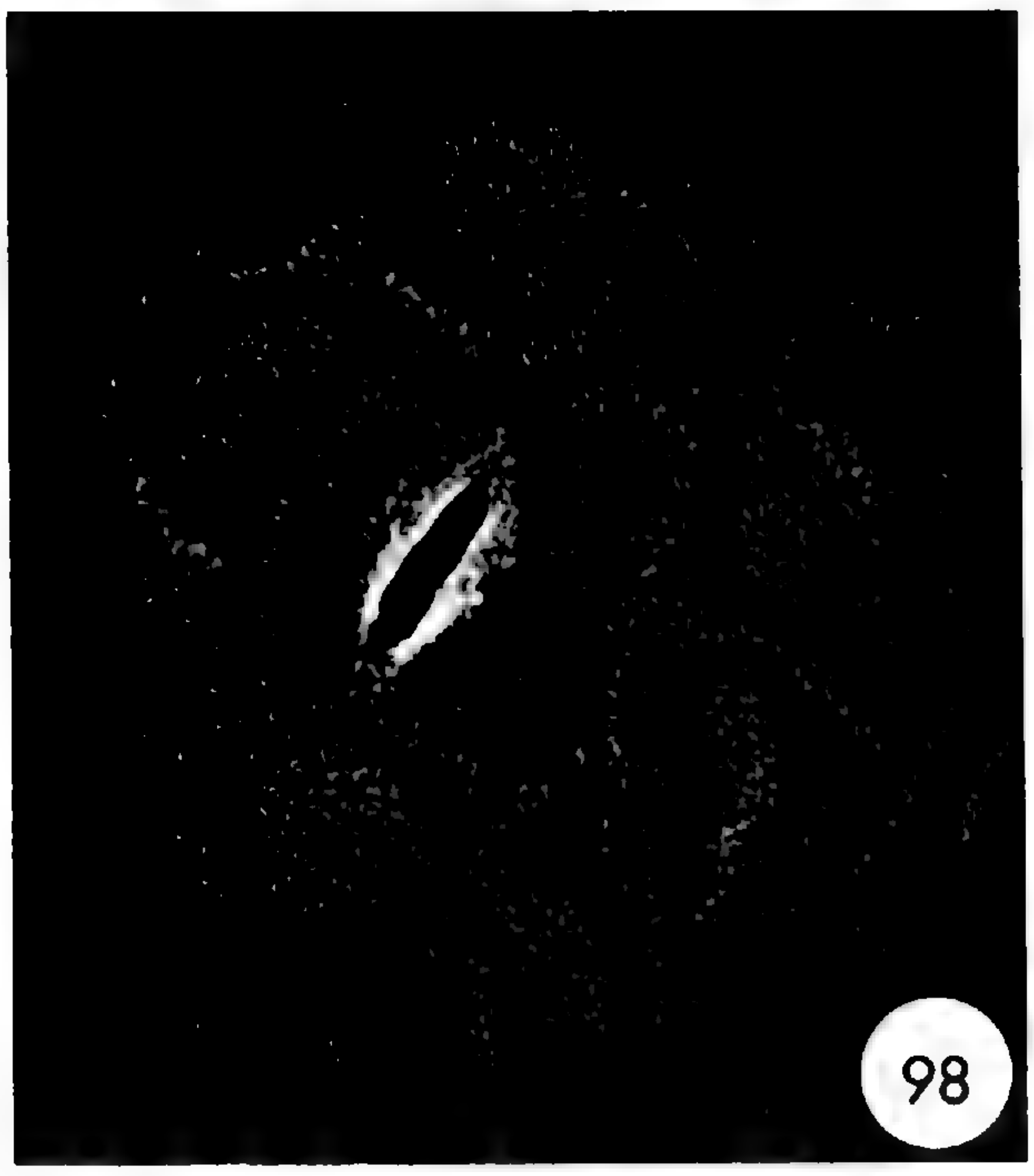

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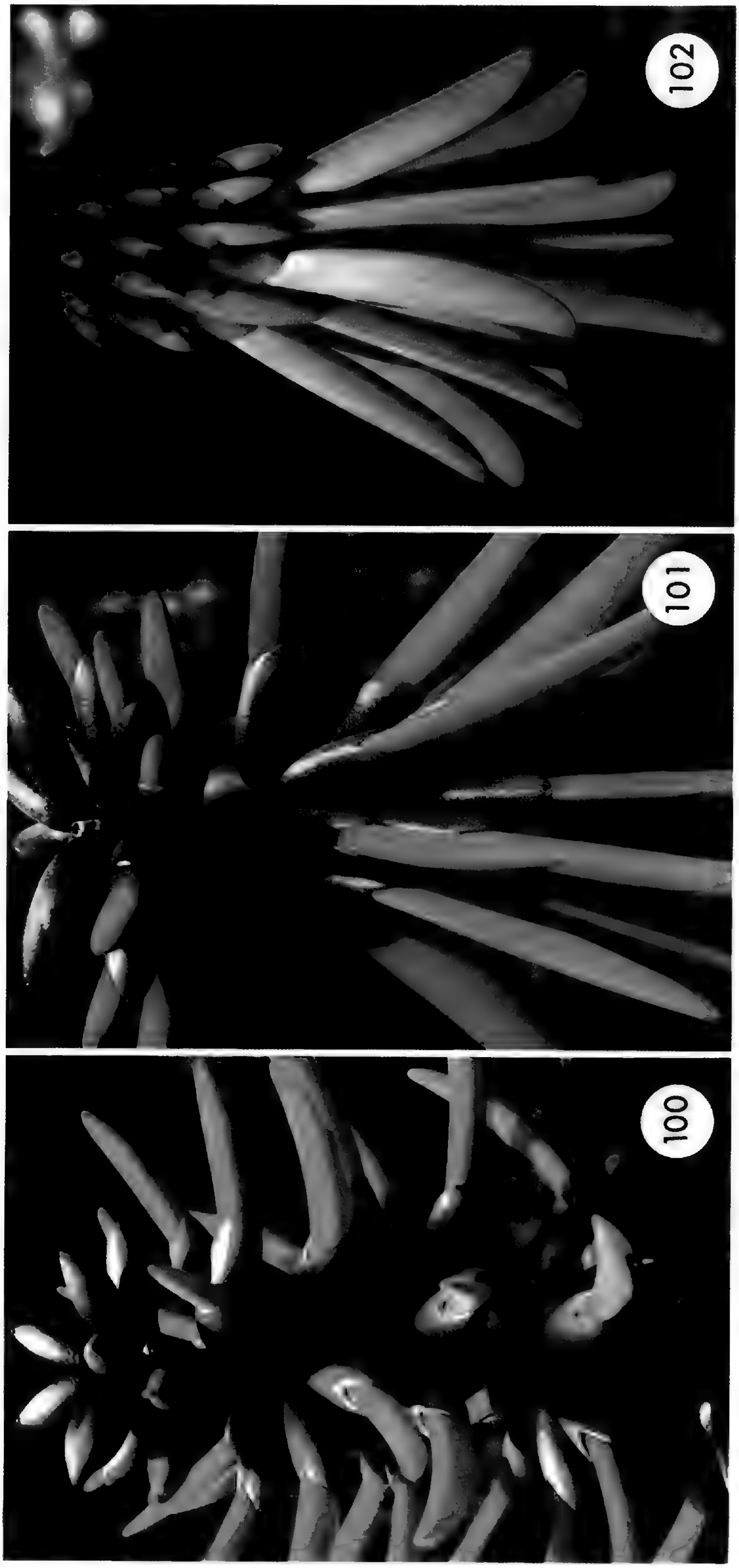

FIGURES 100–102. *Inflorescences of* Erythrina guatemalensis × E. folkersii *and parents.*—*100.* E. guatemalensis, *PT 700018001, female parent.*—*101.* E. guatemalensis × E. folkersii, *HO 82.282.*—*102.* E. folkersii, *PT 700010001, male parent.*

TABLE 19. *Comparison of flowers of F_1 hybrids and their parents in sect.* Erythrina. *Color code in "Standard Color" refers to Berlin & Kay color chart; see Croat (1983).*

	Female Parent	F_1 Hybrid	Male Parent
Figure 103	*E. berteroana* WA 78s564	HO 82.647	*E. guatemalensis* WA 74c1453
CALYX			
Shape	oblong	oblong to elliptic	elliptic
Apex shape	oblique; longer on carinal side	oblique; longer on carinal side	irregular; bilabiate or oblique
Length (cm)			
Vexillar side	2.2–2.3	2.2–2.4	2.3–2.7
Carinal side	2.6–2.7	2.7–2.8	2.6–2.9
Width (cm)			
Greatest	0.8	1.0–1.1	1.2–1.3
Middle	0.8	1.0–1.1	1.2–1.3
Indumentum	glabrous	sparsely puberulent	glabrous
Texture	smooth	minutely papillate	minutely papillate
Color	pale red	red to reddish brown	reddish brown
COROLLA			
Standard			
Color	red 8/7.5	red 8/7.5	red 6/7.5
Length (cm)	8.7	7.5	6.5
Greatest width (cm)	1.6	1.6	1.8
Wings			
Shape	apex acute	apex acute to rounded	apex rounded
Length (cm)	1.2	1.1	1.3
Width (cm)	0.3	0.4	0.3
Keel			
Shape	emarginate; each half acute at apex	apex short-apiculate	apex rounded
Length (cm)	1.0	1.1	1.3
Width (cm)	0.8	1.0	1.0
Figure 104	*E. guatemalensis* WA 74c1453	PT 820547001	*E. tajumulcensis* WA 74c1448
CALYX			
Shape	elliptic	oblong	oblong
Apex shape	variable; bilabiate or oblique	oblique; longer on carinal side	oblique; longer on carinal side
Length (cm)			
Vexillar side	2.3–2.7	2.3–2.5	2.4–2.6
Carinal side	2.6–2.9	2.7–2.8	2.7–3.0
Width (cm)			
Greatest	1.2–1.3	0.9	0.7
Middle	1.2–1.3	0.9	0.7
Indumentum	glabrous	glabrous	glabrous
Texture	minutely papillate	smooth	smooth
Color	reddish brown		red
COROLLA			
Standard	red 6/7.5	red 7/7.5	red 6/7.5
Color	6.5	7.2	9.3
Length (cm)	1.8	1.5	1.3
Greatest width (cm)			

TABLE 19. *Continued.*

	Female Parent	F$_1$ Hybrid	Male Parent
Wings			
Shape	oblong; apex rounded	oblong; apex rounded	oblong, apex rounded
Length (cm)	1.3	1.0	1.0
Width (cm)	0.4	0.4	0.3
Keel			
Shape	apex rounded	emarginate; each half short-apiculate at apex	apex long-acuminate
Length (cm)	1.3	1.1	1.3
Width (cm)	1.0	1.8	1.0
Figure 105	*E. guatemalensis* PT 700018001	HO 82.282	*E. folkersii* PT 700010001
CALYX			
Shape	elliptic; broadest in middle	cuneate; broadest at apex	cuneate; broadest at apex
Apex shape	irregular; oblique or bilabiate	oblique to truncate	oblique; longer on side
Length (cm)			
Vexillar side	2.3–2.7	1.8–1.9	1.8–1.9
Carinal side	2.6–2.9	2.2–2.5	2.1–2.2
Width (cm)			
Greatest	1.2–1.3	1.2–1.3	1.2
Middle	1.2–1.3	1.0	0.8
Indumentum	glabrous	sparsely puberulent	densely puberulent
Texture	minutely papillate	minutely papillate	minutely papillate
Color	reddish brown	reddish brown to purple-brown	light brown
COROLLA			
Standard			
Color	red 6/7.5	red 6/10	red 7/7.5
Length (cm)	6.5	7.0–7.8	8.0
Greatest width (cm)	1.8	2.2	2.4
Wings			
Shape	apex rounded	apex rounded	apex rounded
Length (cm)	1.3	1.1–1.3	1.0
Width (cm)	0.4	0.5	0.5
Keel			
Shape	apex rounded	apex variable; rounded or emarginate	emarginate, each half obtuse at apex
Length (cm)	1.3	1.2–1.3	1.0
Width (cm)	1.0	0.9	1.3
Figure 106	*E. guatemalensis* PT 700018001	HO 82.284 PT 820278002 (2 individuals)	*E. chiapasana* PT 73071001
CALYX			
Shape	elliptic	oblong to elliptic	oblong
Apex shape	variable; bilabiate or oblique	truncate to oblique; 5 apical lobes in bud, absent in anthesis	truncate; 5 apical lobes in bud, absent at anthesis
Length (cm)			
Vexillar side	2.3–2.7	1.7–1.9	1.5–1.6
Carinal side	2.6–2.9	1.7–2.1	1.5–1.6

TABLE 19. *Continued.*

	Female Parent	F$_1$ Hybrid	Male Parent
Width (cm)			
Greatest	1.2–1.3	0.9	0.8
Middle	1.2–1.3	0.8–0.9	0.7
Indumentum	glabrous	sparsely puberulent	densely puberulent
Texture	minutely papillate	smooth	smooth to indistinctly 5-angled
Color	reddish brown	reddish brown to green	green
COROLLA			
Standard			
Color	red 6/7.5	red 5/5 to 5/7.5	red 5/7.5
Length (cm)	6.5	6.5	7.4
Greatest width (cm)	1.8	1.5–1.8	1.4
Wings			
Shape	oblong; apex rounded	oblong; apex rounded	oblong; apex rounded
Length (cm)	1.3	1.5	1.3–1.4
Width (cm)	0.4	0.4	0.4
Keel			
Shape	apex rounded	variable; apex rounded or emarginate	emarginate; each half short-apiculate
Length (cm)	1.3	1.0–1.3	1.3
Width (cm)	1.0	0.9–1.0	0.9

Figure 107	*E. guatemalensis* PT 700018001	HO 82.285 HO 82.288 PT 820276001	*E. macrophylla* PT 750420002
CALYX			
Shape	elliptic; broadest in middle	oblong to elliptic	cuneate; broadest at apex
Apex shape	variable; bilabiate or oblique	truncate to slightly oblique; 5 irregular apical lobes	truncate; 5 prominent, blunt lobes
Length (cm)			
Vexillar side	2.3–2.7	1.8–2.5	2.0
Carinal side	2.6–2.9	2.3–2.6	2.0
Width (cm)			
Greatest	1.2–1.3	1.0–1.2	1.2 (at apex)
Middle	1.2–1.3	1.0–1.2	0.9
Indumentum	glabrous	sparsely to densely puberulent	densely puberulent
Texture	minutely papillate	obscurely 5-angled	longitudinally 5-angled
Color	reddish brown	reddish brown to green	brown to green
COROLLA			
Standard			
Color	red 6/7.5	red 6/7.5 to 6/10	red 5/7.5
Length (cm)	6.5	6.4–7.0	6.4
Greatest width (cm)	1.8	1.7–2.1	1.7
Wings			
Shape	oblong; apex rounded	oblong; apex rounded	oblong; apex rounded
Length (cm)	1.3	1.3–1.6	1.3
Width (cm)	0.4	0.4–0.5	0.4
Keel			
Shape	apex rounded	apex short-apiculate	apex short-apiculate
Length (cm)	1.3	1.1–1.3	1.3
Width (cm)	1.0	1.1–1.2	1.1

TABLE 19. *Continued.*

	Female Parent	F$_1$ Hybrid	Male Parent
Figure 108	*E. macrophylla* PT 750420002	HO 82.763 (2 individuals)	*E. guatemalensis* PT 700018001
CALYX			
Shape	cuneate; broadest at apex	elliptic	elliptic; bilabiate in middle
Apex shape	truncate; 5 prominent apical lobes	variable; bilabiate or truncate; 5 indistinct apical lobes present or lacking	variable; bilabiate or oblique
Length (cm)			
Vexillar side	2.0	1.9–2.2	2.3–2.7
Carinal side	2.0	2.0–2.4	2.6–2.9
Width (cm)			
Greatest	1.2 (at apex)	1.1–1.2	1.2–1.3
Middle	0.9	1.1–1.2	1.2–1.3
Indumentum	densely puberulent	densely puberulent	glabrous
Texture	longitudinally 5-angled	smooth to minutely papillate	minutely papillate
Color	brown to green	reddish brown to green	reddish brown
COROLLA			
Standard			
Color	red 5/7.5	red 5/7.5	red 6/7.5
Length (cm)	6.4	6.5–6.7	6.5
Greatest width (cm)	1.7	1.8	1.8
Wings			
Shape	oblong; apex rounded	oblong; apex rounded	oblong; apex rounded
Length (cm)	1.3	1.3	1.3
Width (cm)	0.4	0.4–0.5	0.4
Keel			
Shape	apex short-apiculate	apex rounded	apex rounded
Length (cm)	1.3	1.0–1.1	1.3
Width (cm)	1.1	1.1–1.2	1.0
Figure 109	*E. chiapasana* PT 721005001	HO 82.278 (2 individuals)	*E. beteroana* PT 700044002
CALYX			
Shape	oblong	oblong	oblong
Apex shape	truncate; 5 indistinct apical knobs	truncate	oblique; longer on carinal side
Length (cm)			
Vexillar side	1.5–1.6	2.2–2.3	2.8
Carinal side	1.5–1.6	2.2–2.4	3.0
Width (cm)			
Greatest	0.8	0.9	0.8
Middle	0.7	0.8–0.9	0.7
Indumentum			
Texture	indistinct longitudinal ridges	indistinct longitudinal ridges	smooth
Color	green	pale green to red	pale red
COROLLA			
Standard			
Color	red 5/7.5	red 6/5 to 8/7.5	red 8/7.5 to 9/7.5
Length (cm)	6.8	8.5	8.3
Greatest width (cm)	1.4	1.6–1.7	1.6

TABLE 19. *Continued.*

	Female Parent	F_1 Hybrid	Male Parent
Wings			
Shape	oblong; apex rounded	oblong; apex acute to rounded	oblong; apex acute
Length (cm)	1.5	1.2	1.0
Width (cm)	0.4	0.4	0.4
Keel			
Shape	emarginate, each half short apiculate	apex rounded to emarginate	deeply emarginate; each half acute at apex
Length (cm)	1.3	1.0	0.8
Width (cm)	0.9	0.9	0.9
Figure 110	*E. macrophylla* PT 750420002	HO 82.281 (2 individuals)	*E. beteroana* PT 700044001
CALYX			
Shape	cuneate; broadest at apex	oblong	oblong, narrow
Apex shape	truncate; 5 prominent apical lobes	truncate; 5 indistinct apical lobes	oblique; longer on carinal side
Length (cm)			
Vexillar side	2.0	2.2–2.4	2.8
Carinal side	2.0	2.2–2.4	3.0
Width (cm)			
Greatest	1.2	1.0–1.1	0.7
Middle	0.9	0.7–0.8	0.7
Indumentum	densely puberulent	sparsely puberulent	glabrous
Texture	longitudinally 5-angled	indistinct longitudinal ridges	smooth
Color	brown to green	green to red	pale red to green
COROLLA			
Standard			
Color	red 5/7.5	red 6/7.5	red 8/7.5
Length (cm)	6.4	7.3–7.4	8.3
Greatest width (cm)	1.7	1.5–1.6	1.3
Wings			
Shape	oblong; apex rounded	oblong; apex acute to rounded	oblong; apex acute
Length (cm)	1.3	1.0–1.2	1.0
Width (cm)	0.4	0.4	0.4
Keel			
Shape	apex short-apiculate	apex apiculate or emarginate	deeply emarginate; each half acute at apex
Length (cm)	1.3	1.0–1.1	0.8
Width (cm)	1.1	0.8–1.0	0.9

of matrocliny or female-dominant inheritance in the *Erythrina* hybrids.

The results, although preliminary, also suggest a difference in the genetics of inheritance of hairs on the one hand, and papillae and lamellae on the other. Hairs are inherited in the hybrids as discrete characters—that is, they are fully formed and of normal size, although they occur at low densities, in crosses between hairy and hairless parents. The formation of hairs may thus be controlled by a single gene or supergene, with modifiers controlling density of the hairs. On the other hand, in crosses between papillate (or lamellate) and nonpapillate parents, papillae (lamellae) may be present but they are much reduced in stature. This suggests that the stature of papillae and lamellae are continuously variable, typical of morphometric traits, and controlled by many genes, each of small effect.

TABLE 20. *Comparison of flowers of* Erythrina atitlanensis *and F_1 hybrid,* E. macrophylla × E. berteroana. *(Photo, Fig. 111.)*

	E. atitlanensis WA 74s98 WA 75s1141	*E. macrophylla* × *E. berteroana* HO 82.281
CALYX		
Shape	oblong	oblong
Apex shape	truncate; 5 indistinct apical lobes	truncate; 5 indistinct apical lobes
Length (cm)		
Vexillar side	1.7–1.8	2.2–2.4
Carinal side	1.8–1.9	2.2–2.4
Width (cm)		
Greatest	1.0	1.0–1.1
Middle	0.7	0.7–0.8
Indumentum	sparsely puberulent	sparsely puberulent
Texture	indistinct longitudinal ridges	indistinct longitudinal ridges
Color	pale green to red	green to red
COROLLA		
Standard		
Color	red 6/7.5	red 6/7.5 to 7/10
Length (cm)	6.5–6.8	7.3–7.4
Greatest width (cm)	1.7	1.5–1.6
Wings		
Shape	oblong; apex rounded	oblong; apex acute or rounded
Length (cm)	1.0	1.0–1.1
Width (cm)	0.4	0.4
Keel		
Shape	apex short-apiculate	apex apiculate or emarginate
Length (cm)	0.8	1.0–1.1
Width (cm)	1.0	0.8–1.0

This suggestion requires confirmation by analysis of segregation in the F_2 generation.

The variation in the four F_1 hybrid siblings derived from a single cross, *Erythrina crista-galli* × *E. guatemalensis*, is illustrated in Figures 76–87. The female parent has an irregular network of low lamellae less than 10 μm tall and lacks epicuticular wax. The male parent has a dense covering of unicellular papillae up to 40 μm tall and has epicuticular wax. The F_1 hybrids exhibit a narrowly segregating array of these characters: they have papillae and/or lamellae intermediate in form and stature between the two parents. Some F_1s resemble the female parent more closely and some resemble the male parent. All the F_1s have epicuticular wax, evidently derived from the male parent. (Other individuals of *E. crista-galli*, besides the one used in this cross, do possess wax.)

The leaf epidermis of three F_1 siblings derived from the cross *Erythrina crista-galli* × *E. fusca*, together with their parents, are illustrated in the two plates comprising Figures 88–99. Also included on these plates are photos of *E. dominguezii*, a species that, based on floral characters, may be a stabilized derivative of hybridization between *E. crista-galli* and *E. fusca* (see discussion of hybrid flowers below). The male parent *Erythrina fusca* has a very unusual epidermal surface with deep and irregularly sized and shaped cavities, knobs and protrusions, appearing under SEM much like the surface of a limestone cavern. The stomata are at the bottom of the cavities.

The F_1 hybrids vary somewhat in surface configuration, but none of them possess either the regular network of lamellae present in *E. crista-galli* or the complex, irregular cavity structure of *E. fusca*. Two of the F_1s have scattered low papillae and one is nearly flat on the abaxial surface. All three F_1s have epicuticular platelets, which are not present in either of the parents.

Erythrina dominguezii (Figs. 93, 99) has scattered balloonlike hairs, not present in *E. crista-galli* or *E. fusca*. Otherwise, the epidermal surface on *E. dominguezii* has no distinctive features. Low

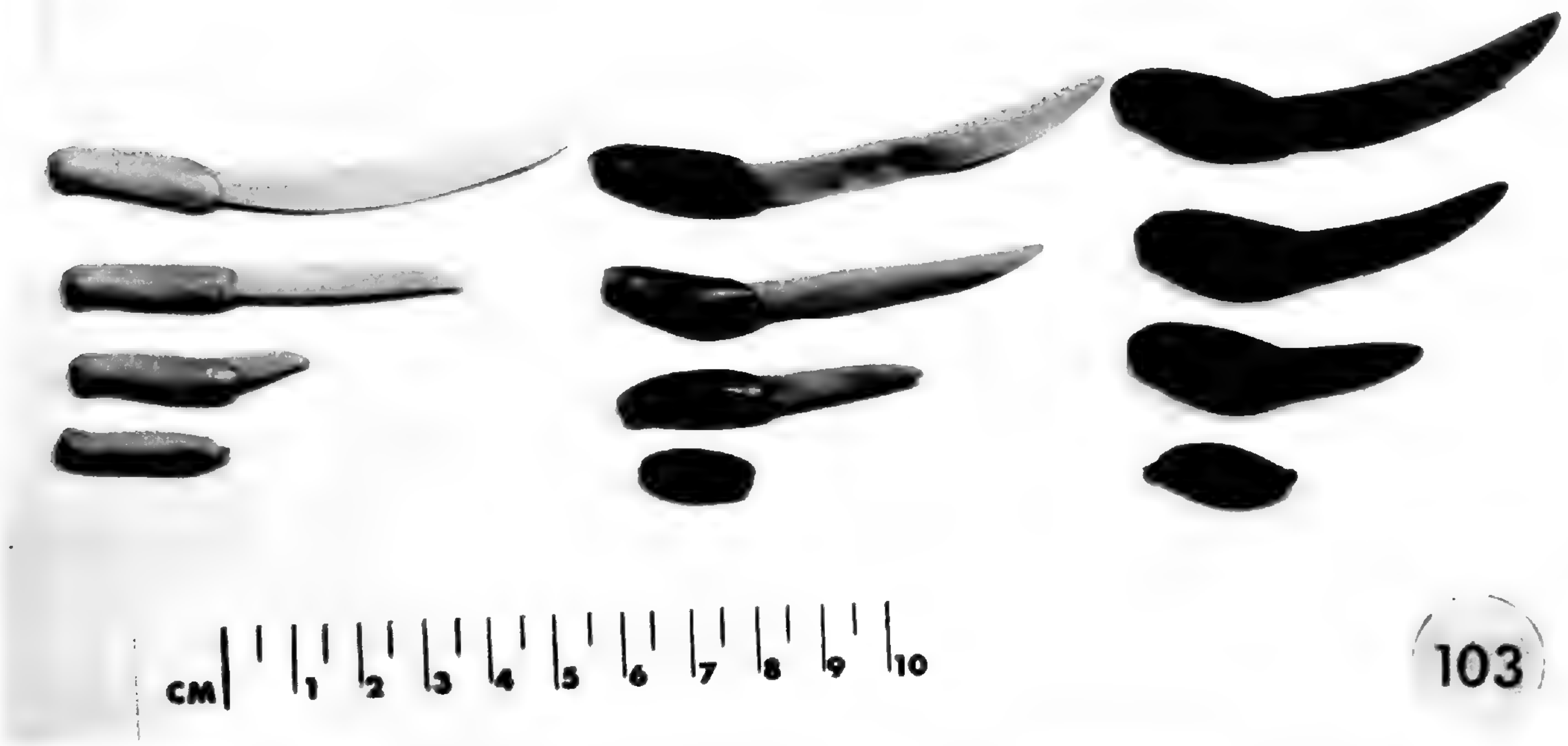

FIGURE 103. *Flowers and buds of* Erythrina berteroana × E. guatemalensis *and parents. Left:* E. berteroana, *WA 78s564, female parent. Center:* E. berteroana × E. guatemalensis, *HO 82.647. Right:* E. guatemalensis, *WA 74c1453, male parent.*

epidermal convolutions similar to the lamellae of *E. crista-galli* are visible at high magnification (Fig. 99) but these are not organized into a regular reticulate pattern.

FLORAL FEATURES: INHERITANCE IN INTERSPECIFIC HYBRIDS

The inheritance of floral morphology and color was examined in the hybrids that flowered by November 1984. These included the hybrids within sect. *Erythrina* and the intersectional hybrid *Erythrina crista-galli* × *E. fusca.*

Materials and Methods

Fresh flowers of the hybrids and parents were fixed in FAA, which preserved their three-dimensional shape, and later measured, described, and photographed, each hybrid together with its par-

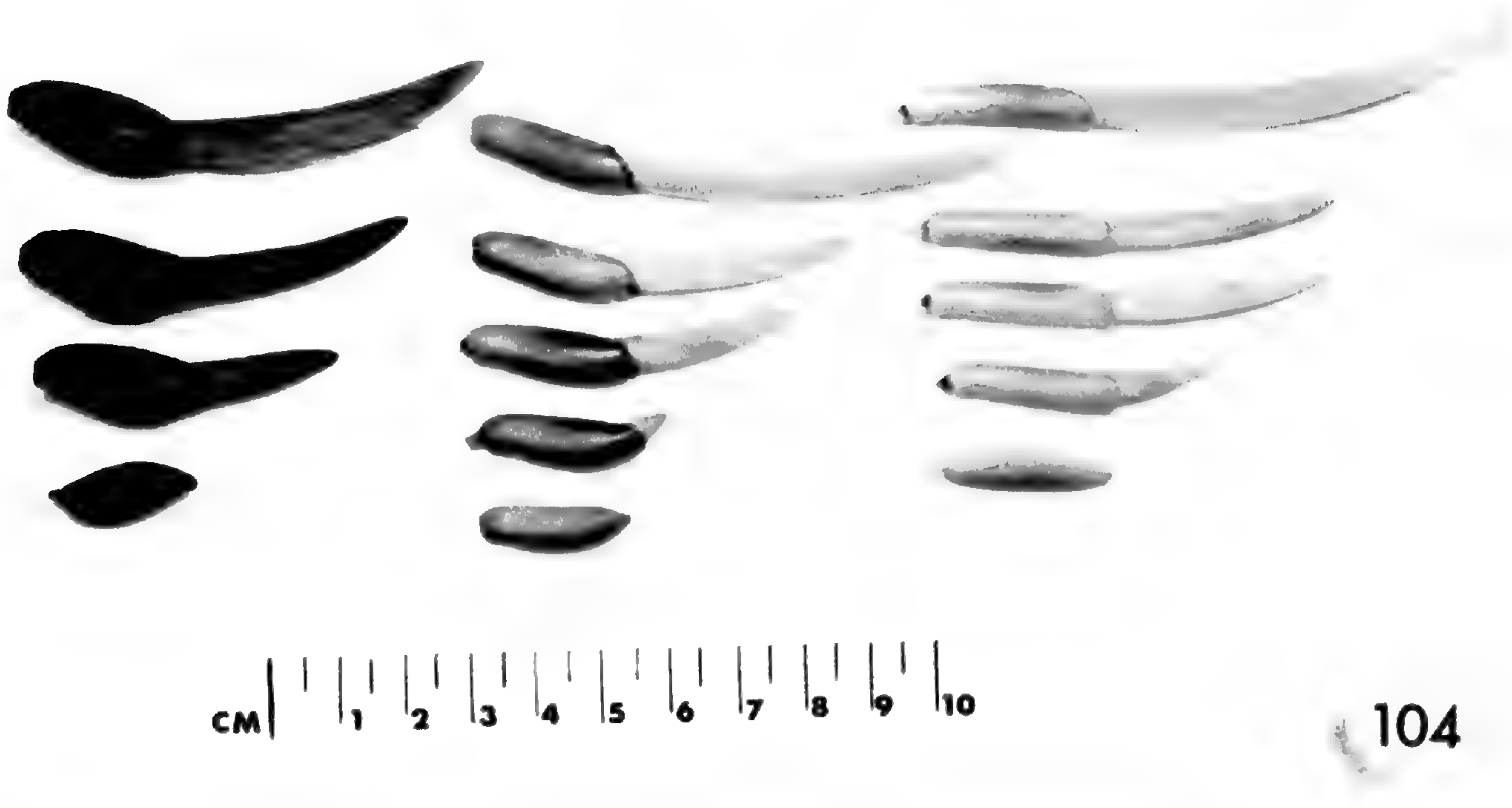

FIGURE 104. *Flowers and buds of* Erythrina guatemalensis × E. tajumulcensis *and parents. Left:* E. guatemalensis, *WA 74c1453, female parent. Center:* E. guatemalensis × E. tajumulcensis, *PT 820547. Right:* E. tajumulcensis, *WA 74c1448, male parent.*

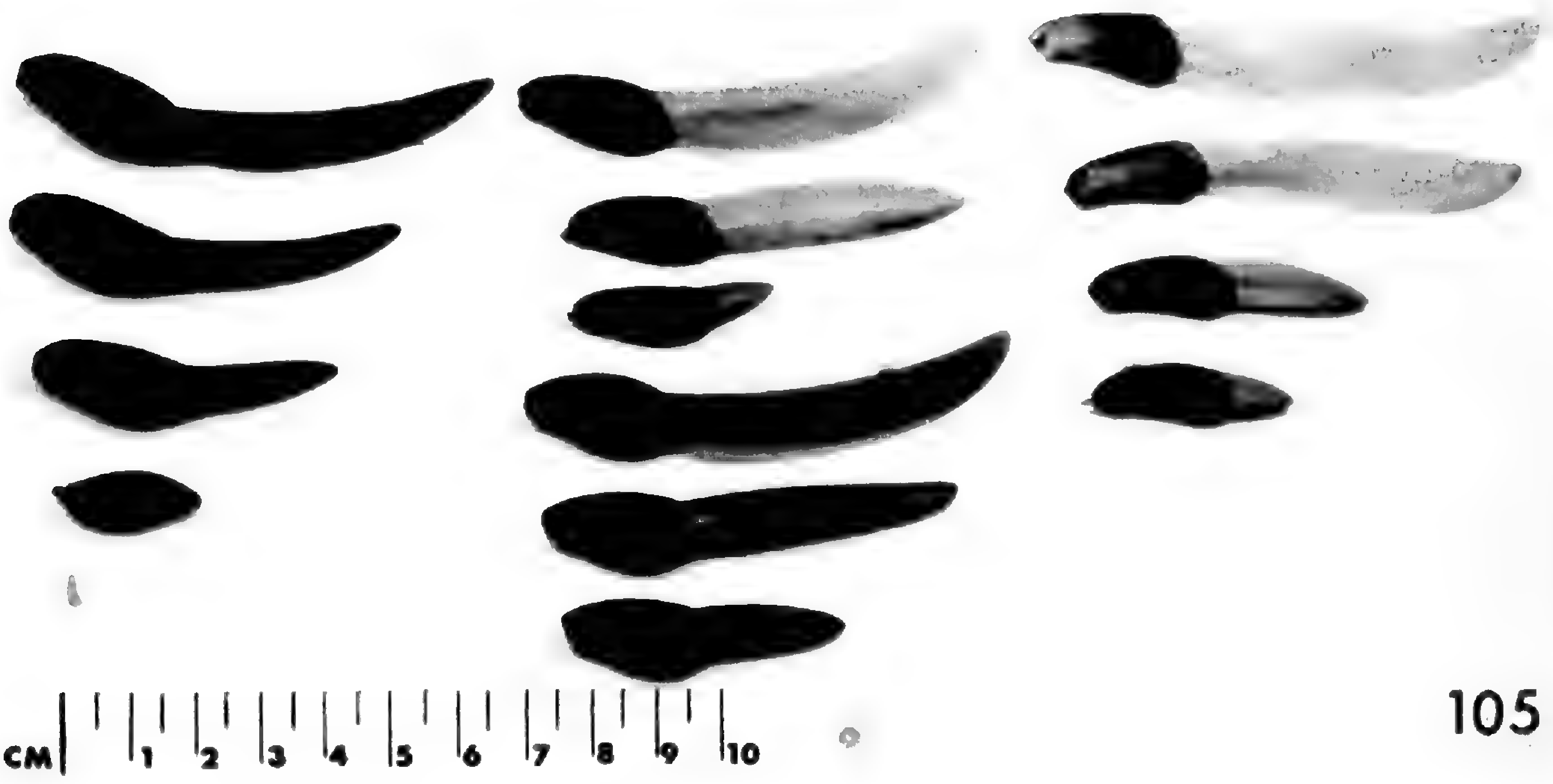

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Figure 105. *Flowers and buds of* Erythrina guatemalensis × E. folkersii *and parents. Left:* E. guatemalensis, *PT 700018001, female parent. Center:* E. guatemalensis × E. folkersii, *two F_1 siblings, HO 82.282. Right:* E. folkersii, *PT 700010001, male parent.*

ents. Color was determined from fresh flowers at the time of collection. A Berlin & Kay color chart (Berlin & Kay, 1969) was used for color descriptions of corolla standards. For use of the Berlin & Kay color chart in botanical descriptions see Croat (1983). Colors are reported in the form "Red 5/7.5." The number preceding the slash refers to brightness (1–9; 1 is brightest) and the number after the slash refers to the hue.

Inflorescences and floral details were photo-

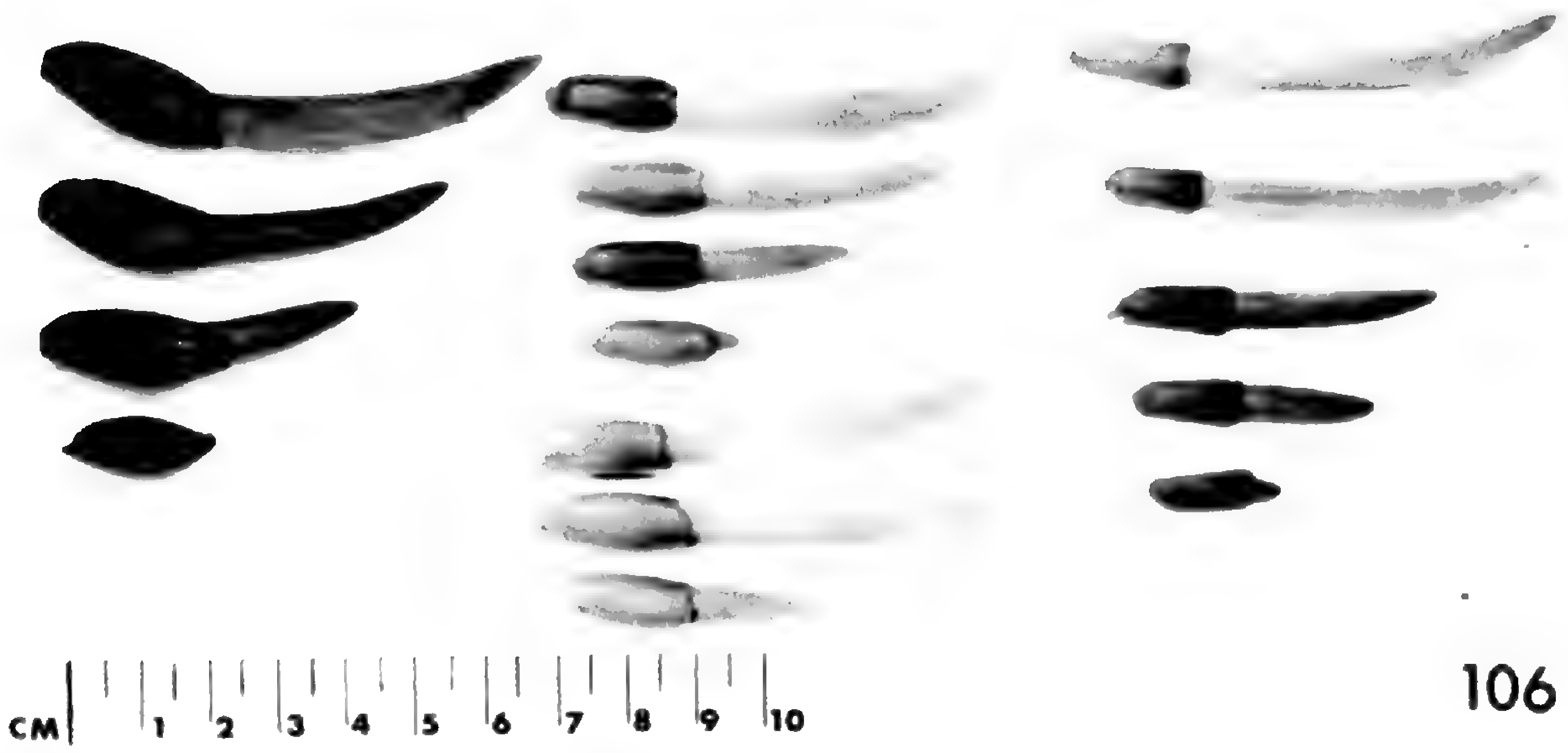

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Figure 106. *Flowers and buds of* Erythrina guatemalensis × E. chiapasana *and parents. Left:* E. guatemalensis, *PT 700018001, female parent. Center:* E. guatemalensis × E. chiapasana, *two F_1 siblings, HO 82.284 and PT 820278002. Right:* E. chiapasana, *PT 730710001, male parent.*

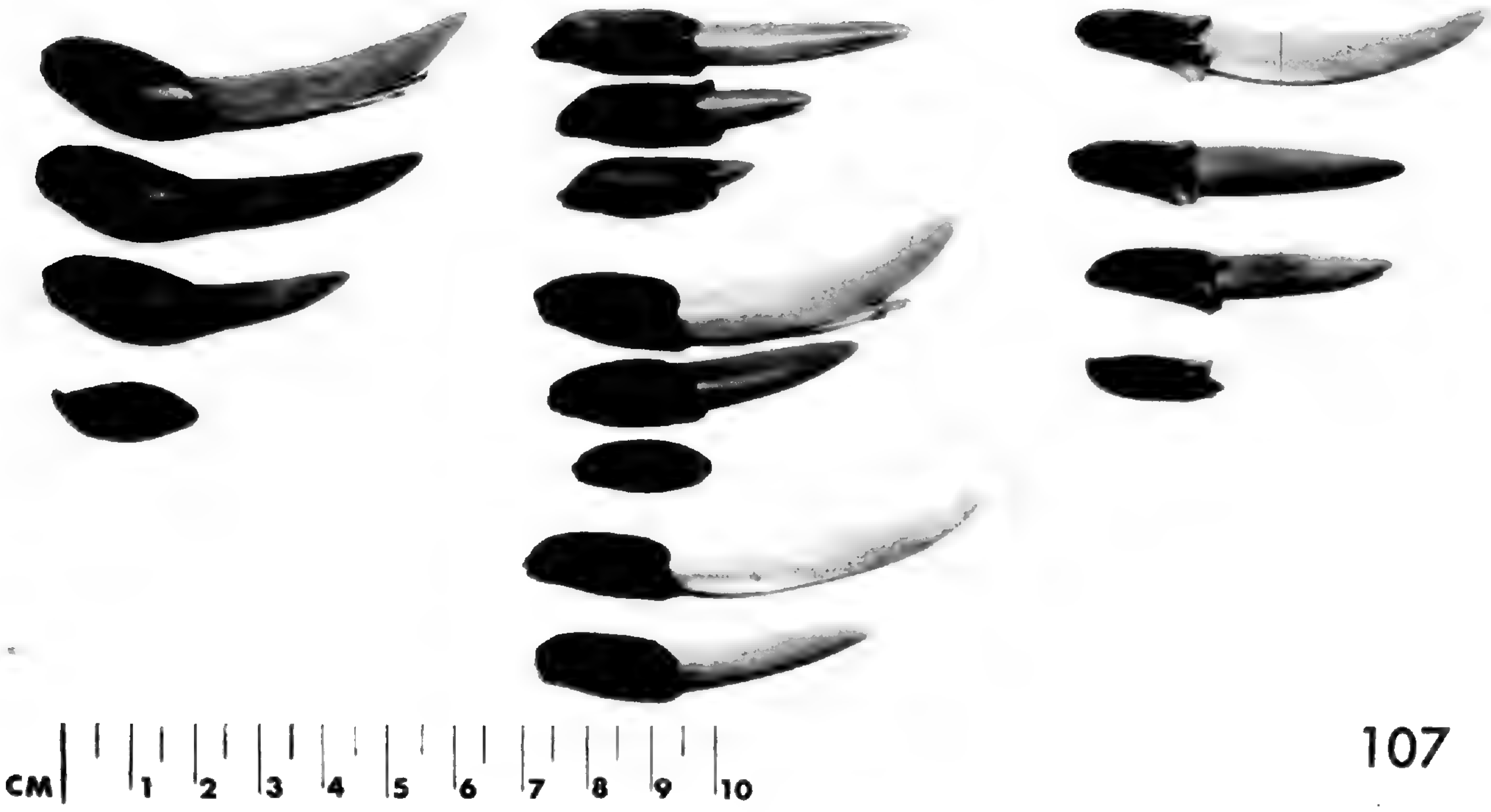

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FIGURE 107. *Flowers and buds of* Erythrina guatemalensis × E. macrophylla *and parents. Left:* E. guatemalensis, *PT 700018001, female parent. Center:* E. guatemalensis × E. macrophylla, *three F_1 siblings, HO 82.285, HO 82.288, PT 820276001. Right:* E. macrophylla, *PT 750420002, male parent.*

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FIGURE 108. *Flowers and buds of* Erythrina macrophylla × E. guatemalensis *and parents. Left:* E. macrophylla, *PT 750420002, female parent. Center:* E. macrophylla × E. guatemalensis, *two F_1 siblings, HO 82.763. Right:* E. guatemalensis, *PT 700018001, male parent.*

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FIGURE 109. *Flowers and buds of* Erythrina chiapasana × E. berteroana *and parents. Left:* E. chiapasana, *PT 721005001, female parent. Center:* E. chiapasana × E. berteroana, *two F_1 siblings, HO 82.278. Right:* E. berteroana, *PT 700044002, male parent.*

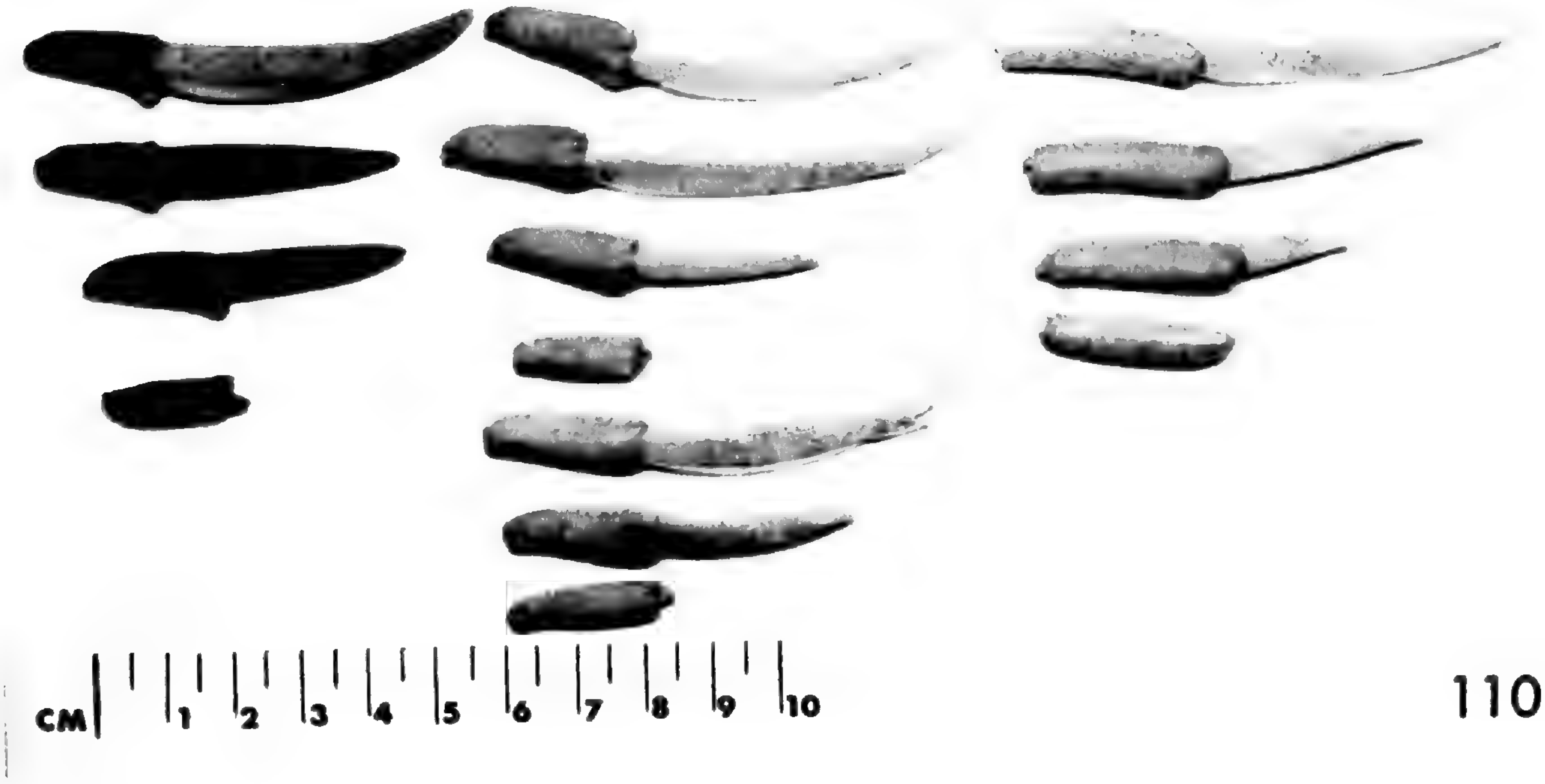

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FIGURE 110. *Flowers and buds of* Erythrina macrophylla × E. berteroana *and parents. Left:* E. macrophylla, *PT 750420002, female parent. Center:* E. macrophylla × E. berteroana, *two F_1 siblings, HO 82.281. Right:* E. berteroana, *PT 700044001, male parent.*

FIGURE 111. *Comparison of flowers of* Erythrina macrophylla × E. berteroana *and* Erythrina atitlanensis. *Left:* E. macrophylla × E. berteroana, *HO 82.281, two F_1 siblings. Top right:* E. atitlanensis, *WA 74s98. Bottom right:* E. atitlanensis, *WA 75s1141.*

graphed at the time of collection. Herbarium vouchers are deposited at Missouri Botanical Garden (MO).

Results

Hybrids within Sect. Erythrina

Inflorescence and Flower Orientation. Species of sect. *Erythrina* all have erect inflorescences, but they differ in the arrangement of the flowers on the inflorescence axis (congested or open), length of the axis, and orientation of the flowers (ascending, horizontal, or descending). These traits are generally intermediate in the hybrids (e.g., Figs. 100–102). In *Erythrina guatemalensis*, the female parent, the flowers are horizontal on an open inflorescence. In *E. folkersii*, the male parent, the flowers descend to nearly vertical on a congested inflorescence. The F_1 hybrid is intermediate in both these traits.

Floral Characters. A comparison of floral characters of the hybrids and their parents within sect. *Erythrina* is summarized in Table 19. The flowers are illustrated in Figures 103–110.

In all characters—color, indumentum, shape, and morphometric dimensions—the F_1 hybrids are intermediate between the two parents. The F_1 siblings from a single cross vary to some extent. There is no evidence of matrocliny or maternal dominance.

Subjectively, some of the hybrids resemble the male parent more closely than the female parent. This is evident in the progeny of the reciprocal hybridizations between *Erythrina guatemalensis* and *E. macrophylla* (Figs. 107, 108). The vestiture and shapes of the calyces of the hybrids are

TABLE 21. *Comparison of flowers of* Erythrina crista-galli × E. fusca, *its parents, and* E. dominguezii.

	E. crista-galli WA 74p840	*E. crista-galli* × *E. fusca* PT 84021001	*E. fusca* PT 840231001	*E. dominguezii* WA 74s865
Orientation	resupinate; standard beneath, open	standard semi-cleistogamous, folded over reproductive parts	standard reflexed	standard semi-cleistogamous, folded over reproductive parts
CALYX				
Color	red	reddish brown	brown	pale orange-pink
Shape	bowl shaped	bowl shaped; slightly asymmetric	asymmetrically bowl shaped	asymmetrically bowl shaped
Length				
Carinal side	1.8 cm	1.6 cm	1.4 cm	1.5 cm
Width at apex	1.0 cm	1.4 cm	2.1 cm	1.4 cm
Apex ornamentation	large subulate tooth, carinal side	narrow tooth, carinal side	large blunt tooth, carinal side	blunt tooth, carinal side
COROLLA				
Standard				
Color	red	orange	orange-pink	pale orange-pink
Length	5.0 cm	6.1 cm	6.5 cm	4.8 cm
Width	3.3 cm	4.9 cm	5.5 cm	3.5 cm
Wings				
Shape	asymmetric; broadest at base	obovate, rounded, cucullate	obovate, cucullate, broadly rounded	small, obovate, cucullate
Length	1.3 cm	1.8 cm	2.9 cm	0.6 cm
Width	0.9 cm	1.0 cm	1.8 cm	0.4 cm
Keel				
Color	red	pale red	ivory at base, red at apex	pale red
Shape	falcate, acute at apex	ovate-falcate, rounded at apex	ovate-falcate, broadly rounded at apex	falcate, acute at apex
Length	4.5 cm	3.4 cm	3.9 cm	1.5 cm
Width	1.0 cm	1.5 cm	1.5 cm	1.0 cm

intermediate and variable, but in both reciprocals the hybrids resemble the male parent somewhat more than the female.

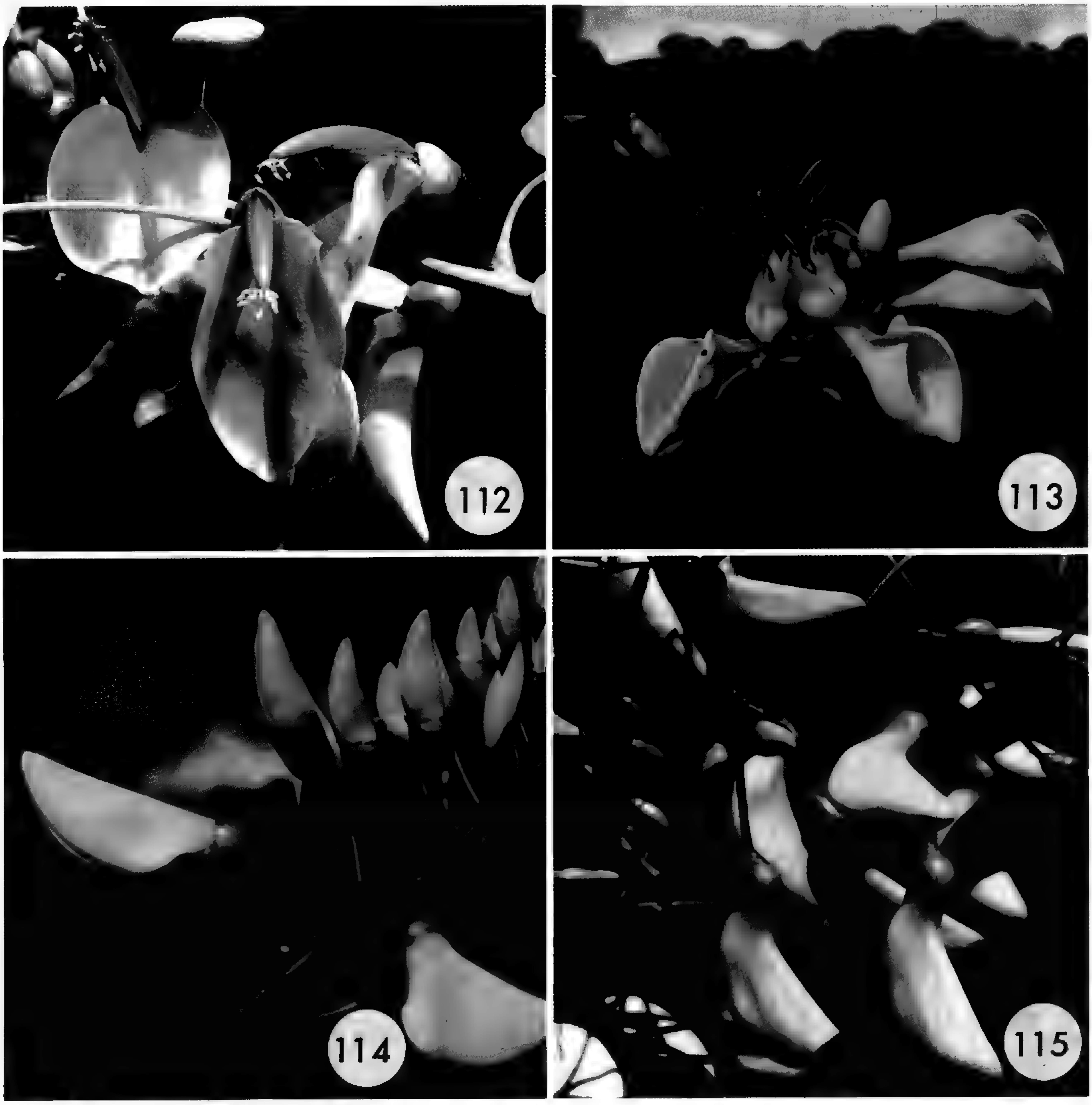
In crosses involving species with tomentose and glabrous calyces, the hybrids are tomentose, but sometimes sparsely so. In color values and morphometric dimensions, the hybrids are generally intermediate between the two parents.

The flower of the hybrid *Erythrina macrophylla* × *E. berteroana* is intermediate between the two parents, and it closely resembles a third recognized species, *E. atitlanensis* (Fig. 111, Table 20). The principal difference is that the calyx of the F_1 hybrid is somewhat longer than that of *E. atitlanensis.* The natural distribution of *Erythrina atitlanensis* is confined to a small area near Lake Atitlan in western Guatemala, and it is geographically and ecologically intermediate between *E. macrophylla* and *E. berteroana.* The possibility that the form known as *E. atitlanensis* represents either a hybridizing population or a stabilized species of hybrid origin will be discussed below.

Flowers of Erythrina crista-galli × E. fusca

The inflorescence and flowers of this intersectional hybrid and its parents are illustrated in Figures 112–117 and described in Table 21. A third species, *E. dominguezii,* is included in the illustrations and descriptions for reasons discussed below.

The morphometric dimensions and proportions of the floral parts of the two parental species are relatively similar, considering the total range of



FIGURES 112–115. *Inflorescences in natural position of* Erythrina crista-galli × E. fusca, *its parents, and* E. dominguezii.—*112.* E. crista-galli, *WA 74p840.*—*113.* E. fusca, *WA 74s99.*—*114.* E. crista-galli × E. fusca, *PT 840231001.*—*115.* E. dominguezii, *PT 740234001.*

variation of these traits in the genus *Erythrina*, but the way in which these parts are arranged and the overall appearance of the flowers are very different. The flower of *E. crista-galli* is resupinate (inverted from the usual position, with the standard below the keel) and the red standard is flattened out, an unusual trait in *Erythrina*. The orange standard of *E. fusca* is reflexed from the clawed base, exposing the reproductive parts, and is broadly folded down the middle.

The flower of the F_1 hybrid *E. crista-galli* × *E. fusca* is different from either parent. The hybrid flower is semicleistogamous, with the standard tightly folded over the wings, keel, and reproductive parts. In this semicleistogamous form, in the orientation of the flowers and the inflorescence, and in the pale pink-orange color of the corolla standard, *E. crista-galli* × *E. fusca* bears a striking resemblance to *E. dominguezii* (Figs. 114–117). Certainly the hybrid resembles *E. dominguezii* more closely in overall appearance than either of its parents. The dimensions of the floral parts are not identical in the F_1 hybrid and in *E. dominguezii* (Fig. 117, Table 21). The overall similarity between the two could be a coincidence, but it is so striking and so unexpected that it raises the possibility that *Erythrina dominguezii* is in fact a hybrid derivative of *E. crista-galli* and *E. fusca*. The distribution of *E. dominguezii* is geographically intermediate but ecologically distinct from *E.*

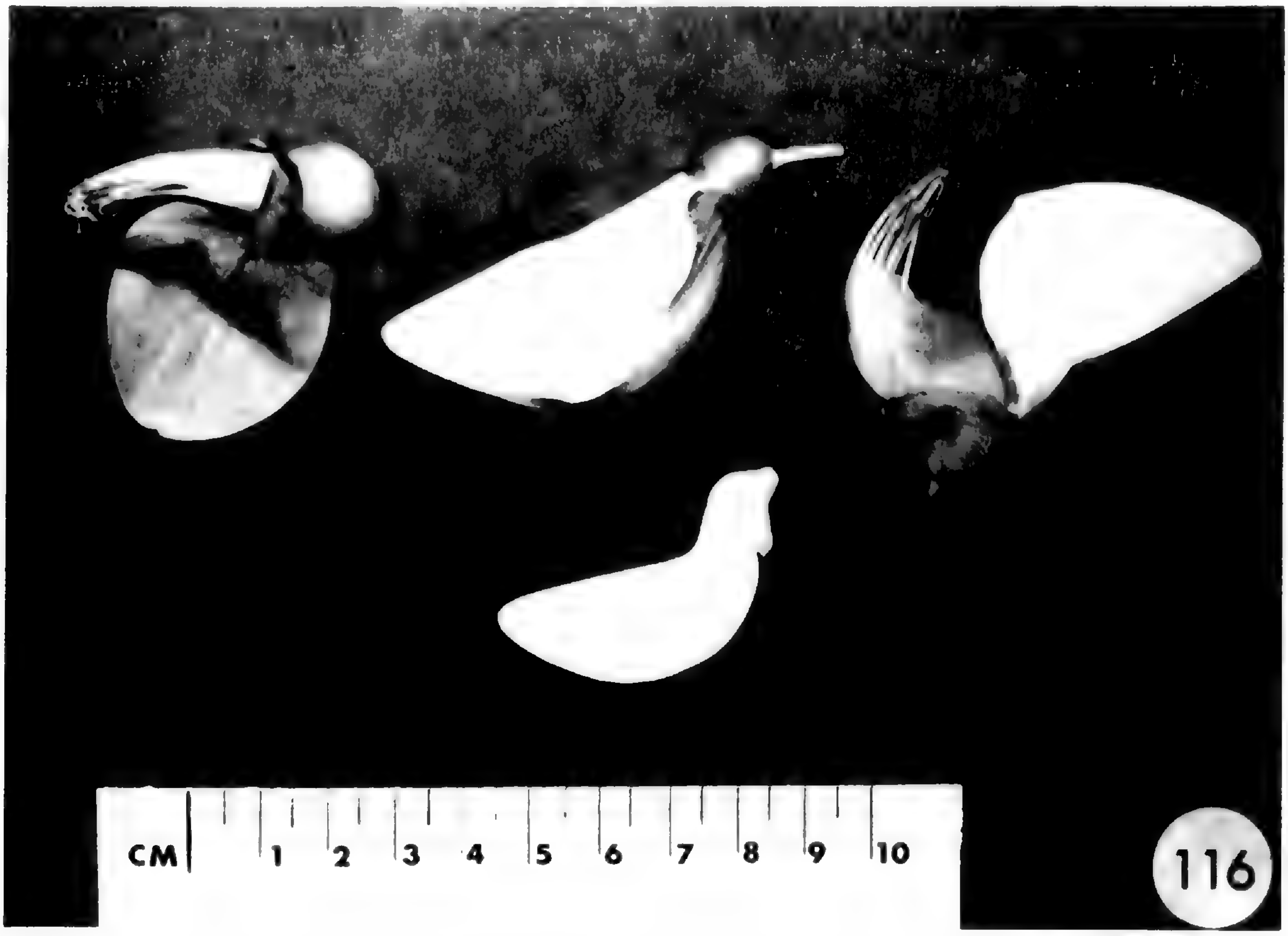


FIGURE 116. *Flowers of* Erythrina crista-galli × E. fusca, *its parents, and* E. dominguezii, *showing approximate natural orientation. Top row, left to right:* E. crista-galli, *WA 75p840, female parent;* E. crista-galli × E. fusca, *PT 840231001;* E. fusca, *WA 74s99, male parent. Bottom center:* E. dominguezii, *PT 740234001.*

crista-galli and *E. fusca.* This will be discussed in greater detail in Section 6.

Conclusions: Inheritance of Phenetic Traits in Interspecific Hybrids

The results of the morphological studies of the F_1 hybrids clearly demonstrate that the progeny are indeed of hybrid origin. Almost universally, the F_1 progeny meet the criterion of intermediacy, and frequently they possess traits present in the male parent but absent in the female parent. Matrocliny is not indicated in *Erythrina* hybrids. Some of the F_1 hybrids closely resemble forms occurring in natural populations and recognized as species.

SECTION 6. NATURAL HYBRIDIZATION AND HYBRID SPECIATION

The Mexican state of Chiapas has great geographical diversity and complexity and a very large flora for an area its size. Climate ranges from semidesert to rainforest, and elevation from sea level to over 4,000 m. The flora of Chiapas contains more than 8,000 plant species and 13 major vegetational formations recognized by Breedlove (1981).

Chiapas, together with adjacent western Guatemala, is also the center of diversity of *Erythrina* sect. *Erythrina.* Eleven species are known to occur in the state, and six of these are endemic or shared only with western Guatemala. Although they are not found in abundance or in large populations, species of *Erythrina* occur in virtually every vegetation type in Chiapas except the upper belts of the cloud forest and elfin forest on the highest peaks.

In common with the usual pattern of distribution in *Erythrina*, the Chiapas species of the genus are mostly allopatric. However, at some localities, particularly at the margins of distribution of the species, different species do come into contact, and there natural hybrids are formed.

One phenomenon that has apparently occurred with *Erythrina* in Chiapas and perhaps elsewhere is spontaneous hybridization in man-made populations. Throughout Mesoamerica many species of *Erythrina* trees are used by the local populace as "living fenceposts." Erythrinas take root readily from woody cuttings and the trunks are ideal posts for stringing barbed wire. Extensive fencerows of the plants line roads and fields in many areas.

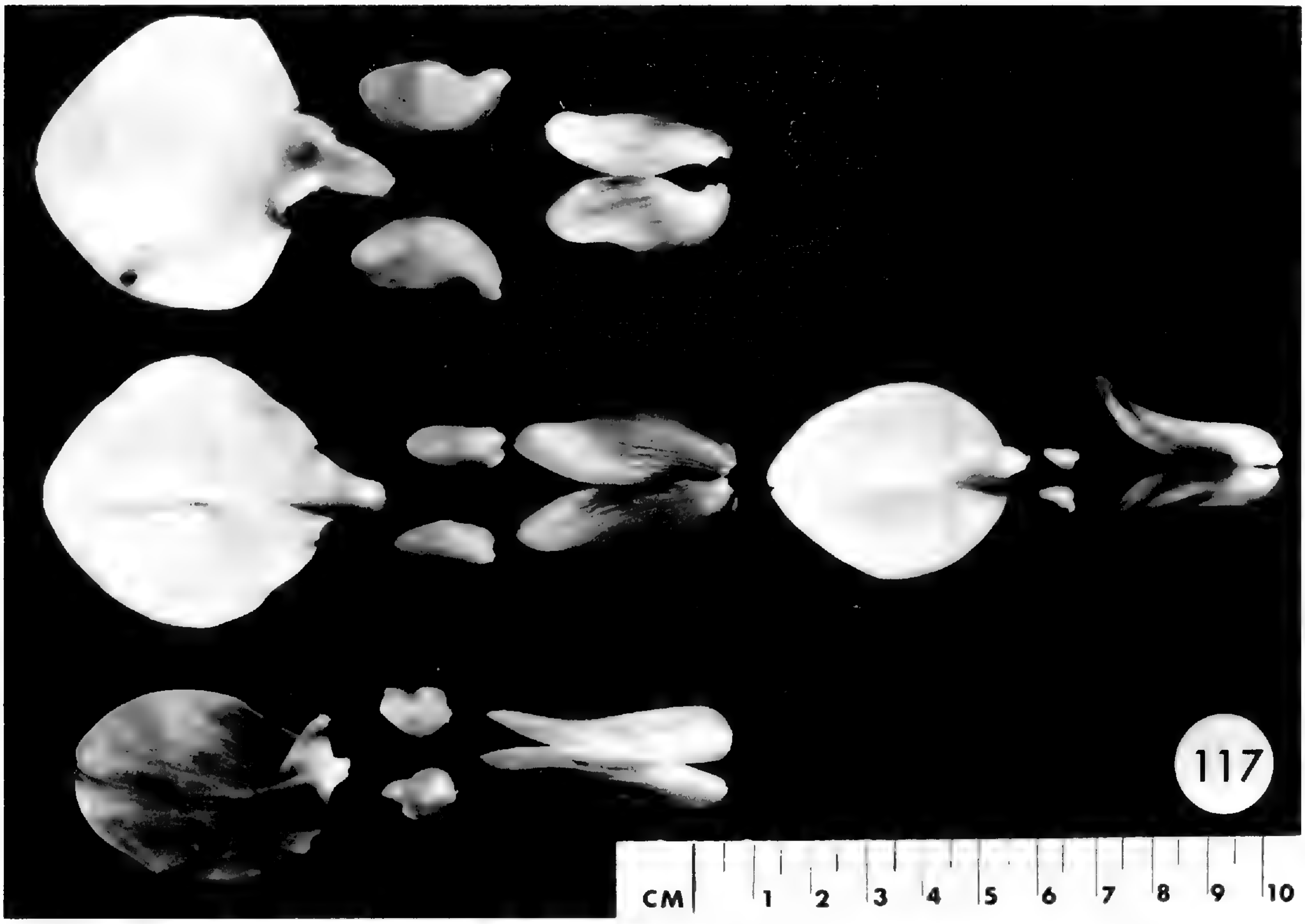


FIGURE 117. *Dissected petals of* Erythrina crista-galli × E. fusca, *its parents, and* E. dominguezii *(each flower, left to right: standard, wings, keel). Top:* E. crista-galli, *WA 74p840, female parent. Center left:* E. crista-galli × E. fusca, *PT 840231001. Center right:* E. dominguezii, *PT 740234001. Bottom:* E. fusca, *WA 74s99, male parent.*

Sometimes two species are cultivated together, and hybrids, apparently produced spontaneously in situ, are occasionally found in these fencerows.

An analysis of hybridizing populations involving three species of *Erythrina* in central Chiapas, *Erythrina chiapasana*, *E. goldmanii*, and *E. pudica*, is presented below. Distributions of these species and their hybrid populations are shown in Figure 118.

Erythrina chiapasana × *E. goldmanii*

Erythrina chiapasana is a tree of the pine–oak forests of the Central Plateau of Chiapas, occurring primarily above 1,500 m. *Erythrina goldmanii* inhabits the dry tropical deciduous forests of the Central Depression of Chiapas, formed by the highland-rimmed valley of the Río Grijalva. At El Sumidero National Park a few km north of the city of Tuxtla Gutierrez, where the Río Grijalva cuts through the limestone of the Central Plateau on its way to the Atlantic Ocean and forms a spectacular 800-m-deep canyon, the two species occur parapatrically and a hybrid zone is found about 2 km wide and extending about 300 m along an elevational gradient (Fig. 119).

Throughout their respective distributions, *Erythrina chiapasana* and *E. goldmanii* exhibit some intraspecific variation, but the two species are readily distinguishable morphologically. The leaves of *E. chiapasana* are densely tomentose with two-armed hairs on the abaxial surface (Fig. 120). The leaves of *E. goldmanii* are glabrous or nearly so at maturity and are aculeate along the midvein and primary veins of the abaxial surface (Fig. 122). The calyx of *E. chiapasana* is green to reddish, densely puberulent, and truncate at the margin without a prominent tooth on the carinal side; the corolla standard is dark red. The calyx of *E. goldmanii* is broader, dark purple brown to nearly black, glabrous, and provided with a prominent apical tooth on the carinal side; the corolla standard is usually pale red.

At El Sumidero both species are at the altitudinal and geographical limits of their ranges. Only individuals with the "pure" *E. chiapasana* phenotype are found in the oak-dominated forest at the plateau summit above 1,100 m; only individuals

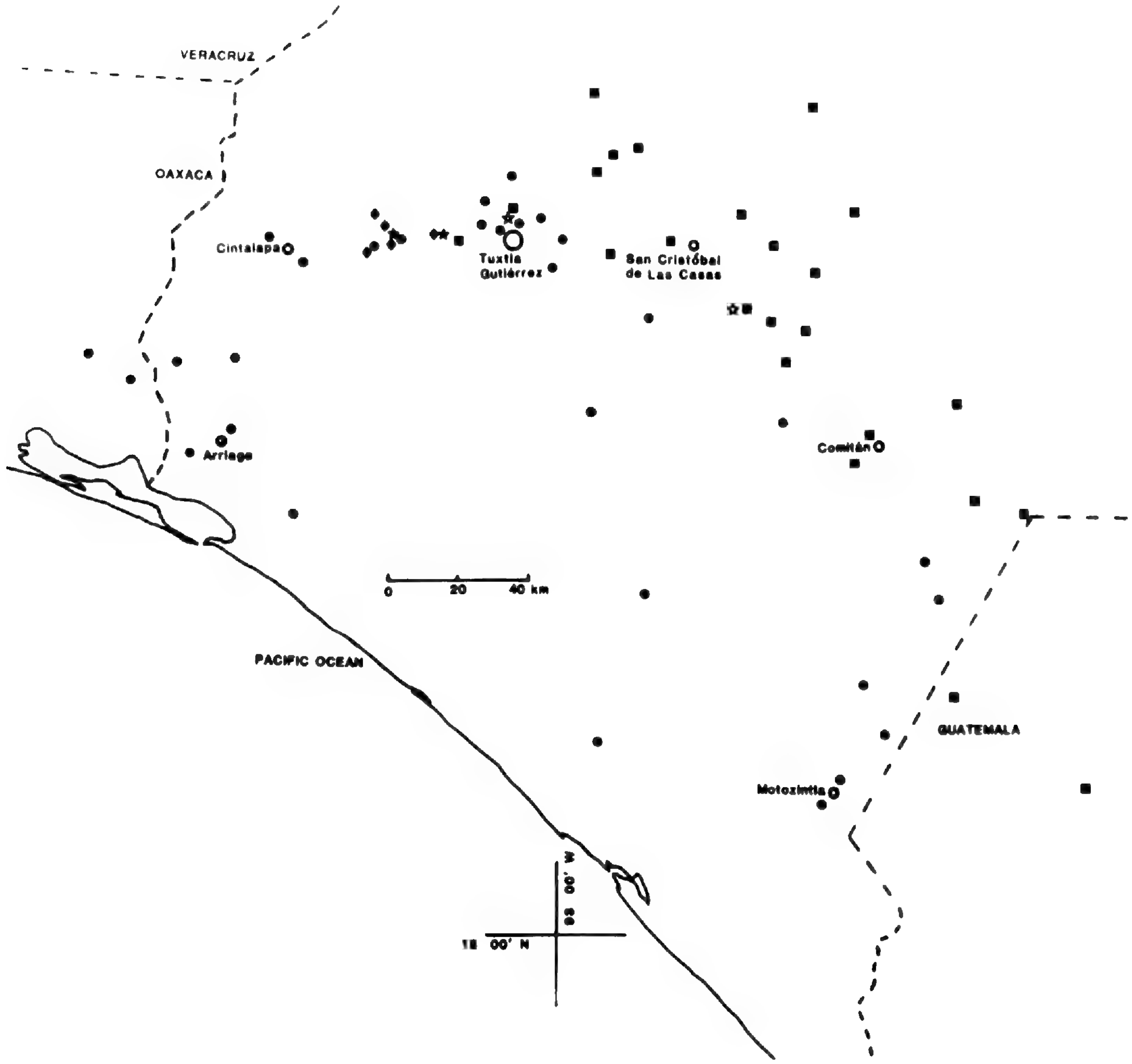


FIGURE 118. *Distribution of* Erythrina chiapasana, E. goldmanii, E. pudica, *and hybrid populations in Chiapas, Mexico. Squares*—E. chiapasana; *circles*—E. goldmanii; *diamonds*—E. pudica; *open stars*—E. chiapasana × E. goldmanii; *solid stars*—E. goldmanii × E. pudica.

with the "pure" *E. goldmanii* phenotype are found in the dry scrub forest below 800 m. In the transition zone near the top of the escarpment between 800 m and 1,100 m there are plants with intermediate phenotypes, or displaying in one individual various combinations of traits of both species. Some individuals, for example, have leaves that are sparsely tomentose on the abaxial surface and are also aculeate on the midvein (Fig. 121). Others have flowers with characters intermediate between the two species, or with various combinations of parental traits such as a puberulent, dark purple-brown calyx with an apical tooth (Fig. 123). Both parental types are also present in the transition zone.

This pattern of variation in the intermediate zone at El Sumidero establishes with reasonable certainty that the population is a hybrid swarm of *Erythrina chiapasana* × *E. goldmanii.* The intermediacy of the traits in this population resembles the patterns of inheritance expressed in the experimentally produced hybrids as discussed in Section 5.

As indicated in Section 4, I attempted to synthesize hybrids between *Erythrina chiapasana* and *E. goldmanii* in the field at El Sumidero using the same techniques of controlled hand-pollination employed in the experimental gardens in Hawaii. Hybrid fruits in both reciprocal crosses were obtained, but the fruit of *Erythrina chiapasana* ♀ × *E. goldmanii* ♂ was destroyed in a brush fire. The reciprocal *E. goldmanii* ♀ × *E. chiapasana* ♂ produced one mature hybrid seed. The F_1 was viable and is now growing in cultivation in Hawaii

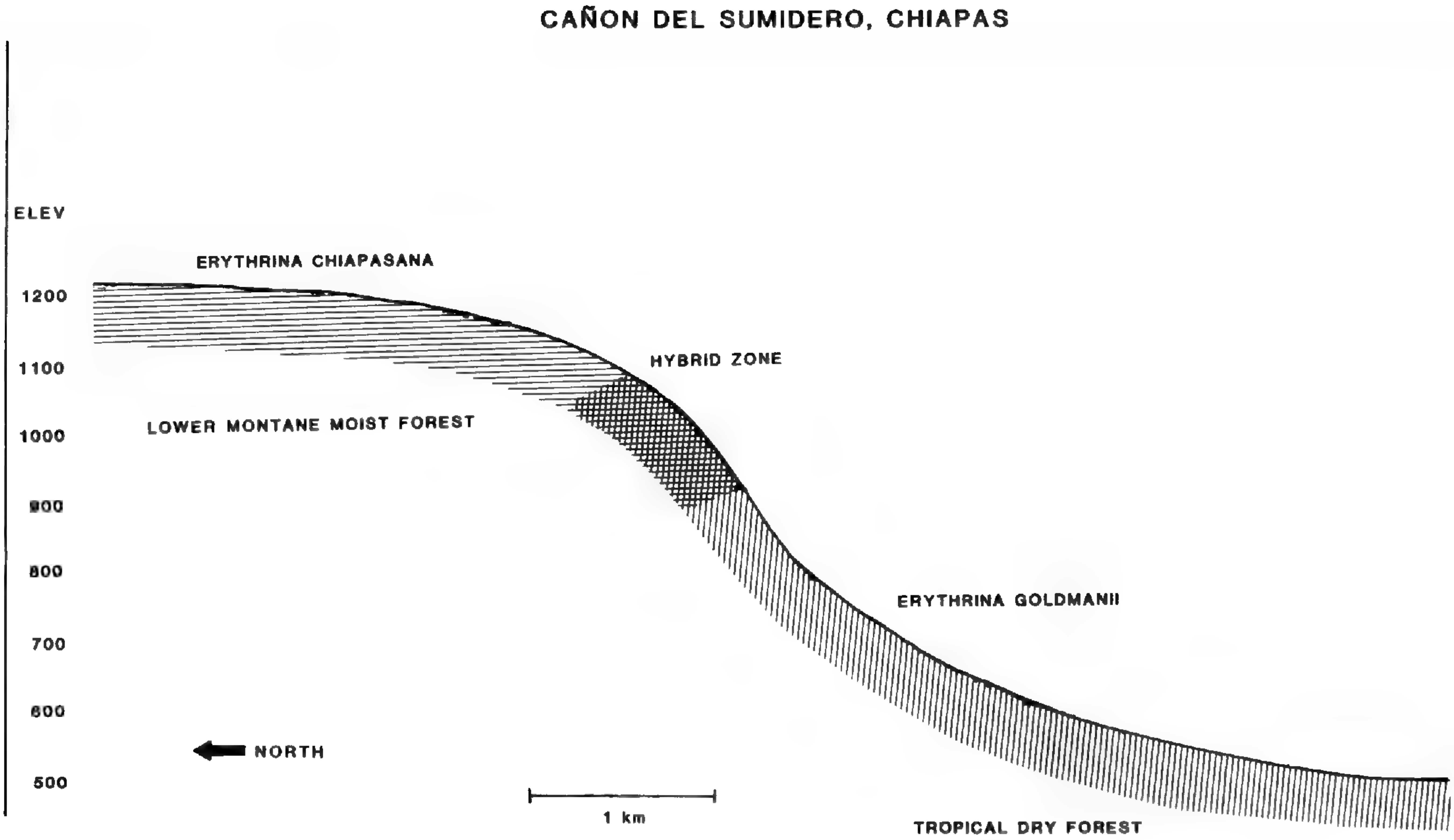


FIGURE 119. *Cross section of slope at El Sumidero, Chiapas, Mexico, showing distribution of* Erythrina chiapasana, E. goldmanii, *and hybrid zone.*

alongside accessions of both parental strains (Table 11). When this artificial hybrid flowers it will be possible to compare it with specimens of the putative natural hybrids from El Sumidero.

As discussed in a separate paper (Neill, 1987), the hummingbird *Heliomaster constantii* pollinates *Erythrina chiapasana* and *E. goldmanii* at El Sumidero and is therefore implicated as the agent directly responsible for interspecific gene flow in the hybridizing *Erythrina* population.

Erythrina goldmanii × *E. pudica*

Erythrina pudica is a locally endemic species that is restricted to the dry valley of the Río de La Venta, a tributary of the Río Grijalva, at the western end of the Central Depression of Chiapas. This is an unusual species, with the flowers drooping to nearly parallel with the erect axis of the inflorescence (Fig. 126). The calyx is truncate without an apical tooth and covered with a dense grayish tomentum; the corolla is very pale pink or orange-pink.

In the vicinity of Ocozocuautla, Chiapas, at the eastern margin of its small range, *Erythrina pudica* occurs sympatrically with *Erythrina goldmanii.* In disturbed scrub forest small hybrid populations are found, with individuals of both parental species as well as intermediates (Figs. 124–126).

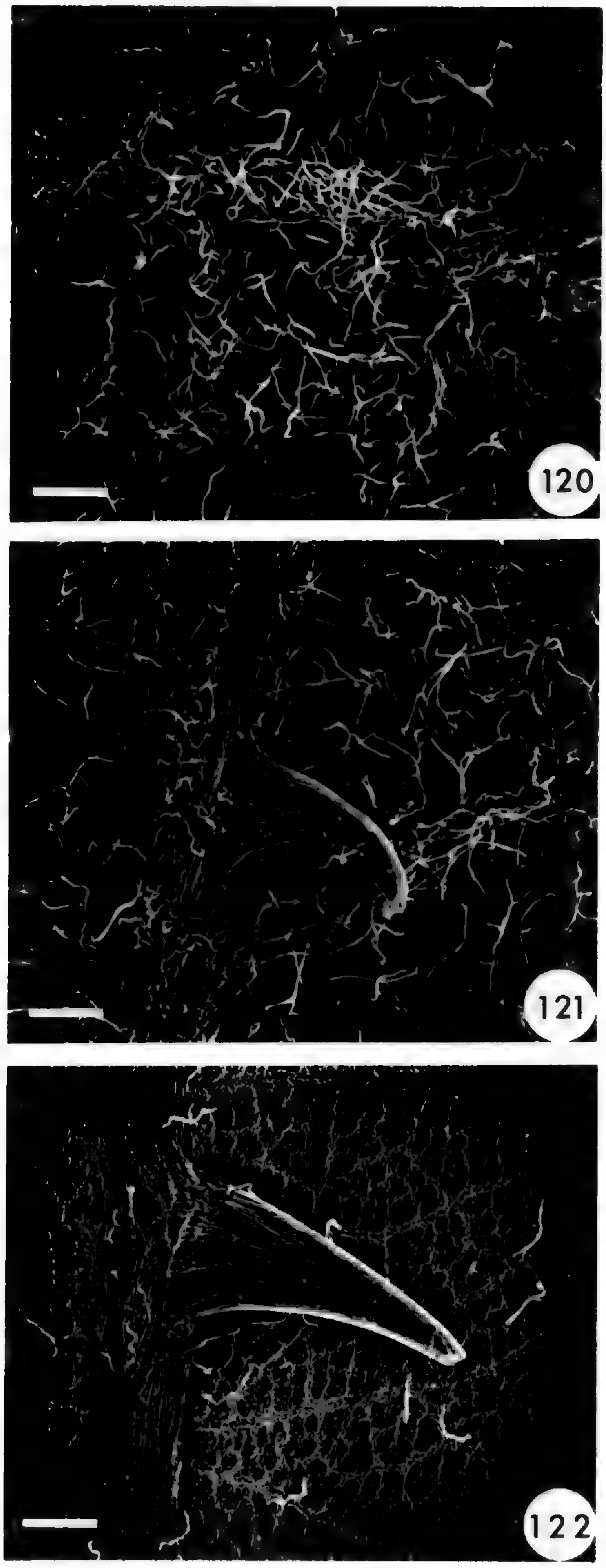
Along the highway 5 km east of Ocozocuautla are living fencerows of *Erythrina* containing both *E. goldmanii* and *E. pudica,* and occasional intermediate and evidently hybrid individuals occur there. These intermediates are similar in appearance to the trees occurring in the adjacent natural hybrid populations. The fencepost hybrids are very likely the progeny of other fencepost trees that received interspecific pollen from foraging hummingbirds moving down the line of mixed species fenceposts. The hybrid seed thus probably germinated directly below its female parent and grew up to become part of the fencerow itself.

Erythrina berteroana × *E. folkersii*

On the Atlantic coastal plain of northern Chiapas and adjacent states the natural vegetation has been almost entirely destroyed and replaced with pastures. There, as elsewhere in Mesoamerica, the pastures and roadsides are commonly lined with living fencerows of *Erythrina* trees. On the Atlantic plain the most frequently used species are *E. berteroana* and *E. folkersii,* which are both native to the region.

Trees morphologically intermediate between *Erythrina berteroana* and *E. folkersii* in shape and vestiture of the calyx and orientation of the flower occur in northern Chiapas. None of the intermediates set seed. Pollen stainability from four collections of the intermediates (Alexander's stain; 500 grains per sample: *Neill 5533, 5540, 5543, 5544*) was 73.2% (range 60.9–86.1%), an unusually low figure for *Erythrina*. These individuals are almost certainly hybrid *Erythrina berteroana* × *E. folkersii*. The reason for the low level of stainable pollen and lack of fruit set is not known; the experimentally produced hybrids within sect. *Erythrina* (Section 4) all had very high pollen fertility.

These intermediates closely match the type specimen of *Erythrina caribaea* Krukoff & Barneby as well as other collections determined by Krukoff as this species. Despite a protracted search, I never found this form occurring in a natural population and never found any seed set on the fencepost trees. It seems reasonable that *Erythrina caribaea* is in fact a hybrid *E. berteroana* × *E. folkersii* and probably occurs only as a cultivated fencepost tree.



FIGURES 120–122. *SEM images, abaxial leaf surfaces of* Erythrina chiapasana, E. goldmanii, *and hybrid from a population at El Sumidero, Chiapas, Mexico.*—*120.* E. chiapasana, Neill 5617.—*121.* E. chiapasana × E. goldmanii, Neill 5618.—*122.* E. goldmanii, Neill 5616. *Scale bars = 0.5 mm.*

HYBRID SPECIATION

In this paper it has been demonstrated that diploid *Erythrina* species are interfertile, that the hybrids are viable and fertile, and that hybridization sometimes occurs in natural populations. What has not yet been shown is the validity of the final hypothesis set forth in the introductory chapter: that hybrid speciation has taken place in *Erythrina*, that some distinct forms recognized as species are stabilized derivatives resulting from hybridization of two parental species, and that this process has been an important element in the evolutionary history of the genus.

Direct and unequivocal evidence relating to this hypothesis is difficult to obtain. Phylogenies based on molecular data of the taxa involved, including studies on isoenzymes and on nucleic acid restriction sites, might in the future provide such evidence. The best evidence available at present is the morphological congruence between certain artificially produced hybrids and certain naturally occurring forms that evidently are stabilized and self-perpetuating populations.

In considering the hypothesis of hybrid speciation, there is no reason to assume that the stabilized derivatives, especially if they became stabilized several generations or more after the original hybridization event, should be precisely intermediate between the parental species or should resemble closely the F_1 hybrids. A limited number of F_1 hybrids is, however, generally the only material available for comparison.

In *Erythrina* some of the artificial F_1 hybrids do resemble naturally occurring forms recognized as species, according to the results of the morphological studies presented in Section 5. *Ery-*

FIGURE 123. *Flowers of* Erythrina chiapasana, E. goldmanii, *and hybrid from a population at El Sumidero, Chiapas, Mexico. Left:* E. chiapasana, Neill 5455. *Center top:* E. chiapasana × E. goldmanii, Neill 5493. *Center bottom:* E. chiapasana × E. goldmanii, Neill 5466. *Right:* E. goldmanii, Neill 5495.

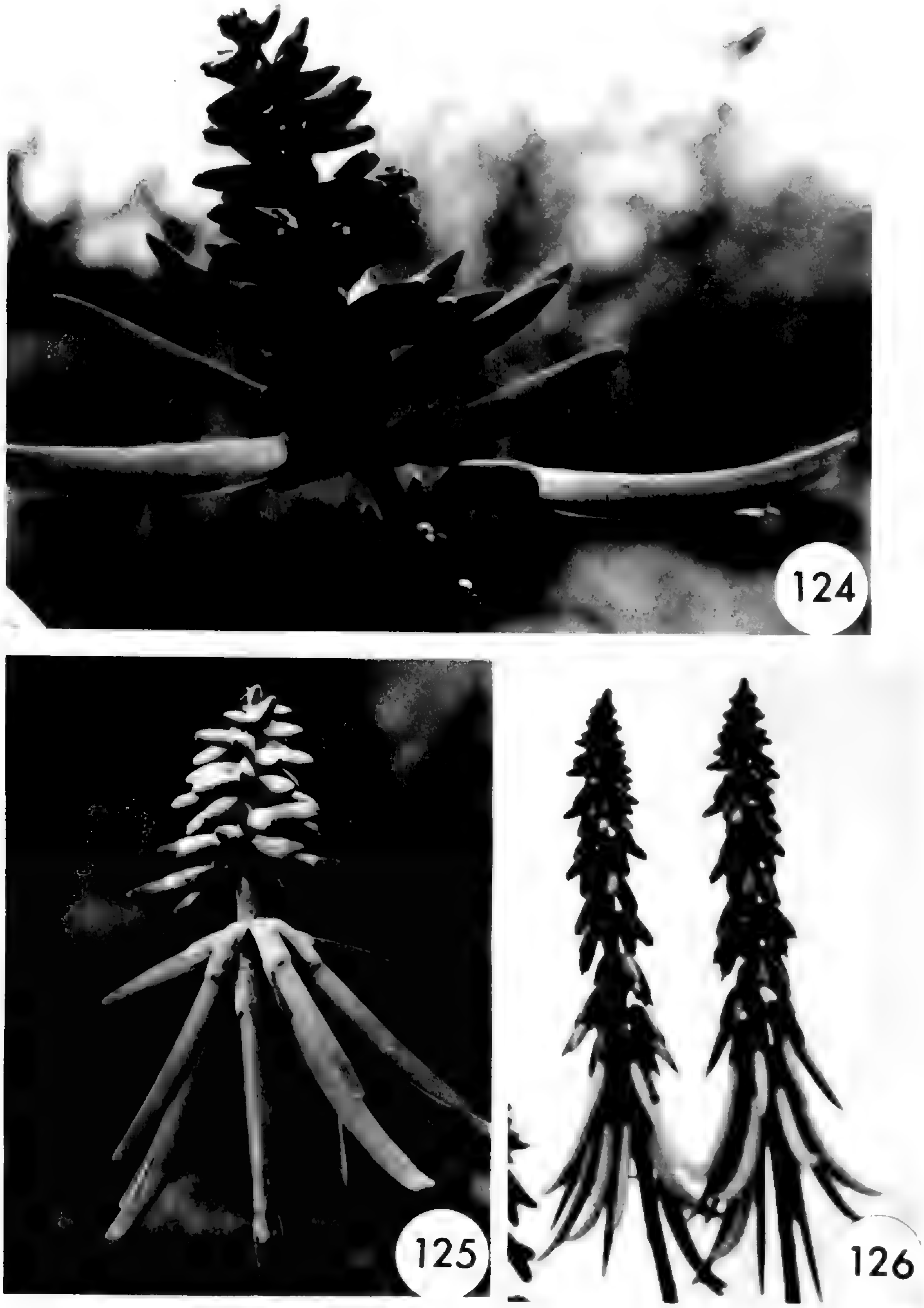
thrina macrophylla × *E. berteroana* bears a close resemblance to *E. atitlanensis*, and *E. crista-galli* × *E. fusca* resembles in certain features *E. dominguezii*. Field studies, which would be valuable for determining whether hybrid speciation could have occurred, were not conducted in either of these situations. The known geographical and ecological distribution of the taxa involved is outlined below.

Erythrina macrophylla is distributed throughout the highlands of Guatemala and western El Salvador, growing in the pine–oak forests above 1,500 m elevation. *Erythrina berteroana*, the most widespread species in sect. *Erythrina*, is common in the Pacific coastal plain of Guatemala and on the lower slopes of the volcanic range that lead up from the plain to the highlands. The intermediate known as *Erythrina atitlanensis* is known only from the vicinity of Lake Atitlan on the southern edge of the highlands. In terms of geography and elevational distribution, *E. atitlanensis* is precisely intermediate between the putative parental species. If hybridization is really implicated in this case, *E. atitlanensis* could be merely an early generation segregate rather than a stabilized, self-perpetuating derivative. Based on comparison of herbarium specimens, the progeny cultivated in Hawaii grown from seed obtained from the population in Guatemala closely resemble the parents. Therefore stabilization of the hybrid form may have taken place.

The case of *Erythrina dominguezii* and its putative parental species *E. crista-galli* and *E. fusca* is more problematic because the three taxa are so morphologically distinct. They are also ecologically distinct. *Erythrina crista-galli* and *E. fusca* are both riparian or estuarine species. *Erythrina crista-galli* is common along the estuary of the Río de La Plata and its tributaries and along the coast of southern Brazil. The more tropical *E. fusca* is distributed widely throughout the Amazon basin and south along the coast of Brazil. The ranges of the two species evidently do overlap in southern Brazil. The putative derivative *Erythrina dominguezii* also occurs in southern Brazil and westward through Paraguay and northern Argentina to eastern Bolivia, but it is an upland species of the dry Chaco forest and cerrado. *Erythrina dominguezii* would never have been suspected as a hybrid derivative of *E. crista-galli* × *E. fusca* were not its resemblance to the artificially produced F_1 so compelling. This situation appears to merit further investigation.

SUMMARY AND CONCLUSION

In the introduction, a set of five hypotheses was stated regarding the species relationships and evolutionary history of *Erythrina*: 1) The numerous species of sect. *Erythrina* can all cross freely with one another, producing fully fertile hybrids. The section forms a homogamic complex in which in-



FIGURES 124–126. *Inflorescences of* Erythrina goldmanii, E. pudica, *and hybrid from a population near Ocozocuautla, Chiapas, Mexico.*—*124.* E. goldmanii, Neill 5510.—*125.* E. goldmanii × E. pudica, Neill 5586.—*126.* E. pudica, Neill 5585.

ternal barriers to hybridization are absent. 2) The interfertile homogamic complex of sect. *Erythrina* extends, to a greater or lesser degree, to species in other sections and subgenera of *Erythrina*. Any diploid *Erythrina* species can hybridize with any other, but crosses between widely divergent taxa are generally difficult to obtain and the resulting F_1s may exhibit varying degrees of sterility. The genus as a whole may be characterized as a series of interfertile homogamic complexes with weak to moderate reproductive barriers between the complexes. 3) The widely foraging hummingbirds that pollinate species of sect. *Erythrina* are capable of effecting interspecific pollen flow between sympatric species of sect. *Erythrina*. 4) Sympatry at the local community level is rare among species of sect. *Erythrina*. Most species are restricted in geographic range and ecological amplitude and are allopatric, separated by habitat differences. However, sometimes different species do come into contact in nature, and then hybridizing populations are formed. 5) Patterns of distribution and phenetic variation in sect. *Erythrina* indicate that some distinct forms recognized as species are stabilized derivatives resulting from hybridization of two parental species. As a consequence of changing climates and dynamic geomorphological processes, and the consequent migration of vegetation types and mixing of floristic elements, formerly allopatric species may have come into contact a number of times. With the temporary breakdown of external isolating barriers, the interfertile species hybridized and the subsequent segregation and stabilization of hybrid derivatives have contributed to the proliferation of species of *Erythrina*.

The data presented in this paper have been marshalled in support of this set of hypotheses. The cytological studies (Section 3) and the experimental hybridization and self-compatibility trials (Section 4) present evidence in support of the first two hypotheses. In spite of the considerable morphological, ecological, and geographic differentiation of *Erythrina*, the species have retained a high degree of chromosomal (structural and genic) homology. Within sect. *Erythrina*, this homology, as evidenced by interspecific compatibility, is virtually complete: there is no detectable difference in the success of interspecific matings as compared with intraspecific matings. At greater taxonomic distances between the two parents (intersectional and intersubgeneric matings), mating success declines to some extent, but the number of successful "wide hybridizations" obtained in the experimental trials indicates that even the most morphologically and ecologically divergent of diploid *Erythrina* species have retained their ancestral chromosomal and genic homology and have not evolved substantial barriers to hybridization in concert with morphological differentiation. *Erythrina* forms a homogamic complex of interfertile species, or perhaps a series of homogamic complexes with weak to moderate barriers between the complexes. *Erythrina* shares this pattern of species relationships with many temperate-zone genera of trees and shrubs. The evidence from *Erythrina* suggests that the patterns of species relationships in predominantly or exclusively tropical groups of woody plants may not differ significantly from the patterns found in their better-known temperate-zone counterparts. Formation of homogamic complexes may be a common phenomenon in tropical woody plants and may be an important factor in the evolution of these taxa.

The patterns of inheritance of phenetic traits in the artificially produced hybrids (Section 5) confirm the true hybrid nature of these plants and demonstrate that matricliny, a potential complicating factor in the inheritance of these traits and in the interpretation of hybridization patterns, is not indicated in *Erythrina* hybrids. The patterns of inheritance in the artificial hybrids reveal the patterns to be expected in the detection and analysis of natural hybridization: for morphometric characters, a rather narrowly segregating array of intermediate types among the hybrids; and for discrete characters such as trichomes, possessed exclusively by either the female or male parent, the inheritance of the character in some of the hybrid offspring, the character being often reduced in size or density.

Evidence for the third hypothesis, concerning the pollination of sect. *Erythrina* by relatively specialized, widely foraging hummingbirds and the relation of this pollination system to *Erythrina* breeding systems, is presented in a separate paper (Neill, 1987). The pollination studies indicate that interspecific pollen flow and potential natural hybridization are likely to occur among sympatric species of sect. *Erythrina*.

Evidence for the fourth and fifth hypotheses, concerning natural hybridization and hybrid speciation in *Erythrina*, is presented in Section 6. Natural hybridization was detected among several co-occurring species of sect. *Erythrina* in Chiapas, Mexico, at the geographical center of diversity of the section. The natural hybrids display the same patterns of inheritance of phenetic traits as the artificial hybrids described earlier. The evidence for hybrid speciation itself is somewhat more equivocal. As stated in the introduction to this paper, the final hypothesis is historical and cannot be tested directly, but can be inferred only by drawing on information obtained by testing the first four.

The information presented throughout this paper does make plausible the hypothesis of hybrid speciation in *Erythrina*. Moreover, the research reported here provides a unique base of information for further studies of species relationships and the evolutionary history of *Erythrina*, as a model of evolutionary processes in flowering plants that may be common to many tropical woody genera. Perhaps the most incisive research that could be carried out at this point in the continuing biosystematic investigation of *Erythrina* would entail studies of isoenzymes and particularly of nucleic acid restriction sites among the taxa, as well as the inheritance of these molecular character states in the hybrids of known origin, followed by the construction of phylogenies combining molecular data with the presently available evidence on morphological and biogeographic patterns and the data from crossing experiments. The collection of *Erythrina* species and hybrids now available in cultivation at the

Hawaiian botanical gardens provides an ideal resource for such studies, and it is my hope that my colleagues specializing in chemosystematics and molecular phylogenetics do take advantage of this resource to investigate further the patterns of evolution in this interesting genus.

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APPENDIX I. *Species, sections, and subgenera of* Erythrina. *All recognized taxa in* Erythrina *are included in this list. I do not recognize infraspecific taxa in* Erythrina. *Proposed taxonomic changes are anticipated here, prior to their formal designation. The numbering sequence of Krukoff & Barneby (1974) is followed for reference to that work, and because the numbers were used to designate the hybrids. There are gaps in the number sequence because of reduction of species to synonymy. Species reduced to synonymy since Krukoff & Barneby (1974) are indicated at the end of this list.*

Erythrina L.
I. Subgenus *Micropteryx* (Walp.) F. G. Baker
  1. Sect. *Duchassaingia* (Walp.) Krukoff
    1. *Erythrina fusca* Lour.
  2. Sect. *Cristae-galli* Krukoff
    2. *Erythrina crista-galli* L.
    3. *Erythrina falcata* Benth.
  3. Sect. *Micropteryx*
    4. *Erythrina dominguezii* Hassler
    5. *Erythrina ulei* Harms
    6. *Erythrina verna* Velloso
    7. *Erythrina poeppigiana* (Walp.) O. F. Cook

II. Subgenus *Erythrina*
  4. Sect. *Suberosae* Krukoff
    8. *Erythrina suberosa* Roxb.
    9. *Erythrina microcarpa* Koord. & Valeton
    10. *Erythrina stricta* Roxb.
    11. *Erythrina resupinata* Roxb.
  5. Sect. *Arborescentes* Krukoff
    12. *Erythrina arborescens* (Roxb.) Walp.
  6. Sect. *Hypaphorus* (Hassk.) Krukoff
    13. *Erythrina subumbrans* (Hassk.) Merr.
  7. Sect. *Breviflorae* Krukoff
    14. *Erythrina breviflora* A. DC.
    14a. *Erythrina petraea* Brandegee
    14b. *Erythrina oaxacana* (Krukoff) Krukoff
    14c. *Erythrina batolobium* Barneby & Krukoff
  8. Sect. *Edules* Krukoff
    15. *Erythrina edulis* Triana ex M. Micheli
    15a. *Erythrina megistophylla* Diels
  9. Sect. *Stenotropis* (Hassk.) Krukoff
    16. *Erythrina speciosa* Andrews
  10. Sect. *Pseudo-edules* Krukoff & Barneby
    17. *Erythrina polychaeta* Harms
    18. *Erythrina schimpfii* Diels
  11. Sect. *Leptorhizae* Krukoff
    19. *Erythrina montana* Standley

APPENDIX I. *Continued.*

    20. *Erythrina leptorhiza* A. DC.
    21. *Erythrina horrida* A. DC.
    21a. *Erythrina sousae* Krukoff
  12. Sect. *Erythrina*
    22. *Erythrina herbacea* L.
    23. *Erythrina standleyana* Krukoff
    24. *Erythrina flabelliformis* Kearney
    25. *Erythrina americana* Miller
    27. *Erythrina pudica* Krukoff & Barneby
    27a. *Erythrina krukoviana* Neill, sp. nov. ined.
    28. *Erythrina lanata* Rose
    29. *Erythrina goldmanii* Standley
    31. *Erythrina folkersii* Krukoff & Mold.
    32. *Erythrina tuxtlana* Krukoff & Barneby
    33. *Erythrina smithiana* Krukoff
    34. *Erythrina cochleata* Standley
    35. *Erythrina hondurensis* Standley
    36. *Erythrina chiapasana* Krukoff
    37. *Erythrina atitlanensis* Krukoff & Barneby
    38. *Erythrina cobanensis* Krukoff & Barneby
    39. *Erythrina williamsii* Krukoff & Barneby
    40. *Erythrina tajumulcensis* Krukoff & Barneby
    41. *Erythrina chiriquensis* Krukoff
    42. *Erythrina macrophylla* A. DC.
    43. *Erythrina guatemalensis* Krukoff
    44. *Erythrina globocalyx* Porsch & Cuf.
    45. *Erythrina steyermarkii* Krukoff & Barneby
    46. *Erythrina florenciae* Krukoff & Barneby
    47. *Erythrina berenices* Krukoff & Barneby
    48. *Erythrina huehuetenangensis* Krukoff & Barneby
    49. *Erythrina lanceolata* Standley
    50. *Erythrina costaricensis* M. Micheli
    51. *Erythrina barqueroana* Krukoff & Barneby
    53. *Erythrina berteroana* Urban
    54. *Erythrina rubrinervia* H.B.K.
    55. *Erythrina mexicana* Krukoff
    56. *Erythrina salviiflora* Krukoff & Barneby
    56a. *Erythrina santamartensis* Krukoff & Barneby
    57. *Erythrina castillejiflora* Krukoff & Barneby
    57a. *Erythrina thyrsiflora* Gómez & Gómez

Appendix I. *Continued.*

- 13. Sect. *Gibbosae* Krukoff & Barneby
  - 58. *Erythrina gibbosa* Cuf.
- 14. Sect. *Corallodendra* Krukoff
  - 59. *Erythrina amazonica* Krukoff
  - 60. *Erythrina similis* Krukoff
  - 61. *Erythrina peruviana* Krukoff
  - 62. *Erythrina mitis* Jacq.
  - 63. *Erythrina pallida* Britton & Rose
  - 64. *Erythrina corallodendrum* L.
  - 65. *Erythrina eggersii* Krukoff
  - 66. *Erythrina buchii* Urban
  - 67. *Erythrina leptopoda* Urban & Ekman
- 14a. Sect. *Fidelenses* Neill, sect. nov. ined.
  - 68. *Erythrina elenae* Howard & Briggs
- 15. Sect. *Cubenses* Krukoff
  - 69. *Erythrina cubensis* C. Wright
- 16. Sect. *Olivianae* Krukoff & Barneby
  - 70. *Erythrina oliviae* Krukoff
- 17. Sect. *Caffrae* Barneby & Krukoff
  - 71. *Erythrina caffra* Thunb.
  - 72. *Erythrina lysistemon* Hutchinson
- 18. Sect. *Humeanae* Barneby & Krukoff
  - 73. *Erythrina humeana* Sprengel
  - 74. *Erythrina zeyheri* Harvey
- 19. Sect. *Acanthocarpae* Barneby & Krukoff
  - 75. *Erythrina acanthocarpa* E. Meyer

III. Subgenus *Tripterolobus* Barneby & Krukoff

- 20. Sect. *Tripterolobus* Barneby & Krukoff
  - 76. *Erythrina greenwayi* Verdcourt

IV. Subgenus *Chirocalyx* (Meisner) Harvey

- 21. Sect. *Bruceanae* Barneby & Krukoff
  - 77. *Erythrina brucei* Schwein.
- 22. Sect. *Macrocymbium* (Walp.) Barneby & Krukoff
  - 78. *Erythrina vogelii* Hooker f.
  - 79. *Erythrina senegalensis* A. DC.
- 23. Sect. *Dilobochilus* Harms
  - 80. *Erythrina excelsa* Baker
- 24. Sect. *Dichilocraspedon* Harms
  - 81. *Erythrina mildbraedii* Harms
- 25. Sect. *Chirocalyx*
  - 82. *Erythrina pygmaea* Torre
  - 83. *Erythrina mendesii* Torre
  - 84. *Erythrina baumii* Harms
  - 85. *Erythrina decora* Harms
  - 86. *Erythrina livingstoniana* Baker
  - 87. *Erythrina tholloniana* Hua
  - 88. *Erythrina addisoniae* Hutchinson & Dalziel
  - 89. *Erythrina droogmansiana* DeWild. & T. Durand
  - 90. *Erythrina orophila* Ghesq.
  - 91. *Erythrina sacleuxii* Hua
  - 92. *Erythrina haerdii* Verdc.
  - 93. *Erythrina sigmoidea* Hua
  - 94. *Erythrina latissima* E. Meyer
  - 95. *Erythrina abyssinica* Lam.

V. Subgenus *Erythraster* Barneby & Krukoff

- 26. Sect. *Erythraster*
  - 96. *Erythrina variegata* L.
  - 97. *Erythrina tahitensis* Nad.
  - 97a. *Erythrina sandwicensis* Degener
  - 98. *Erythrina euodiphylla* Hassk.
  - 99. *Erythrina vespertilio* Benth.
  - 100. *Erythrina merrilliana* Krukoff
  - 101. *Erythrina velutina* Willd.
  - 103. *Erythrina grisebachii* Urban
  - 104. *Erythrina burtii* Baker f.
  - 105. *Erythrina burana* R. Chiovenda
  - 106. *Erythrina perrieri* R. Viguier
  - 107. *Erythrina schliebenii* Harms ex Mildbr.
  - 108. *Erythrina melanacantha* Taubert ex Harms

Species reduced to synonymy since Krukoff & Barneby (1974):

Erythrina caribaea Krukoff & Barneby
= *E. berteroana* Urban × *E. folkersii* Krukoff & Mold.
Erythrina coralloides A. DC. = *E. americana* Miller
Erythrina insularis F. M. Bailey = *E. vespertilio* Benth.

The first two reductions to synonymy are proposed for the first time in this paper. The third reduction follows Krukoff's treatment in his post-1974 publications on *Erythrina.*

APPENDIX II. Erythrina *hybridization trials. This appendix summarizes the results of the interspecific hybridization trials for each species combination. For many of the species combinations, more than one accession was employed as the male and/or female parents. The identity of the individual parents is presented in Tables 11–13 only for the successful trials resulting in viable hybrid plants.*

The hybridization trials are grouped into five categories:

I. *Narrow hybridizations within sect.* Erythrina.
II. *Narrow hybridizations, excluding sect.* Erythrina.
III. *Intersectional hybridizations: female parent in sect.* Erythrina.
IV. *Intersectional hybridizations: male parent in sect.* Erythrina.
V. *Intersectional hybridizations: excluding sect.* Erythrina.

In categories III–V, the number in parentheses after the species name refers to the section to which the species belongs (see Table 1). An asterisk indicates a wide (intersubgeneric) hybridization.

Hybrid # = a number assigned to each hybrid combination, made up from the numbers assigned to the parental species as listed in Krukoff & Barneby (1974)
Pol = number of flowers hand-pollinated in the hybrid combination
Frt = number of pollinations producing mature fruits
Sds = total number of normal-sized seeds produced in the hybrid combination
Ger = number of seeds that germinated
Liv = surviving progeny; number of live F_1 plants in the hybrid combination

Female Parent	Male Parent	Hybrid #	Pol	Frt	Sds	Ger	Liv
I. Narrow hybridizations within sect. *Erythrina*							
americana	*berteroana*	25×53	3	1	1	1	1
americana	*herbacea*	25×22	7	0	0	0	0
atitlanensis	*berteroana*	37×53	4	0	0	0	0
atitlanensis	*guatemalensis*	37×43	1	0	0	0	0
berteroana	*chiapasana*	36×53	4	0	0	0	0
berteroana	*folkersii*	53×31	14	0	0	0	0
berteroana	*guatemalensis*	53×43	21	1	8	6	6
berteroana	*rubrinervia*	53×54	3	0	0	0	0
berteroana	*salviiflora*	53×56	3	0	0	0	0
berteroana	*standleyana*	53×23	2	0	0	0	0
berteroana	*tajumulcensis*	53×40	4	0	0	0	0
chiapasana	*berteroana*	36×53	7	1	12	8	8
chiapasana	*folkersii*	36×31	1	0	0	0	0
chiapasana	*guatemalensis*	36×43	16	0	0	0	0
chiapasana	*macrophylla*	36×42	2	0	0	0	0
chiapasana	*tajumulcensis*	36×40	3	0	0	0	0
costaricensis	*berteroana*	50×53	12	0	0	0	0
folkersii	*berteroana*	31×53	22	0	0	0	0
folkersii	*guatemalensis*	31×43	5	0	0	0	0
goldmanii	*chiapasana*	29×53	12	1	1	1	1
guatemalensis	*berteroana*	43×53	13	4	25	14	8
guatemalensis	*chiapasana*	43×36	10	2	15	9	9
guatemalensis	*folkersii*	43×31	4	1	5	5	2
guatemalensis	*herbacea*	43×22	12	0	0	0	0
guatemalensis	*macrophylla*	43×42	7	4	17	12	8
guatemalensis	*salviiflora*	43×56	2	1	7	1	1
guatemalensis	*standleyana*	43×23	15	3	7	3	2
guatemalensis	*tajumulcensis*	43×40	23	6	17	9	9
herbacea	*americana*	22×25	2	2	4	3	3
herbacea	*berteroana*	22×53	14	2	3	1	1
herbacea	*chiapasana*	22×36	1	0	0	0	0
herbacea	*guatemalensis*	22×43	4	1	2	2	2
herbacea	*standleyana*	22×23	8	0	0	0	0
herbacea	*tajumulcensis*	22×40	2	0	0	0	0
macrophylla	*americana*	22×25	4	1	3	2	1
macrophylla	*atitlanensis*	42×37	1	0	0	0	0
macrophylla	*berteroana*	42×53	4	2	8	4	4

APPENDIX II. *Continued.*

Female Parent	Male Parent	Hybrid #	Pol	Frt	Sds	Ger	Liv
macrophylla	*chiapasana*	42×36	6	1	3	0	0
macrophylla	*folkersii*	42×31	7	1	2	1	1
macrophylla	*guatemalensis*	42×43	17	2	6	4	4
macrophylla	*herbacea*	42×22	8	0	0	0	0
macrophylla	*salviiflora*	42×56	8	0	0	0	0
macrophylla	*standleyana*	42×23	2	0	0	0	0
macrophylla	*tajumulcensis*	42×40	9	1	1	0	0
rubrinervia	*berteroana*	54×53	2	0	0	0	0
salviiflora	*berteroana*	56×53	19	0	0	0	0
salviiflora	*guatemalensis*	56×43	3	0	0	0	0
standleyana	*berteroana*	23×53	19	0	0	0	0
standleyana	*guatemalensis*	23×43	8	0	0	0	0
standleyana	*herbacea*	23×22	10	0	0	0	0
tajumulcensis	*berteroana*	40×53	12	0	0	0	0
tajumulcensis	*guatemalensis*	40×43	8	1	4	4	4
tajumulcensis	*herbacea*	40×22	2	0	0	0	0
tajumulcensis	*macrophylla*	40×42	5	0	0	0	0
I. Total			417	39	142	90	75
II. Narrow (intrasectional) hybridizations: excluding sect. *Erythrina*							
		1. Sect. *Cristae-galli*					
crista-galli	*falcata*	2×3	22	2	4	1	1
falcata	*crista-galli*	3×2	14	4	7	0	0
		2. Sect. *Chirocalyx*					
abyssinica	*latissima*	95×94	3	1	2	1	1
abyssinica	*sacleuxii*	95×91	2	0	0	0	0
		3. Sect. *Erythraster*					
perrieri	*variegata*	106×96	10	4	12	10	9
sandwicensis	*variegata*	97a×96	8	0	0	0	0
tahitensis	*sandwicensis*	97×97a	7	0	0	0	0
tahitensis	*variegata*	97×96	26	0	0	0	0
tahitensis	*velutina*	97×102	19	0	0	0	0
variegata	*perrieri*	96×106	6	0	0	0	0
variegata	*vespertilio*	96×99	6	0	0	0	0
II. Total			123	11	25	12	11
III. Intersectional hybridizations: female parent in sect. *Erythrina*							
*berteroana**	*fusca* (1)	53×1	21	0	0	0	0
*chiapasana**	*fusca*	36×1	5	0	0	0	0
*folkersii**	*fusca*	31×1	8	0	0	0	0
*guatemalensis**	*fusca*	43×1	35	0	0	0	0
*herbacea**	*fusca*	22×1	10	1	4	4	4
*macrophylla**	*fusca*	42×1	10	1	3	0	0
*berteroana**	*crista-galli* (2)	53×2	2	0	0	0	0
*guatemalensis**	*crista-galli*	43×2	64	1	2	0	0
*herbacea**	*crista-galli*	22×2	10	0	0	0	0
*macrophylla**	*crista-galli*	42×2	20	0	0	0	0
*herbacea**	*dominguezii* (3)	22×4	3	0	0	0	0
guatemalensis	*stricta* (4)	43×10	5	0	0	0	0
guatemalensis	*arborescens* (5)	43×12	3	0	0	0	0
guatemalensis	*speciosa* (9)	43×16	10	0	0	0	0
herbacea	*speciosa*	22×16	2	0	0	0	0
macrophylla	*speciosa*	42×16	11	0	0	0	0
berteroana	*pallida* (14)	53×63	4	0	0	0	0

APPENDIX II. *Continued.*

Female Parent	Male Parent	Hybrid #	Pol	Frt	Sds	Ger	Liv
guatemalensis	*amazonica (14)*	43×59	58	1	1	0	0
guatemalensis	*corallodendrum (14)*	43×64a	2	2	6	0	0
guatemalensis	*caffra* (17)	43×71	1	0	0	0	0
guatemalensis	*lysistemon (17)*	43×72	23	2	3	1	0
herbacea	*caffra*	22×71	2	0	0	0	0
guatemalensis	*humeana* (18)	43×73	5	1	1	0	0
herbacea	*humeana*	22×73	5	1	2	2	2
*guatemalensis**	*senegalensis* (22)	43×79	8	3	3	1	1
*guatemalensis**	*abyssinica* (25)	43×95	9	2	2	1	1
*guatemalensis**	*latissima* (25)	43×94	6	0	0	0	0
*macrophylla**	*abyssinica*	42×95	2	0	0	0	0
*macrophylla**	*latissima*	42×94	4	0	0	0	0
*guatemalensis**	*perrieri* (26)	43×106	12	0	0	0	0
*guatemalensis**	*sandwicensis (26)*	43×97a	25	0	0	0	0
*guatemalensis**	*variegata (26)*	43×96	26	0	0	0	0
*guatemalensis**	*vespertilio (26)*	43×99	4	1	2	0	0
*herbacea**	*perrieri*	22×106	8	0	0	0	0
*herbacea**	*variegata*	22×96	8	0	0	0	0
*macrophylla**	*sandwicensis*	42×97a	4	0	0	0	0
*macrophylla**	*variegata*	42×96	8	0	0	0	0
*macrophylla**	*vespertilio*	42×99	1	0	0	0	0
III. Total			444	16	29	9	8
IV. Intersectional hybridizations: male parent in sect. *Erythrina*							
fusca (1)*	*berteroana*	1×53	70	0	0	0	0
*fusca**	*folkersii*	1×31	8	0	0	0	0
*fusca**	*guatemalensis*	1×43	11	0	0	0	0
crista-galli (2)*	*guatemalensis*	2×43	10	4	15	10	8
stricta (4)	*guatemalensis*	10×43	6	0	0	0	0
arborescens (5)	*guatemalensis*	12×43	24	1	1	0	0
speciosa (9)	*berteroana*	16×53	3	0	0	0	0
corallodendrum (14)	*berteroana*	64×53	3	0	0	0	0
pallida (14)	*berteroana*	63×53	4	0	0	0	0
pallida (14)	*fusca*	63×1	2	0	0	0	0
humeana (18)	*berteroana*	73×53	3	0	0	0	0
abyssinica (25)*	*guatemalensis*	95×43	3	0	0	0	0
perrieri (26)*	*berteroana*	106×53	2	0	0	0	0
perrieri (26)*	*guatemalensis*	106×43	8	0	0	0	0
variegata (26)*	*guatemalensis*	96×43	7	0	0	0	0
variegata (26)*	*herbacea*	96×22	8	0	0	0	0
IV. Total			176	5	16	10	8
V. Intersectional hybridizations: excluding sect. *Erythrina*							
fusca (1)	*crista-galli* (2)	1×2	38	0	0	0	0
*fusca**	*lysistemon* (17)	1×72	1	0	0	0	0
*fusca**	*variegata* (26)	1×96	17	0	0	0	0
crista-galli (2)	*fusca* (1)	2×1	35	11	33	8	7
crista-galli	*dominguezii* (3)	2×4	34	0	0	0	0
*crista-galli**	*arborescens* (5)	2×12	1	0	0	0	0
*crista-galli**	*speciosa* (9)	2×16	14	2	2	2	1
*crista-galli**	*amazonica* (14)	2×59	18	1	1	0	0
*crista-galli**	*abyssinica* (25)	2×95	3	0	0	0	0
*crista-galli**	*perrieri* (26)	2×106	8	0	0	0	0
*crista-galli**	*sandwicensis* (26)	2×97a	5	2	3	0	0
*crista-galli**	*variegata* (26)	2×96	23	2	3	2	1
dominguezii (3)	*crista-galli* (2)	4×2	8	0	0	0	0

Appendix II. *Continued.*

Female Parent	Male Parent	Hybrid #	Pol	Frt	Sds	Ger	Liv
arborescens (5)*	*crista-galli* (2)	12×2	15	1	1	0	0
arborescens	*humeana* (18)	12×73	7	0	0	0	0
*arborescens**	*sandwicensis* (26)	12×97a	15	0	0	0	0
speciosa (9)*	*fusca* (1)	16×1	3	0	0	0	0
*speciosa**	*crista-galli* (2)	16×2	33	0	0	0	0
speciosa	*lysistemon* (17)	16×72	64	3	7	4	4
caffra (17)*	*fusca* (1)	71×1	5	1	2	2	2
lysistemon (17)*	*fusca* (1)	72×1	10	0	0	0	0
lysistemon	*speciosa* (9)	72×16	46	3	8	4	3
*lysistemon**	*abyssinica* (25)	72×95	11	0	0	0	0
*lysistemon**	*latissima* (25)	72×94	4	0	0	0	0
senegalensis (22)*	*fusca* (1)	79×1	8	0	0	0	0
abyssinica (25)*	*fusca* (1)	95×1	5	0	0	0	0
*abyssinica**	*crista-galli* (2)	95×2	2	0	0	0	0
*abyssinica**	*humeana* (18)	95×73	5	1	1	0	0
*abyssinica**	*sandwicensis* (26)	95×97a	1	0	0	0	0
*abyssinica**	*variegata* (26)	95×96	1	0	0	0	0
latissima (25)*	*lysistemon* (17)	94×72	16	0	0	0	0
*latissima**	*humeana* (18)	95×73	5	0	0	0	0
perrieri (26)*	*fusca* (1)	106×1	3	0	0	0	0
variegata (26)*	*fusca* (1)	96×1	32	0	0	0	0
*variegata**	*crista-galli* (2)	96×2	2	0	0	0	0
*variegata**	*speciosa* (9)	96×16	6	0	0	0	0
*variegata**	*senegalensis* (22)	96×79	7	0	0	0	0
V. Total			511	27	61	22	18

APPENDIX III. *Sources of cultivated* Erythrina *used as parentals in successful interspecific hybridizations. (W): Accession obtained from known wild populations; (NW): Accession obtained from cultivated source, or otherwise not from a known wild population.*

Vouchers (from plants cultivated in Hawaiian gardens) are deposited at MO. Location of voucher from original wild collection of seed is indicated here if known.

Erythrina abyssinica Lam. PT 770034001
Kenya: Nairobi. *E. Taylor 17.* (NW)

Erythrina abyssinica Lam. PT 731006002
Kenya: Nairobi, cultivated tree in yard of Cunningham van Someren. (NW)

Erythrina americana Miller WA 75c1171
Mexico: Mexico City, cultivated tree. *L. S. Ayres s.n.* (Waimea received as cutting from Los Angeles State & County Arboretum # 565874) (NW)

Erythrina berteroana Urban PT 730311001
Guatemala: Suchitepequez. Nahualate, Finca El Salvador. *B. A. Krukoff 1973-13* (NY). (W)

Erythrina berteroana Urban PT 700044001, -002
Panama: Canal Zone. Tree cultivated at Summit Gardens. *W. S. Stewart s.n.* (NW)

Erythrina berteroana Urban WA 74s864
Guatemala: Suchitepequez. Municipio Chicacao. *B. A. Krukoff 1968-508* (NY). (W)

Erythrina berteroana Urban WA 78s564
Panama: Canal Zone. Between Madden Dam and Chilibre. *J. Folson 3661* (MO). (W)

Erythrina caffra Thunb. WA 74c1456
South Africa: Cape Province, Grahamstown, elev. 2,400 ft. *Roy Bayliss s.n.* (Waimea received as cutting from Foster Garden # 69.265) (W)

Erythrina chiapasana Krukoff PT 721005001
Guatemala: Huehuetenango, near La Estancia. *B. A. Krukoff 1969-68* (NY). (W)

Erythrina chiapasana Krukoff PT 730710001
Guatemala: Huehuetenango, near La Estancia. *B. A. Krukoff 1973-16* (NY). (W)

Erythrina crista-galli L. PT 740283001
Paraguay: near Asunción. *Conrad & Die 2191.* (W)

Erythrina crista-galli L. WA 74p840
South Africa. Cultivated tree; seed received from Wm. J. Tijmens, Univ. of Stellenbosch. (Waimea received as live plant from PT 72s352) (NW)

Erythrina falcata Benth. PT 750086001
Argentina. Thays Botanical Garden, cultivated tree. *E. Pingitore s.n.* (NW)

Erythrina folkersii Krukoff & Mold. PT 700010001
Guatemala: Izabal, at junction of road to Puerto Barrios and Mathias Calves. *B. A. Krukoff 1969-109* (NY). (W)

Erythrina fusca Lour. PT 740230005, WA 74599
Guatemala: Escuintla. *B. A. Krukoff 1972-12* (NY). (W)

Erythrina guatemalensis PT 700018001, WA 74c1453
Guatemala: Alta Verapaz, along Cobán–Salama road, near Santa Cruz, elev. 1,280 m. *B. A. Krukoff 1969-195* (NY). (W) Note: The tree at Waimea Arboretum WA 74c1453 was grown from a cutting taken from PT 700018001, so the two accessions are genetically identical.

Erythrina guatemalensis Krukoff PT 720999002
Guatemala: Huehuetenango, near Barillas. *B. A. Krukoff 1969-200* (NY). (W)

Erythrina guatemalensis Krukoff PT 750419001
Guatemala: Huehuetenango, near Barillas. *B. A. Krukoff s.n.* (W)

Erythrina herbacea L. PT 75c1103
California: Los Angeles State & County Arboretum # 54s1201, cultivated. (NW)

Erythrina herbacea L. WA 76s187
Florida: Miami, Fairchild Garden, cultivated. (NW)

Erythrina humeana Sprengel WA 74p1382
South Africa: locality unknown. *D. Millington s.n.* (NW)

Erythrina latissima E. Meyer PT 750281004
South Africa: Natal. Cultivated tree at Pine Town Gardens. *Ian Whitton 750401.* (NW)

Erythrina lysistemon Hutchinson PT 750280002, -003
South Africa: Natal, Durban. *Ian Whitten s.n.* (1975) (W)

Erythrina macrophylla A. DC. PT 750420002, WA 75s1136
Guatemala: Sololá, near Godinez. Elev. 6,145 ft. *B. A. Krukoff 1975-4* (NY). (W)

APPENDIX III. *Continued.*

Erythrina perrieri R. Viguier WA 74s857
Madagascar: Maintirano, near Bekopaka. *Fred Meyer s.n.* (W)

Erythrina salviiflora Krukoff & Barneby PT 721000002
Guatemala: Suchitepequez, Municipio Chicacao, Finca El Naranjo. Elev. 1,070 m. *B. A. Krukoff 1969-58* (NY). (W)

Erythrina senegalensis A. DC. WA 74s100
Nigeria: Coastal area. Seeds received from B. A. Krukoff; collector unknown. (W)

Erythrina speciosa Andrews PT 730708001, PT 730742002
Brazil: São Paulo. Cultivated tree at São Paulo Botanical Garden. *B. A. Krukoff 1973-20* (NY). (NW)

Erythrina standleyana Krukoff WA 76s1056
California: Escondido. Cultivated tree. (NW) Originally collected as seed by Fred Meyer from wild tree, Yucatán, Mexico.

Erythrina tajumulcensis Krukoff & Barneby WA 74c1448
Guatemala: San Marcos, near Aldea Feria, along road from San Marcos to San Rafael de La Costa. *B. A. Krukoff 1969-249* (NY). (Waimea received as cutting from PT 700015001) (W)

Erythrina variegata L. WA 74s892
Hawaii: Honolulu, Mid-Pacific Country Club, cultivated (white-flowered form). *Beatrice Krauss s.n.* (NW)

Erythrina variegata L. WA 76s996
Mariana Islands: Saipan Unai, Laulau Beach. *Derral Herbst s.n.* (W)

THE BIOSYSTEMATICS OF *LUDWIGIA* SECT. *MICROCARPIUM* (ONAGRACEAE)[1]

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ABSTRACT

Ludwigia *sect.* Microcarpium *is a polyploid complex of 14 species distributed primarily in the southeastern United States. Several of the species are variable and taxonomically difficult; the boundaries of many are blurred by intermediate forms. Relationships among the species are often reticulate and in some cases difficult to specify precisely. Data from the study of meiosis in artificial and natural hybrids were used to analyze relationships among the species. Among diploid (*$n = 8$*) species,* L. linearis *and* L. linifolia *are similar in morphology but differ chromosomally by one reciprocal translocation.* F_1 *hybrids between them are vigorous, have 47–48% stainable pollen, and produce moderate quantities of viable seeds. Another diploid,* L. microcarpa, *is morphologically and genetically distinct from* L. linearis *and* L. linifolia. *Hybrids between* L. microcarpa *and either other diploid are vigorous but produce only 6% stainable pollen and no viable seeds. They formed mostly univalents at meiotic metaphase I, with up to three sometimes heteromorphic bivalents. The fourth diploid,* L. stricta, *has not been studied biosystematically. The eight morphologically distinct tetraploid (*$n = 16$*) taxa can be crossed in any combination, producing fertile offspring with complete association of their 16 bivalents. No extant diploids are believed to have been involved directly in forming the tetraploids of sect.* Microcarpium. Ludwigia alata, *a hexaploid (*$n = 24$*), is morphologically similar to the tetraploids, and chromosome pairing in experimental hybrids suggests that it originated after hybridization between a tetraploid and* L. microcarpa *or populations ancestral to that species. Two chromosome numbers are present in the* L. curtissii *complex (*L. simpsonii, $n = 24$*;* L. curtissii, $n = 32$*). The hexaploid complement of* L. simpsonii *appears to include three different diploid genomes, one of which is identical with that of* L. microcarpa. *Present data are not sufficient to determine if the diploid* L. linearis–L. linifolia *lineage was involved in parentage of the hexaploid* L. simpsonii, *but morphological evidence suggests it was not. It is highly probable, however, that the octoploid* L. curtissii *was derived after hybridization between the diploid* L. linearis–L. linifolia *lineage and the hexaploid* L. simpsonii.

Ludwigia contains some 82 species, which are classified into 23 sections (Raven, 1963; Ramamoorthy, 1979; Ramamoorthy & Zardini, 1987). It is the only member of the monotypic tribe Jussiaeeae and is the fourth largest genus in Onagraceae (after *Epilobium*, *Oenothera*, and *Fuchsia*). It has existed since at least the Eocene (Eyde & Morgan, 1973), and increasing evidence suggests it represents the earliest surviving evolutionary offshoot of the family (review in Ramamoorthy & Zardini, 1987; Eyde, 1981), or, in cladistic terms, the "sister group" of all other genera of the family. Study of this genus is therefore critical to understanding the overall evolutionary pattern in Onagraceae, a subject to which Peter H. Raven and his associates have devoted much time and energy over the past 30 years.

Thirteen species of *Ludwigia* are restricted to the Old World, 59 to the New World, and 10 are common to both hemispheres (Ramamoorthy,

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1980). Most sections are tropical and subtropical, but *Ludwigia* also has several well-developed temperate offshoots, particularly in North America (Raven & Tai, 1979).

Most native North American *Ludwigia* species have four sepals, four stamens, pluriseriate and free seeds with narrow raphes, and a herbaceous habit (Raven, 1963). With a few exceptions they are confined to the Atlantic and Gulf coastal plains of the United States. The 23 haplostemonous species represented here are placed in three sections: sect. *Ludwigia*, with 4 species (Munz, 1944, 1965; Raven, 1963); sect. *Dantia*, with 5 species (Schmidt, 1967); and sect. *Microcarpium*, a diverse group of 14 species (Table 1), which constitutes the subject of this study.

Section *Microcarpium* was selected for the present study because it represents a diverse polyploid complex (Raven & Tai, 1979) in which abundant natural hybridization occurs and in which the relationships among species are not clear. In a comparative study of the reproductive structures in *Ludwigia*, Eyde (1978) considered sect. *Microcarpium* as "remarkably diverse," at least with respect to surface-cell orientation of the seeds. The fact that several polyploid species were reported to have two different chromosome numbers (Raven & Tai, 1979) may reflect either difficulties in identification or their diverse genetic backgrounds. Duke (1955) noted the varying degree of intergradation exhibited between North Carolina *Ludwigia* species, and he suspected one population to be of hybrid origin between two species of sect. *Microcarpium*. A critical study of herbarium material has revealed many specimens exhibiting various intermediate morphological characteristics. Two such natural hybrids, *L. lanceolata* × *L. pilosa* and *L. suffruticosa* × *L. pilosa*, have even been given specific and varietal names (*L. simulata* Small and *L. suffruticosa* Walter var. *pubens* Torrey & A. Gray, respectively). Conclusive evidence of intergradation among species, however, can only be obtained through experimental hybridization.

Schmidt's (1967) work in establishing the phylogenetic relationships among species belonging to *Ludwigia* sect. *Dantia* has proved helpful in the study of sect. *Microcarpium*. Both of these sections were grouped, along with the monotypic East Asian section *Miquelia*, in the "*Microcarpium* complex" on the basis of reproductive structures and overall evolutionary patterns in *Ludwigia* (Eyde, 1981). Schmidt (1967) demonstrated through artificial hybridization and cytological observations of hybrid microsporocytes in sect. *Dantia* that hybrids between plants of different ploidy levels consistently exhibited typical "Drosera-type" chromosome pairing; i.e., homologous genomes in the F_1 generations always formed bivalents and nonhomologous genomes remained unpaired.

Schmidt (1967) also studied two naturally occurring intersectional hybrids. Meiotic observations of the hybrid between *L. palustris* ($n = 8$; sect. *Dantia*) and *L. glandulosa* ($n = 16$; sect. *Microcarpium*) revealed very little association between chromosomes, with 0–3 weakly joined bivalents. The other natural hybrid examined, involving *L. simpsonii* ($n = 24$, cited as *L. curtissii* by Schmidt; sect. *Microcarpium*) and *L. repens* ($n = 24$; sect. *Dantia*), yielded 48 unpaired chromosomes at meiosis. These observations suggest that in the related sect. *Microcarpium*, "Drosera-type" chromosome pairing also occurs. This characteristic is helpful in studying genetic relationships among species in such a polyploid complex.

The purpose of the present study was to determine the evolutionary relationships of the taxa comprising sect. *Microcarpium*. Toward this end I have considered extensive cytological evidence from my experimental hybridizations. This has been supplemented with data on morphology, pollination biology, crossing relationships, geographical distribution, and field observations of morphological variation and habitat preference. In addition, more than 7,000 herbarium specimens have been examined.

MATERIALS AND METHODS

Specimens were collected from wild populations and were propagated from seeds or clonal transplants in the experimental greenhouse at the Missouri Botanical Garden (with the exception of some strains that were obtained as seeds from the Kew Seed Bank). Members of sect. *Microcarpium* can be cloned easily from their vegetative parts and cultivated in the greenhouse by standard procedures. Parental seeds usually germinated readily one or two weeks after they were sown. However, it took one or two months or even longer for some of the hybrid seeds to germinate. Plants of sect. *Microcarpium* normally flower the first year.

In an insect-free greenhouse, several flowers of each parental strain were (1) artificially self-pollinated to test for self-compatibility, (2) left alone to test for self-pollination, and (3) emasculated and left alone to test for apomixis. Plants of all species studied were found to be self-compatible and nonapomictic. Except for a few species, in which selfing is prevented physically, members of sect. *Microcarpium* are capable of mechanical self-pollination.

All experimental crosses were therefore made by first emasculating the ovulate parent before self-pollination could occur, and then applying pollen from the pollen parent to its stigmas. Generally, several different parental strains were used in each cross; in a given trial all pollen parents were from the same population. The seeds resulting from successful hybridizations were sown early the following spring. Usually six seedlings of each artificial hybrid were randomly selected and transplanted into five-inch pots. A few of the F_2 families were also grown to maturity. About five to six months were required to produce a flowering hybrid after germination.

Flower buds to be examined for meiotic behavior were fixed in a 3:1 mixture of 95% ethanol and glacial acetic acid and stored in the refrigerator. Prior to staining, the buds were hydrolyzed for 5–8 minutes at 60°C using a 1:1 mixture of concentrated HCl and 95% ethanol. They were then squashed in FLP orcein (Jackson, 1973). Somatic chromosome counts for some of the parental strains were obtained from actively growing root tips pretreated for three to four hours in 8-hydroxyquinoline, then fixed as above for at least ten minutes. The root tips were then hydrolyzed in 1 N HCl for 8–10 minutes at 60°C and squashed in the FLP orcein. Semipermanent slides were prepared and preserved in the freezer. Cytological observations were made using a Zeiss Universal Large Research Microscope. All analyzable chromosome configurations (mostly diakinesis or metaphase I) were documented with camera lucida drawings or photomicrographs using Kodak Panatomic-X film. Negatives and drawings are deposited at the Institute of Botany, Academia Sinica, Taipei.

Fertility of greenhouse parental individuals, experimental hybrids, and suspected naturally occurring hybrids was estimated by determining the percentage of stainable pollen using the malachite green-acid fuchsin-orange G stain of Alexander (1969), which stains pollen walls green and cytoplasm red. Pollen grains with uniformly red cytoplasm were scored as fertile; partially stained or unstained grains were considered sterile. In many hybrids, however, and especially those of heteroploid crosses, the stainable pollen grains differ substantially in size, and some probably are not functional, as was suggested by Uhl (1976). At least 200 tetrads (when pollen shed as tetrads) or 400 single grains (when pollen shed singly) per plant were scored.

Seeds of members of sect. *Microcarpium* are so small (ca. 0.4–0.7 mm long) that studying the shapes and orientations of their surface cells under a dissecting microscope is very difficult. However, they are transparent enough to be examined under a light microscope. Photographs of seeds were taken with strong back illumination using Kodak Panatomic-X film. Polarized light was sometimes used.

Herbarium specimens prepared from all experimental plants, both parental and hybrid (with the exception of the very small individuals such as those which did not develop much further than the cotyledonous stage), are deposited at MO. Experimental hybrids are designated by a formula consisting of the acronym (Tables 3–15; Figs. 5, 21) for the two parents, connected by the multiplication sign (×), with the ovulate parent listed first.

DIAGNOSTIC FEATURES

Discussion of the morphological features is limited to those useful in delimiting members of sect. *Microcarpium* and in recognizing hybrids. A more complete discussion of morphological variability in this group can be found in Peng (in press). Characters that are functionally related to the pollination biology will be examined in more detail later in this paper. Some relevant diagnostic characters are summarized in Table 1.

HABIT

Plants of this section are all erect perennial herbs about 15–100 cm tall. They produce sprawling, leafy stolons along the surface of the ground in winter, although some species may also send out stolons in the summer while they are still flowering. In *Ludwigia suffruticosa*, however, underground rhizomes with scalelike leaves are also produced.

FLOWERS

The flowers have four sepals, four stamens, and a four-loculed ovary. Only *L. linearis*, *L. linifolia*, and *L. stricta*, all diploid, consistently have four yellow petals. The only other diploid species, *L. microcarpa*, and tetraploid, hexaploid, and octaploid species are apetalous. Vestigial petals are, however, occasionally present in normally apetalous species, especially *L. curtissii*. Loss of petals apparently represents the derived status, which is reflected in the fact that all polyploid species lack petals. Absence of petals does not in itself indicate autogamy, however, since nectary discs on top of the ovaries of all species produce various amounts of nectar that is fed on by insects. Furthermore, in the apetalous species—*L. alata*, *L. suffruticosa*, *L. pilosa*, and *L. sphaerocarpa*—the sepals are either cream-colored or yellow and are quite showy.

One aspect of the floral morphology of particular

TABLE 1. *Some characters of* Ludwigia *sect.* Microcarpium.

Taxon	Chromosome Number	Petals Present (+) or Absent (−)	Pollen Shed Singly (S) or as Tetrads (T)	Seed Surface Cell Shape and Orientation[a]
L. alata Elliott	$n = 24$	−	S	T
L. curtissii Chapman	$n = 32$	−[b]	S	T
L. glandulosa Walter				
subsp. *glandulosa*	$n = 16$	−	T	P
subsp. *brachycarpa* (Torrey & A. Gray) Peng	$n = 16$	−	T	T
L. lanceolata Elliott	$n = 16$	−	T	I
L. linearis Walter	$n = 8$	+	T	P or T[c]
L. linifolia Poiret	$n = 8$	+	T	I
L. microcarpa Michaux	$n = 8$	−	S	T
L. pilosa Walter	$n = 16$	−	T	I
L. polycarpa Short & Peter	$n = 16$	−	T	P
L. ravenii Peng	$n = 16$	−	T	T
L. simpsonii Chapman	$n = 24$	−	S	T
L. sphaerocarpa Elliott	$n = 16$	−	T	P and T[d]
L. stricta (Wright ex Griseb.) Wright	$n = 8$	+	T	I
L. suffruticosa Walter	$n = 16$	−	S	I

[a] Letter codes I, P, T indicate seeds with surface cells more or less isodiametric, in columns parallel elongate to the seed length, and transversely elongate to the seed length, respectively.

[b] Flowers with 1–3 (sometimes 4) vestigial petals sometimes observed.

[c] Seed surface cells elongate parallel to the seed length are predominantly exhibited by the subglabrous populations, whereas cells elongate transversely to the seed length are prevalent in more strigillose populations.

[d] Seed surface comprised of a mixture of cells both parallel and transversely elongate to the seed length. Sometimes the orientation of these columnar cells is irregular.

interest in *L. linearis* is the presence in the anthers of transverse septa composed of tapetum and parenchyma which divide the sporogenous tissue into packets (Eyde, 1977; Tobe & Raven, 1986). This character is shared only by an unrelated South American species, *L. latifolia* (Benth.) Hara, and five other genera of Onagraceae.

POLLEN

Pollen morphology of Onagraceae has been studied intensively by Ting (1966), Brown (1967), Skvarla et al. (1975, 1976, 1978), and Praglowski et al. (1983). Unique palynological features of the family include: protruding papillose apertures; mechanisms of tetrad and polyad cohesion; the fine structure of the exine; and viscin threads, which are extensions of the exine that tend to bind the grains together in masses. Pollen of sect. *Microcarpium* is quite uniform, being characterized by isopolar grains frequently with prominent colpal extensions and with a psilate exine (Praglowski et al., 1983). Most species shed pollen in tetrads, although in *L. alata*, *L. curtissii*, *L. microcarpa*, *L. simpsonii*, and *L. suffruticosa* grains are shed singly (in monads), a characterisic found sporadically in other species of *Ludwigia* (Praglowski et al., 1983). Pollen shed as monads is thought to be the ancestral condition in *Ludwigia* (Praglowski et al., 1983), but in view of the relationships suggested by Eyde (1977, 1978, 1981), the monad pollen in sect. *Microcarpium* was probably derived secondarily from tetrad pollen. In any event, this character, along with the seed-surface cell pattern, is useful in distinguishing closely related species like *L. alata* ($n = 24$; monads) and *L. lanceolata* ($n = 16$; tetrads), which have different chromosome numbers but are otherwise difficult to distinguish. It is also highly helpful in detecting natural hybrids when their suspected parents differ in this character.

CAPSULES

Fruit anatomy of *Ludwigia* has been studied by Eyde (1978), who reported that the fruit wall in *L. alata* is thickest in the placental radii, contrasting markedly with the fruit wall in sect. *Dantia* and in most other species of sect. *Microcarpium*. The shape, size, and vestiture of capsules are very

FIGURES 1–4. Photographs of seeds of some members of *Ludwigia* sect. *Microcarpium.*—1. *L. lanceolata,* Florida: Highlands Co., *Peng 4183* (MO).—2. *L. glandulosa* subsp. *glandulosa,* Florida: Santa Rosa Co., *Dille 412* (MO).—3. *L. alata,* Florida: Wakulla Co., *Morar 11* (FSU).—4. *L. sphaerocarpa,* South Carolina: Jasper Co., *Dille 348* (MO). Scale bar = 0.4 mm.

diverse within sect. *Microcarpium.* Capsule shape ranges from obpyramidal to subcylindrical, oblong-obovate, turbinate, or subglobose, and length ranges from 1 to 12 mm. In *L. alata* and *L. lanceolata,* the capsules are narrowly to markedly four-winged. The surface vestiture ranges from glabrous to strigillose or hirtellous. These characters are of paramount importance in distinguishing the species and detecting hybrids. Furthermore, the lengths of persistent bracteoles at or near the capsule base is often a diagnostic character in species delimitation and hybrid recognition.

SEEDS

The seeds are small, 0.4–0.7 mm long, and are cylindric, ellipsoid, reniform, or ovoid in shape. Their surface cells are diverse in shape and orientation (Eyde, 1978). They are either more or less isodiametric (Fig. 1) or are in parallel columns that are predominantly either elongate parallel (Fig. 2) or transversely elongate (Fig. 3) to the seed length, with minor variation on the two ends and areas near the raphe (Table 1). Like capsule morphology, seed-surface pattern provides excellent diagnostic characters for identifying the species and detecting natural hybrids.

In *L. sphaerocarpa* the seed-surface cells (Fig. 4) are less regularly oriented than in the other species. They are arranged in columns both transversely elongate and parallel to the seed length, with the former alignment often dominant in the central part of the seed. In this species, it is also not uncommon to have some seeds with variously oriented cells, a pattern that supports the suggestion of a hybrid origin for *L. sphaerocarpa* (see below).

REPRODUCTIVE BIOLOGY

Raven (1979) thoroughly reviewed reproductive biology of Onagraceae. Two-thirds (56 of 82) of all species in *Ludwigia* modally self-pollinate, and of the 26 that modally outcross, most accomplish that by separation of the stigma and anthers (Raven, 1979; Ramamoorthy & Zardini, 1987). There are no known instances in *Ludwigia* of protandry, protogyny, or male sterility, such as are found in other genera of Onagraceae (Raven, 1979). In nine species of *Ludwigia,* however, outcrossing is reinforced by genetic self-incompatibility, which occurs in about a quarter of all outcrossing species in the family (Raven, 1979).

All members of sect. *Microcarpium* are genetically self-compatible perennials that are mostly facultatively autogamous. Shortly after the flowers open in the morning, the anthers dehisce and the stigma becomes receptive. The anthers spread and are held away from the stigma shortly after anthesis, but in most species, petalous or apetalous, the anthers arch over a few hours later and attach firmly to the sticky stigma, thus effecting self-pollination.

Self-pollination, as well as cross-pollination, however, can also be achieved by insect vectors without having the anthers attached to the stigma mechanically. Bumble bees, honeybees, wasps, moths, and ants were observed visiting populations of *L.*

pilosa in the field (Peng, 1984). Raven (pers. comm.) also observed numerous wasps attracted by flowers of *L. sphaerocarpa*. The presence of plentiful confirmed natural hybrids (see below) suggests substantial cross-pollination by insects in the field.

CYTOLOGY

The first cytological study of a member of sect. *Microcarpium* was made by Gregory & Klein (1960) who, in the course of investigating the meiotic chromosomes of several onagraceous genera, recorded five counts for four species (cited as five species). These authors were the first to document polyploidy in the genus. One diploid population of *L. linifolia* that they studied was subsequently examined mitotically by Kurabayashi et al. (1962), who called attention to the fact that the chromosomes of *Ludwigia* and those of tribe Epilobieae are the smallest in Onagraceae, and also that they may differ conspicuously in size within a single genome. The proximal ends of the chromosome arms are heavily pycnotic and appear even in interphase nuclei as very distinct and definite chromocenters.

Based on a review of the literature and the study of 302 individuals from 282 naturally occurring populations from throughout the range of the genus, Raven & Tai (1979) presented a comprehensive chromosome number report for 38 of the 45 species of *Ludwigia* exclusive of sect. *Myrtocarpus* sensu lato. The basic chromosome number for the genus was established as $x = 8$ with no aneuploidy but extensive polyploidy. In my description of a new species of sect. *Microcarpium*, *L. ravenii* (Peng, 1984), I reported $2n = 32$ for this species, which has been misidentified as *L. pilosa* in the past. *Ludwigia stricta*, a Cuban endemic, is here reported as a diploid, with $n = 8$. Through these efforts, chromosome counts are now available for all taxa recognized in sect. *Microcarpium*. Section *Microcarpium* is shown to be a diverse polyploid complex, with four diploids, eight tetraploids, two hexaploids, and an octoploid. *Ludwigia alata*, *L. curtisii*, and *L. suffruticosa*, reported as having more than one chromosome number (Raven & Tai, 1979), will be discussed below.

In the present paper, I am reporting 78 more counts representing 75 populations of 14 species and one additional subspecies in sect. *Microcarpium* (Table 2). The chromosome number of *L. stricta* is here reported for the first time. These, along with 69 previously reported counts by Raven & Tai (1979), constitute our present knowledge of cytology of sect. *Microcarpium*. Because several taxonomic changes have been made, including a new combination (Peng, 1986), and because a new species, *L. ravenii*, has recently been recognized (Peng, 1984), I have checked the identification of voucher specimens cited by Raven & Tai (1979) and included these previously published counts in Table 2, using the currently accepted names. All counts are gametic except those indicated by "$2n =$ ". Original counts reported by Raven & Tai (1979) are indicated by asterisks; those reported by others are accompanied by references.

Raven & Tai (1979), while reporting two chromosome numbers for *L. alata*, stated that "Chromosome counts are now available for all taxa except . . . *L. stricta* . . . and, if it is distinct from *L. alata*, *L. lanceolata* Ell." Indeed, the last two species are similar in many aspects, especially in sharing obpyramidal capsules with winged corners, which is the key character in recognizing this species pair. However, upon examination of microscopic characters, such as seed surface architecture and the way pollen grains are shed, characters which previously have not been used by monographers (Munz, 1944, 1965), it has become clear that the two are distinct species. *Ludwigia alata* consistently sheds pollen singly (Praglowski et al., 1983) and has seed-surface cells in parallel columns transversely elongate to the seed length (Fig. 3), whereas *L. lanceolata* sheds pollen as tetrads (Praglowski et al., 1983) and invariably has nearly isodiametric seed-surface cells (Fig. 1). Their seeds differ in size and shape as well. Furthermore, these differences are correlated with chromosome number. Based on the 15 counts available (Table 2), *L. alata* is hexaploid with $n = 24$, whereas *L. lanceolata* is tetraploid with $n = 16$. The only exception is a specimen collected from Collier Co., Florida (*Raven 18672*), which Raven & Tai (1979) correctly identified as *L. alata* and reported to have $n = 16$. In order to verify this report, the same population was sampled again in 1980 (*Peng 4242*). Plants from this population yielded a count of $n = 24$. It seems likely, therefore, that the reported count of $n = 16$ resulted from confusion or interchange of samples. The questionable count has therefore been omitted from Table 2.

For *L. suffruticosa* there are 11 chromosome counts available at present, ten with $n = 16$, and one with $n = 24$ for a collection (*Raven 18651*) from Hillsborough Co., Florida (Raven & Tai, 1979). Four other populational counts obtained from the same county consistently show $n = 16$. It is possible that plants with $n = 24$ have arisen

TABLE 2. *Chromosome numbers in* Ludwigia *sect.* Microcarpium, *with voucher information. Voucher specimens for original counts are at the Missouri Botanical Garden (MO); those of earlier reports, identified by an asterisk, are indicated in Raven & Tai (1979).*

Ludwigia alata Elliott ($n = 24$)

U.S.A. FLORIDA: Collier Co., *Peng 4242* ($2n = 48$), *Peng 4267* ($2n = 48$); Franklin Co., *Godfrey 70575, Peng 4344*; Levy Co., *Dille 392*; Martin Co., *Peng 4203* ($n = 24$; $2n = 48$); Wakulla Co., *Raven 18608**. GEORGIA: Charlton Co., nr. Cravens Hammock, *Raven in 1974** ($2n = 48$). SOUTH CAROLINA: Horrey Co., *Raven 18719**.

Ludwigia curtissii Chapman ($n = 32$)

BAHAMA ISLANDS. Grand Bahama Island, *Correll & Popenoe 51315.*

U.S.A. FLORIDA: Collier Co., *Peng 4231, 4276, 4283*; Dade Co., *Godfrey 63396** ($2n = 64$); Franklin Co., *Godfrey 71148*; Hendry Co., *Peng 4285, 4287*; Hillsborough Co., *Dille 435*; Martin Co., *Peng 4199*; Monroe Co., *Godfrey 63519** ($2n = 64$); Palm Beach Co., *Popenoe 1962*; Sarasota Co., *Raven 18662** ($2n = 64$).

Ludwigia glandulosa Walter subsp. *glandulosa* ($n = 16$)

U.S.A. ALABAMA: Macon Co., *Raven 18562**. ARKANSAS: *Demaree 46645** (*Raven 65-42*, $2n = 32$). FLORIDA: Jefferson Co., *Raven 18617**; Leon Co., *Godfrey* (Gregory & Klein, 1960); Madison Co., *Raven 18628**; Santa Rosa Co., *Dille 412*. GEORGIA: Emanuel Co., *Peng 4013* ($2n = 32$). LOUISIANA: St. Tammany Parish, *Raven 18576*, 18577**. MISSISSIPPI: Jones Co., *Raven 18569**. NORTH CAROLINA: Columbus Co., *Broome 865, 897* TEXAS: Liberty Co., *Raven 19427**.

Ludwigia glandulosa subsp. *brachycarpa* (Torrey & A. Gray) Peng ($n = 16$)

U.S.A. LOUISIANA: Cameron Parish, *Peng 4367*. TEXAS: Fort Bend Co., *Raven 19398** (as *L. glandulosa*), *Raven 19405** (as *L. glandulosa*).

Ludwigia lanceolata Elliott ($n = 16$)

U.S.A. FLORIDA: Highlands Co., *Dille 370* ($2n = 32$), *Peng 4183, 4193, Raven 18681** (as *L. alata*), *Raven 18684** (as *L. alata*), *Raven 19727** (as *Raven 17927*, typographic error, $2n = 32$, as *L. alata*).

Ludwigia linearis Walter ($n = 8$)

U.S.A. ALABAMA: Baldwin Co., *Raven 18590**. ARKANSAS: *Demaree 46898** (*Raven 65-43*, $2n = 16$). FLORIDA: Madison Co., *Raven 18627**. GEORGIA: Emanuel Co., *Peng 4023* ($2n = 16$). LOUISIANA: St. Tammany Parish, *Dille 420, Raven 18579**. MISSISSIPPI: Jackson Co., *Raven 18585**. NORTH CAROLINA: Cumberland Co., *Lloyd 1026**; Johnston Co., *Lloyd 1121**. SOUTH CAROLINA: Horry Co., *Raven 18721**; Jasper Co., *Dille 350, Peng 3935* ($2n = 16$).

Ludwigia linifolia Poiret ($n = 8$)

MEXICO. TABASCO: Municipio Huimanguillo, *Cowan 2632* (also $2n = 16$), *Cowan 3111.*

U.S.A. FLORIDA: Franklin Co., *Peng 4343*; Hillsborough Co., *Dille 427*; Okaloosa Co., *Raven 18593**; Wakulla Co., *Godfrey 77091* ($2n = 16$). MISSISSIPPI: Hancock Co., *Raven 18581**; Jackson Co., *Demaree 37879* ($n = 8$, Gregory & Klein, 1960; $2n = 16$, Kurabayashi et al., 1962).

TABLE 2. *Continued.*

Ludwigia microcarpa Michaux ($n = 8$)

U.S.A. FLORIDA: Charlotte Co., *Peng 4294*; Clay Co., *Dille 359, Raven 18692**; Franklin Co., *Peng 4348*; Hillsborough Co., *Raven 18641**; Jackson Co., *Godfrey 77093*; Wakulla Co., *Raven 18601*, 18610**. NORTH CAROLINA: Jones Co., *Peng 3800.*

Ludwigia pilosa Walter ($n = 16$)

U.S.A. FLORIDA: Franklin Co., *Peng 4345*; Leon Co., *Kral in 1963** (*Raven 65-44*, $2n = 32$); Madison Co., *Raven 18625**; Walton Co., *Raven 18594**. GEORGIA: Camden Co., *Raven 18701**; Emanuel Co., *Peng 4025* ($2n = 32$). MISSISSIPPI: Hancock Co., *Dille 419* ($2n = 32$), *Raven 18580**; Jackson Co., *Raven 18583**; Jones Co., *Raven 18568**. SOUTH CAROLINA: Colleton Co., *Raven 18717**; Horry Co., *Dille 342*; Jasper Co., *Raven 18712**.

Ludwigia polycarpa Short & Peter ($n = 16$)

U.S.A. MASSACHUSETTS: Middlesex Co., *Raven 16514**. MICHIGAN: Washtenaw Co., *Raven 16523**. MISSOURI: Franklin Co., *Dille 328* ($2n = 32$), *Dille 436* ($2n = 32$); Lincoln Co., *Dille 443* (also $2n = 32$).

Ludwigia ravenii Peng ($n = 16$)

U.S.A. FLORIDA: Clay Co., *Raven 18690** (as *Raven 19690*, typographic error; as *L. pilosa*). SOUTH CAROLINA: Berkeley Co., *Peng 4402* ($2n = 32$, Peng, 1984).

Ludwigia simpsonii Chapman ($n = 24$)

U.S.A. FLORIDA: Charlotte Co., *Peng 4293*; Collier Co., *Dille 378, Munz & Gregory 23476* (Gregory & Klein, 1960, as *L. curtissii*), *Peng 4232, 4234, 4246, 4248, 4254, 4261, 4262, 4268, 4271*; Hillsborough Co., *Raven 18649** (also $2n = 48$, as *L. curtissii*); Lee Co., *Peng 4289*; Martin Co., *Munz & Gregory 23481* (Gregory & Klein, 1960); Sarasota Co., *Dille 383, Peng 4313, Raven 18664** (as *Raven 18640*, typographic error).

Ludwigia sphaerocarpa Elliott ($n = 16$)

U.S.A. Without definite locality, *Monoson 55* (Gregory & Klein, 1960). FLORIDA: Franklin Co., *Dille 402*; Madison Co., *Raven 18626*, 18630**; Taylor Co., *Raven 18620**; Wakulla Co., *Dille 401, Peng 4339*. INDIANA: Starke Co., *Raven 16525**. MASSACHUSETTS: Plymouth Co., *Raven 16516**. SOUTH CAROLINA: Jasper Co., *Dille 348* ($2n = 32$).

Ludwiga stricta (Wright ex Griseb.) Wright ($n = 8$)[a]

CUBA. *A. Leiva s.n. in 1982* ($2n = 16$).

Ludwigia suffruticosa Walter ($n = 16$)

U.S.A. FLORIDA: Glades Co., *Raven 18678** ($2n = 32$); Hillsborough Co., *Dille 423, 424, 434, Peng 4327*; Lake Co., *Raven 18637*; Leon Co., *Dille 421, Raven 18595** (as *Raven 18585*, typographic error); Polk Co., *Lakela 24806** (*Raven 19704*, $2n = 32$); Taylor Co., *Raven 18619**.

[a] Chromosome number here determined for the first time.

directly from tetraploids by fusion of an unreduced gamete from one parent with a normal gamete from the other, as Raven & Tai (1979) postulated. Meiosis was normal (Raven & Tai, 1979), and pollen from the voucher specimen was fully viable as judged by staining results. The count of $n = 24$ should be reconfirmed and investigated further if additional individuals are located; it is omitted from Table 2.

Ludwigia curtisii is another species Raven & Tai (1979) reported as having two chromosome numbers. They considered this species, along with *L. simpsonii* and *L. spathulifolia,* to comprise a single species complex, within which diagnostic characters such as capsule size and leaf shape (Munz, 1944, 1965) were not correlated with chromosome numbers. The present study, however, indicates that *L. simpsonii* is specifically distinct from *L. curtissii* and that *L. spathulifolia* should be treated as a variant of *L. curtissii* with slightly larger capsules.

In addition to being high polyploids (hexaploid and octoploid), plants of this complex are unique among species of sect. *Microcarpium* in having the capsules split along four longitudinal lines opposite the loculi at maturity (Peng & Tobe, 1987). Capsules from other species in sect. *Microcarpium* dehisce either by separation of the walls from the indurate nectary disc (Munz, 1944, 1965; Raven, 1963) or by irregular disintegratoin of the fruit wall (Peng & Tobe, 1987). Technical characters, such as the way pollen grains are shed and seed-surface cell shape and orientation, are not useful in distinguishing these taxa; they have both pollen grains shed singly and seed-surface cells in parallel columns transversely elongate to the seed length. They have turbinate or slightly broadly turbinate capsules 1.5–4.5 mm long and are extremely variable in cauline leaf shape, which ranges from obovate to spatulate-oblanceolate, narrowly oblanceolate, or sublinear. No consistent correlation was found between leaf shape and capsule size. When plants of distinct leaf shape and capsule size were collected and cultivated in an experimental greenhouse, the leaf shapes tended to converge and become spatulate-oblanceolate, but the capsule sizes remained constant.

Based on counts from 30 populations, including seven reported by Raven & Tai (1979), differences in chromosome number are indeed correlated with mature capsule size. All plants with $n = 24$ have mature capsules 1.5–2(–2.5) mm long, while all plants with $n = 32$ have mature capsules (2–)2.5–4(–4.5) mm long. The morphology of plants with $n = 24$ fits very closely the description of *L. simpsonii,* whereas the morphology of plants with $n = 32$ clearly corresponds to that of *L. curtissii* (including *L. spathulifolia*).

Compared with plants with $n = 32$, plants with $n = 24$ have generally diminutive floral parts: shorter bracteoles, sepals, stamens, and ovaries. Further, plants with $n = 24$ rarely exhibit vestigial petals, whereas those with $n = 32$ frequently have 1–3 caducous petals on at least some flowers. Vegetatively, plants with $n = 24$ are erect to ascending, or sometimes are prostrate and rooting at the nodes. They are pale green with slender stems often much branched from below or above. The leaves are sometimes quite small, tending to be opposite or subopposite at the lower nodes. By contrast, plants with $n = 32$ are usually dark green or sometimes purplish, have stouter erect stems branched above, and leaves usually alternate throughout.

Although *L. simpsonii* and *L. curtissii* frequently are sympatric, they are ecologically distinct and seldom actually intermix. Plants with $n = 24$ tend to grow along roadsides with other weeds in moist sandy soil. Plants with $n = 32$ grow far from roadsides in black muck and often in deep standing water, often mixed with tall grasses or sedges.

In view of this evidence, *L. simpsonii* is considered a hexaploid with $n = 24$, and *L. curtissii* (including *L. spathulifolia*) an octoploid with $n = 32$.

A collection from Clay Co., Florida (*Raven 18690*) was originally identified as *L. pilosa* and determined to be tetraploid with $n = 16$ (Raven & Tai, 1979). A more detailed morphological study reveals that this is best treated as *L. ravenii* (Peng, 1984). Nearly all previous collections of *L. ravenii* were initially identified as *L. pilosa* by their respective collectors: the two species are similar in being densely hirtellous, a distinct character not shared by any other member of sect. *Microcarpium. Ludwigia ravenii* may be distinguished readily from *L. pilosa* by having oblong-obovoid capsules and seed-surface cells predominantly in parallel columns transversely elongate to the seed length, and by having shorter sepals, filaments, and styles. Furthermore, unlike *L. pilosa,* which is nearly always hirtellous on the lower half of the style and between the lobes of the nectary disk, all 28 collections of *L. ravenii* are completely glabrous in these areas.

Among the voucher specimens for *L. glabrous* ($n = 16$, Raven & Tai, 1979), a collection from Fort Bend Co., Texas (*Raven 19398*), with short capsules and seed-surface cells in parallel columns transversely elongate to the seed length, has been placed under subsp. *brachycarpa* in Table 2. Another collection (*Raven 19405*) from the same county is preserved in two duplicate specimen sheets: one of them (FLAS) belongs to subsp.

TABLE 3. *Strains of* Ludwigia *used in artificial hybridization experiments.*

L. alata (ALA)[a]
- (a) Franklin Co., Florida, *Godfrey 70575.*
- (b) Levy Co., Florida, *Dille 392.*

L. curtissii (CUR)
- (a) Hillsborough Co., Florida, *Dille 435.*
- (b) Martin Co., Florida, *Peng 4199.*
- (c) Collier Co., Florida, *Peng 4231.*
- (d) Collier Co., Florida, *Peng 4283.*
- (e) Palm Beach Co., Florida, *Popenoe 1962.*
- (f) Franklin Co., Florida, *Godfrey 71148.*

L. glandulosa subsp. *glandulosa* (GLA)
- (a) Santa Rosa Co., Florida, *Dille 412.*
- (b) Emanuel Co., Georgia, *Peng 4013.*
- (c) Columbus Co., North Carolina, *Broome 897.*
- (d) Columbus Co., North Carolina, *Broome 865.*

L. glandulosa subsp. *brachycarpa* (BRA)
- (a) Cameron Parish, Louisiana, *Peng 4367.*

L. lanceolata (LAN)
- (a) Highlands Co., Florida, *Dille 370.*
- (b) Highlands Co., Florida, *Peng 4193.*

L. linearis (LIE)
- (a) Jasper Co., South Carolina, *Dille 350.*
- (b) St. Tammany Parish, Louisiana, *Dille 420.*
- (c) Jasper Co., South Carolina, *Peng 3935.*
- (d) Emanuel Co., Georgia, *Peng 4023.*

L. linifolia (LIF)
- (a) Municipio Huimanguillo, Tabasco, Mexico, *Cowan 2632.*
- (b) Hillsborough Co., Florida, *Dille 427.*
- (c) Wakulla Co., Florida, *Godfrey 77091.*
- (d) Franklin Co., Florida, *Peng 4343.*

L. microcarpa (MIC)
- (a) Clay Co., Florida, *Dille 359.*
- (b) Jackson Co., Florida, *Godfrey 77093.*
- (c) Jones Co., North Carolina, *Peng 3800.*
- (d) Franklin Co., Florida, *Peng 4348.*

L. pilosa (PIL)
- (a) Horry Co., South Carolina, *Dille 342.*
- (b) Hancock Co., Mississippi, *Dille 419.*
- (c) Emanuel Co., Georgia, *Peng 4025.*

L. polycarpa (POL)
- (a) Franklin Co., Missouri, *Dille 328.*
- (b) Franklin Co., Missouri, *Dille 436.*
- (c) Lincoln Co., Missouri, *Dille 443.*

L. simpsonii (SIM)
- (a) Collier Co., Florida, *Dille 378.*
- (b) Sarasota Co., Florida, *Dille 383.*
- (c) Collier Co., Florida, *Peng 4234.*
- (d) Collier Co., Florida, *Peng 4246.*
- (e) Sarasota Co., Florida, *Peng 4313.*

L. sphaerocarpa (SPH)
- (a) Jasper Co., South Carolina, *Dille 348.*
- (b) Wakulla Co., Florida, *Dille 401.*
- (c) Wakulla Co., Florida, *Dille 402.*

TABLE 3. *Continued.*

L suffruticosa (SUF)
- (a) Hillsborough Co., Florida, *Dille 423.*
- (b) Hillsborough Co., Florida, *Dille 424.*
- (c) Hillsborough Co., Florida, *Dille 434.*

[a] Three-letter abbreviations are used for each taxon in Tables 3–14 and Figures 5, 6, 21, 22.

brachycarpa; the other (DS), however, is a mixture of two plants of subsp. *L. glandulosa* with one of subsp. *brachycarpa*. This is arbitrarily placed under subsp. *brachycarpa* in Table 2; both taxa have the same chromosome number.

The following collections counted by Raven & Tai (1979) as $n = 16$ are considered to represent hybrid populations of *L. pilosa* × *L. sphaerocarpa* and have been excluded from Table 2: Florida: Highlands Co., *Raven 18683* (as *L. pilosa*); Clay Co., *Raven 18680* (as *L. sphaerocarpa*); Columbia Co., *Raven 18634* (as *L. sphaerocarpa*). South Carolina: Beaufort Co., *Raven 18716* (as *L. sphaerocarpa*); Colleton Co., *Raven 18718* (as *L. sphaerocarpa*).

EXPERIMENTAL HYBRIDIZATION

An extensive artificial hybridization program was carried out among members of sect. *Microcarpium* with the following objectives: (1) to determine chromosome homologies and relationships of taxa with the same and with different ploidy levels; (2) to study whether chromosome repatterning has played a role in the diversification of the species; (3) to study the genetic isolating mechanisms that may have permitted preservation of the genetic integrity of the taxa; and (4) to examine the variation pattern generated by hybridization, which is useful in studying natural hybrid populations.

Over 1,000 reciprocal crosses have been made among the 12 species and one additional subspecies of sect. *Microcarpium*. *Ludwigia ravenii* and *L. stricta* were not included because living plants were not available at the time these studies were conducted. Most of the attempted crosses resulted in seed set. Some of the failures probably resulted from damage by the sharp forceps used to emasculate the flowers and to transfer the pollen to these usually small-flowered plants. In these cases, additional attempts were made using either the same or different parental strains, and seed set was usually obtained. The only consistent failure occurred in some crosses involving *L. microcarpa* as pollen parent. This species is the smallest in

TABLE 4. *Percentages of stainable pollen in hybrids between species of* Ludwigia *sect.* Microcarpium. Ludwigia pilosa *group, diploid group, and* L. curtissii *complex are separated by lines.*

	♂												
♂	ALA	BRA	GLA	LAN	PIL	POL	SPH	SUF	LIE	LIF	MIC	SIM	CUR
ALA *n* = 24	·	·	47	62	52	53	71	63	1	0	·	·	·
BRA *n* = 16	·	·	97	56	·	67	·	·	·	·	·	·	·
GLA *n* = 16	46	96	·	·	·	·	·	62	2	·	0	3	·
LAN *n* = 16	64	·	·	·	96	83	95	95	·	·	0	11	4
PIL *n* = 16	43	87	84	75	·	·	98	78	·	0	·	·	6
POL *n* = 16	43	·	·	83	83	·	·	·	·	0	·	·	25
SPH *n* = 16	47	·	·	87	·	·	·	·	1	·	·	15	17
SUF *n* = 16	61	·	·	·	·	·	·	·	·	·	·	·	·
LIE *n* = 8	·	·	·	·	·	0	1	·	·	48	·	·	·
LIF *n* = 8	·	·	0	1	·	·	·	·	47	·	·	·	·
MIC *n* = 8	15	·	2	·	·	13	4	·	0	6	·	9	2
SIM *n* = 24	20	·	·	·	·	·	·	·	·	·	·	·	81
CUR *n* = 32	·	·	5	·	·	32	31	9	0	10	2	89	·

stature and in flower size and has the shortest style and smallest pollen grains among members of sect. *Microcarpium*. The few ovulate parents that failed to set seed in these crosses were of taxa with styles 3–6 times longer than those of *L. microcarpa*. Rather than genetic disharmony, it is likely that these failures were due to the improbability of small grains containing sufficient food reserves to support pollen tube growth through long styles (review in Lee, 1978), since the reciprocal crosses using shorter-styled *L. microcarpa* as ovule parent invariably set seeds.

As all plants in sect. *Microcarpium* are self-compatible and modally autogamous, self-pollination sometimes interfered with the hybridizations, especially in crosses involving a small-flowered ovulate parent. Part of the seed set may thus reflect a small to moderate amount of self-pollination despite regular emasculation. The seedlings resulting from self-pollination, however, can almost always be distinguished from those resulting from hybridization by the leaf color or shape, or even by growth rate, when both types of seedlings were grown together.

The strains utilized in the crossing experiments are presented in Table 3. The results of the artificial hybridizations are summarized in Figure 5 and indicate three more or less interfertile groups in sect. *Microcarpium*: (1) all the tetraploid taxa plus *L. alata*, a hexaploid; (2) *L. linearis* and *L. linifolia*, both diploid species; and (3) the *L. curtissii* complex (hexa- and octoploids). Data on the percentages of stainable pollen in hybrids (Table 4) support this interpretation.

The crossing results will be discussed in the following order: (I) the diploid group (including *L. linearis*, *L. linifolia*, and *L. microcarpa*); (II) the *L. pilosa* group (including all tetraploids and a single hexaploid, *L. alata*); (III) the *L. curtissii* complex (including *L. curtissii* and *L. simpsonii*); (IV) crosses between the diploid group and the *L. pilosa* group; (V) crosses between the diploid group

♀ \ ♂	ALA	BRA	GLA	LAN	PIL	POL	SPH	SUF	LIE	LIF	MIC	SIM	CUR
ALA n=24			◉	◉	◉	◉	◉	◉	○	○	—	X	X
BRA n=16			●	◉		◉			X	X		X	
GLA n=16	◉	●		◉	•	●	•	◉	○	X	○	⊙	
LAN n=16	◉	•	•		●	●	●	●	X	X	○	○	○
PIL n=16	◉	●	●	●		•	●	●	X	○	—		⊙
POL n=16	◉			●	●		•	•	X	○			⊙
SPH n=16	◉		•	●	•	•		•	○	X	X		⊙
SUF n=16	◉		•	•	•	•	•		X	X	—		
LIE n= 8	X			X	X	○	○	X		◉	—		○
LIF n= 8	X	X	○	○	X	X	X	X	◉		—	X	X
MIC n= 8	○		○	X	X	○	○		○	○		⊙	○
SIM n=24	⊙			X	X			X	○	⊙	⊙		●
CUR n=32		X	⊙	X	X	⊙	⊙	○	○	X		●	

● F_1 hybrids producing abundant seeds (usually >80% of potental number)

◉ F_1 hybrids producing fewer seeds (e.g., often about 1/2 of potential number)

⊙ F_1 hybrids producing very few seeds (< 5% of potential number)

○ F_1 hybrids flowering, but setting no seeds

X F_1 hybrid seed formed failed to germinate or died soon after germination

• Hybridization resulted in abundant seed set , but seeds not sown

— Hybridization failed to result in seed set

FIGURE 5. Summary of artificial hybridization between species of *Ludwigia* sect. *Microcarpium. Ludwigia pilosa* group, diploid group, and *L. curtissii* complex are separated by lines.

TABLE 5. *Meiotic configurations and pollen stainability in interspecific* Ludwigia *diploid hybrids.*

Hybrid Combination	Modal Meiotic Configuration Observed	Number of Cells with Modal Configuration/ Total Number of Cells Examined	Pollen Stainabilty (%)
LIE d × LIF c	1IV + (4–6)II + (4–0)I	6/20	48
LIF c × LIE d	1IV + (5–6)II + (2–0)I	5/9	47
MIC b × LIE c	(0–1)II + (16–14)I	5/10	0
MIC b × LIF c	(2–3)II + (12–10)I	4/4	6

and the *L. curtissii* complex; and (VI) crosses between the *L. pilosa* group and the *L. curtissii* complex.

HYBRIDS WITHIN THE DIPLOID GROUP (*LUDWIGIA LINEARIS, L. LINIFOLIA,* AND *L. MICROCARPA*)

These interspecific crosses resulted in significant seed set except for a few cases in which *L. microcarpa* was pollen donor. As suggested earlier, these failures were probably due to the inability of the small pollen grains of *L. microcarpa* to grow through the long styles of *L. linearis* and *L. linifolia*. Four hybrid combinations were obtained (Table 5) and grown to flowering.

Meiotic analysis and pollen stainability

Meiosis was normal in the examined natural populations of the diploid parental strains. The chromosomes regularly formed eight bivalents, with no univalents or multivalents observed. In the reciprocal crosses between *L. linearis* and *L. linifolia*, meiotic configurations ranged from eight bivalents to four bivalents and eight univalents; a ring or chain quadrivalent was observed in 11 of the 29 cells examined. In a single cell, a hexavalent was observed; trivalents were observed occasionally. In the translocation heterozygote, chiasma frequency and quadrivalent frequency are interdependent to a certain extent, as McCollum (1958) suggested. If chiasmata are formed in each of the four paired arms of the cross-shaped configuration at pachytene, then the four chromosomes form a ring at metaphase I; progressively lower numbers of chiasmata will give a chain of three plus a univalent, two bivalents, or four univalents. The observation of the quadrivalent in meiosis of the diploid hybrid indicates that the strains of *L. linearis* and *L. linifolia* hybridized differ by at least one reciprocal translocation, which may help to account for the inviability in about half of the pollen in the hybrid. This is the first demonstration of a reciprocal translocation in *Ludwigia*. The interpretation of the single cell recorded as having a hexavalent is uncertain, and the observation should be confirmed.

The reciprocal hybrids between *L. linearis* and *L. linifolia* produced many aborted seeds. However, *L. linearis* has the highest number of seeds per capsule (about 700) among species of sect. *Microcarpium*. F_1 plants resulting from reciprocal crosses involving *L. linearis* and *L. linifolia* were also very fecund, and their output of viable seeds per capsule was therefore quite substantial, although reduced. An F_2 family of nearly 100 plants was grown for each of the reciprocal crosses. Some 25% of these plants died in the seedling stage, and another 25% were very weak. About 10–15% of the F_2s flowered. Pollen stainability of the seven F_2 plants examined ranged from 1 to 52% (1, 7, 10, 15, 22, 32, 52%). None of the F_2s that survived were as vigorous and floriferous as the F_1 plants.

In diakinesis and first metaphase of *L. microcarpa* × *L. linearis* and *L. microcarpa* × *L. linifolia* univalents predominated. The bivalents ranged from 0 to 3, the rest being univalents. Heteromorphic bivalents were observed in at least a few cells. The paired chromosomes were sometimes held together by a matrix connection instead of by a chiasma. However, a maximum of three true bivalents, held together by chiasmata, were observed in a few cells. The few paired chromosomes did not always line up in the equatorial plane, more often being randomly placed like univalents. Micronuclei were present at the tetrad stage. Pollen grains were shed both singly and as (loose) tetrads. Their sizes varied. The stainability was 0% in *L. microcarpa* × *L. linearis* and 6% in *L. microcarpa* × *L. linifolia*, which seemed to accord with the fact that no or one bivalent(s) were observed in the former and two or three were observed in the latter.

Morphology of the hybrids

Reciprocal hybrids between *L. linearis* and *L. linifolia* resembled each other morphologically. They were vigorous and floriferous. In overall habit and capsule shape they were more similar to *L. linearis*. In floral details, however, the hybrids were intermediate between the parents. For example, the divided sporogenous tissue in the anthers, which is characteristic of *L. linearis*, also appeared in the hybrids, although the packets were fewer and shallower. Seed set was variable from capsule to capsule, but was generally fairly high.

Ludwigia microcarpa, a small, highly autogamous herb with minute, apetalous flowers and obovate-spatulate to spatulate leaves, differs from both *L. linearis* and *L. linifolia* in nearly every morphological aspect. Hybrid combinations between *L. microcarpa* and *L. linearis* and those involving *L. microcarpa* and *L. linifolia* were vigorous and morphologically intermediate between the parents. Both produced small flowers with four yellow petals and reached the maximum height of the taller parents. Hybrids between *L. microcarpa* and *L. linearis* were about 70 cm tall and had very narrowly elliptic leaves, whereas those between *L. microcarpa* and *L. linifolia* were about 35 cm tall and had oblanceolate to narrowly obovate leaves. Neither hybrid set fruit—the ovaries simply withered.

HYBRIDS WITHIN THE *LUDWIGIA PILOSA* GROUP

Parental strains of this group consisted of one hexaploid species, *L. alata* ($n = 24$), and seven tetraploid entities ($n = 16$). All interspecific reciprocal crosses attempted invariably yielded abundant seed. As many hybrid combinations as greenhouse space and time allowed were grown (Fig. 5; Tables 6, 7). Hybrid seedlings were nearly always vigorous. Occasionally a few plants assumed stunted growth or exhibited some morphological abnormality. These are considered to represent chance combinations of disharmonious genotypes from the two parents. For each hybrid combination, only the healthy F_1 individuals were grown to maturity for study.

Meiotic analysis and pollen stainability

Meiosis was normal in all parental strains of the tetraploid species as well as in *L. alata*, the only hexaploid in this group. From diakinesis to metaphase I, 16 and 24 bivalents, respectively, were invariably observed in these taxa; no univalents or multivalents were detected. Disjunction and microspore formation also appeared to be normal. The pollen stainability of the parental strains was 95–100%.

As all the hybrids between tetraploid taxa exhibited a similar pattern of meiotic behavior, the data for these are pooled and discussed together. Hybrids between the tetraploid taxa and *Ludwigia alata* (hexaploid) were likewise similar with respect to meiotic behavior; these data will also be treated as a group.

(1) Hybrids between tetraploid taxa (Table 6)

In very many cases, meiosis in these hybrids appeared normal, exhibiting 16 bivalents from diakinesis to metaphase I. The majority of cells exhibited complete chromosome pairing, but 2–6 (very rarely 8–10) univalents were often encountered in prepared slides. In many cases these univalents appeared to have resulted from precocious separation of the bivalents (probably because no chiasmata developed). This was suggested by their shapes and nonrandom locations on the metaphase plates. Nevertheless, meiotic anaphase I was generally regular, and no micronuclei were observed in the tetrad stage. Occasionally bivalents had a slightly stretched or attenuated appearance. This stretching may result from a failure of terminal chiasmata to disjoin properly (Grant, 1952). A few cells with 2–3 bivalents associated side by side were seen. This association is apparently not due to chiasmata but rather to the "sticky" matrix bands typical of the "pseudobivalents" in hybrids of other taxa (e.g., *Bromus*, Walters, 1954).

Despite the few meiotic irregularities observed, the pollen stainability of the tetraploid hybrids was generally high (Tables 4, 6). Of the 17 hybrid combinations examined, 6 had estimated pollen stainabilities of 95–98%. With a few exceptions, most other hybrids exhibited 75–87% stainable pollen.

Two hybrids failed to flower in the closed greenhouse: *L. glandulosa* subsp. *brachycarpa* × *L. lanceolata* and *L. sphaerocarpa* × *L. glandulosa* subsp. *glandulosa*. These were then moved to an open, netted greenhouse. Here, the hybrids between *L. sphaerocarpa* × *L. glandulosa* subsp. *glandulosa* produced a single flower; its pollen stainability was not studied. The hybrid *L. glandulosa* subsp. *brachycarpa* × *L. lanceolata* was very vigorous and produced many flowers two

TABLE 6. *Meiotic configurations and pollen stainability in interspecific* Ludwigia *tetraploid hybrids.*

Hybrid Combination	Modal Meiotic Configuration Observed	Number of Cells with Modal Configuration/ Total Number of Cells Examined	Pollen Stainability (%)
BRA × GLA b	16II	10/10	97
BRA × LAN a	15II + 2I	4/12	56
BRA × POL c			67
GLA b × BRA	16II	15/25	96
GLA d × POL b	Fruiting specimen showed plump capsules with abundant seeds.		
GLA b × SUF b			62
LAN a × PIL a	16II	12/13	96
LAN a × POL c	16II	14/19	83
LAN a × SPH b	16II	9/13	95
LAN a × SUF a	14II + 4I	4/6	95
PIL c × BRA	16II	5/5	87
PIL b × GLA d	(14–16)II + (4–0)I	5/6	84
PIL b × LAN a	16II	14/15	75
PIL b × SPH b	15II + 2I	5/7	98
PIL b × SUF a			78
POL c × LAN a			83
POL c × PIL b			83
POL c × SPH b	Fruiting specimen showed plump capsules with abundant seeds.		
SPH b × GLA c	Fruiting specimen showed plump capsules with abundant seeds.		
SPH c × LAN a			87

months after transfer. Its pollen stainability was estimated to be only 56%, significantly lower than one would expect, since this plant has as much chromosome pairing (13–16 pairs) as other hybrids that exhibited 75–98% stainable pollen.

Jones (1976) noted that environmental factors may exert considerable influence on production of presumably normal stainable pollen. She found that plants of some *Aster* species moved out from the greenhouse to the field consistently yielded significantly reduced fractions of normal pollen. Whether this is the case for *L. glandulosa* subsp. *brachycarpa* × *L. lanceolata* remains to be confirmed by growing them in a closed experimental greenhouse. It is also possible that the low observed pollen stainability is the result either of genic interaction between the parents or of the pronounced meiotic irregularities discussed earlier. However, the present sample size is not large enough to establish that hybrids from the cross *L. glandulosa* subsp. *brachycarpa* × *L. lanceolata* indeed exhibit a higher degree of meiotic irregularity than other hybrids.

Reciprocal hybrids between tetraploid taxa generally exhibited similar values for pollen stainability (Tables 4, 6). Different values were obtained for the reciprocal crosses between *L. lanceolata* and *L. pilosa* (96% and 75%), but different strains of *L. pilosa* were used in these crosses.

These data suggest that the tetraploid species in sect. *Microcarpium* in general have high chromosome homology, and complete pairing is frequently observed in almost all interspecific hybrids. The few meiotic irregularities occasionally observed (a few univalents, slightly attenuated bivalents, and sticky bivalents) have little effect on the hybrid fertility (as estimated by pollen stainability). This was further substantiated by abundant seed sets of all the hybrids.

A small family of vigorous F_2 individuals was reared for two randomly selected hybrids: *L. pilosa* × *L. glandulosa* subsp. *glandulosa* (17 plants) and *L. lanceolata* × *L. suffruticosa* (19 plants). These populations were small, owing to the limited space and time available to handle them. They generally received less care than the F_1s. Therefore, the several plants that were weak or died may not necessarily reflect F_2 weakness or breakdown. For example, the organic potting soil that was used was easily spoiled since all pots were continuously kept in standing water and were sprayed with insecticide periodically. Had the potting soil not been changed as needed, the plants might have remained vegetative, become weak, or even died.

TABLE 7. *Meiotic configurations and pollen stainability in hybrids resulting from crosses between tetraploid* Ludwigia *species and the hexaploid species (*L. alata*).*

Hybrid Combination	Modal Meiotic Configuration Observed	Number of Cells with Modal Configuration/ Total Number of Cells Examined	Pollen Stainability (%)
ALA a × GLA c	16II + 8I	10/16	47
GLA d × ALA a	(15–16)II + (10–8)I	7/9	46
ALA a × LAN a	16II + 8I	15/29	62
LAN a × ALA a	(15–16)II + (10–8)I	4/4	64
ALA a × PIL a	(12–16)II + (16–8)I	10/10	52
PIL a × ALA a	(15–16)II + (10–8)I	6/9	43
ALA a × POL a			50
ALA a × POL b			56
POL a × ALA a	(11–15)II + (18–10)I	8/11	43
ALA a × SPH b	16II + 8I	13/22	71
SPH a × ALA a	(13–16)II + (14–8)I	2/7	47
ALA a × SUF a	16II + 8I	5/6	63
SUF c × ALA a	(14–16)II + (12–8)I	7/7	61

All F_2s that did grow were vigorous. In the cross *L. pilosa* × *L. glandulosa* subsp. *glandulosa*, the only individual that flowered was quite unlike either the parents or the F_1s in morphology but had 91% stainable pollen. In *L. lanceolata* × *L. suffruticosa*, about 10 F_2 individuals flowered, some of which resembled the intermediate F_1s, whereas others were similar to *L. lanceolata*. Pollen stainability was quite different from plant to plant, ranging from 1% to 97% (1, 12, 51, 63, 74, 97%) in the six plants studied. Meiosis of an F_2 individual (pollen stainability not assessed) was nearly normal. Complete chromosome pairing was nearly always exhibited, although 2–4 univalents were occasionally seen. Some of the univalents were formed as a result of precocious disjunction of the bivalents.

(2) Hybrids between tetraploid taxa and hexaploid species (Table 7)

The hexaploid *L. alata* ($n = 24$) was crossed reciprocally to nearly all of the tetraploid ($n = 16$) taxa. All crosses resulted in vigorous, floriferous, pentaploid hybrids. Meiosis in the F_1 individuals typically exhibited a maximum of 16 bivalents and 8 scattered univalents, although exceptional configurations of 17 bivalents and 6 univalents were observed in *L. alata* × *L. lanceolata* (one cell), *L. alata* × *L. sphaerocarpa* (four cells), and *L. pilosa* × *L. alata* (one cell). One or two trivalents were seen occasionally in diakinesis and metaphase I of the following hybrids: *L. alata* × *L. glandulosa* subsp. *glandulosa* (one trivalent in two cells; two trivalents in one cell), *L. alata* × *L. lanceolata* (one trivalent in four cells; two trivalents in one cell), *L. alata* × *L. sphaerocarpa* (two trivalents in one cell), and *L. polycarpa* × *L. alata* (one trivalent in two cells; two trivalents in one cell). Groups of 2–4 bivalents (often of similar shape and size) "sticking" to one another sidewise were observed in meiotic metaphase but not in diakinesis. These associations were obviously not a result of chiasmata formation. Eight univalents would normally be expected in these hybrids. Observations of additional univalents at metaphase I either represent precociously separated bivalents or chromosomes which have no homologue. Present observations suggest that in most cells which had more than eight univalents, these "extras" are often precociously separate bivalents, judged by their shapes and locations.

Pseudobivalents (Walters, 1954) composed of two univalents held together by matrix bands were seen at least in a few metaphase I cells. One to six (rarely to ten) bivalents of stretched appearance were also seen occasionally. Some metaphase I cells in *L. alata* × *L. suffruticosa* were peculiar in having attenuated ends on the bivalents. Lagging univalents were uniformly found in meiotic anaphase I and II of all hybrids, and micronuclei occurred in nearly all the sporads.

Pollen stainability was in the range 43–71%, rather high for pentaploid hybrids exhibiting the above meiotic irregularities. All F_1 plants produced some aborted and some viable seeds in the plump capsules. An F_2 family (*L. glandulosa* subsp. *glandulosa* × *L. alata*) of 32 vigorous plants was grown and many individuals probably flowered but were not studied in detail. One morphologically intermediate plant was examined, however, and had 31% stainable pollen.

Morphology of the hybrids

Because of an apparently chance distribution of dominance between parents, some hybrids are likely to possess some characters of one parent, some of the other, and some (due to incomplete dominance or polygenic inheritance) that are intermediate (Stace, 1975). The net result is that hybrids are nearly always intermediate in overall morphology between the two parents. This is the situation within sect. *Microcarpium*. Genomic interaction resulting in a new character state has not been observed in these plants. With the exceptions of *L. glandulosa* subsp. *glandulosa* × *L. polycarpa* and *L. sphaerocarpa* × *L. glandulosa* subsp. *glandulosa*, all hybrids were very vigorous and flowered over a period of at least a month. Even in these two exceptional hybrids, if additional seeds were sown, or if different parental strains were crossed, vigorously growing hybrids would, I believe, be expected. This is because of the occurrence of a natural hybrid population of *L. sphaerocarpa* × *L. glandulosa* subsp. *glandulosa*. As there are very many naturally occurring hybrid populations between members of the *L. pilosa* group, it is valuable to discuss the morphology of artificial hybrids between these taxa. Since all reciprocal hybrids resembled each other, the discussion of characters that follows is limited to crosses in only one direction.

(1) Tetraploid hybrids

Ludwigia glandulosa subsp. *glandulosa* × *L. polycarpa*. These were dwarfs 5–20 cm in height at maturity, with an ascending habit. Despite their abnormal appearance, all produced a few flowers, set plump capsules with abundant seeds, and survived in the experimental greenhouse for two consecutive years. In general they were intermediate in vegetative and reproductive features, especially in shapes and sizes of floral parts and capsules. Like their parents, the hybrids shed pollen grains as tetrads and had seed-surface cells in parallel columns elongate to the seed length.

Ludwigia glandulosa subsp. *glandulosa* × *L. glandulosa* subsp. *brachycarpa*. The intermediacy of these hybrids was apparent in capsule size (4.5–5.5 mm long) and seed surface, which exhibited a mixture of columnar cells elongate and transversely elongate to the seed length (Fig. 6).

Ludwigia lanceolata × *L. pilosa*. The parents did not differ in seed-surface cell pattern or in the way their pollen grains were shed. The hybrids showed intermediate morphology in all aspects. Diagnostic characters include hirtellous pubescence and oblong-obpyramidal, 4-angled, unwinged capsules.

Ludwigia lanceolata × *L. polycarpa*. The hybrids were morphologically intermediate between the parents. Diagnostic characters include the 4-angled capsules and seed-surface cells (Fig. 7) basically similar in orientation to those of *L. polycarpa* (Table 1) but arranged in shorter columns. Some of them appeared more or less isodiametric in shape.

Ludwigia lanceolata × *L. sphaerocarpa*. The hybrids were again intermediate. The obpyramidal capsules were puberulent and very slightly winged, and the seed surface was composed of some more or less isodiametric cells and numerous, variously oriented short columnar cells (Fig. 8).

Ludwigia lanceolata × *L. suffruticosa*. The hybrids were generally intermediate in morphology. The stems were much branched as in *L. lanceolata*, but with a slightly congested and branched terminal inflorescence. The lower margins of sepals, bracteoles, and peduncles were slightly hirtellous. The capsules were weakly 4-winged and the seed-surface cells were subisodiametric as in both parents. Pollen grains were shed singly as in *L. suffruticosa*.

Ludwigia pilosa × *L. glandulosa* subsp. *glandulosa*. These hybrids were similar to *L. glandulosa* subsp. *glandulosa* in having subcylindric capsules, which were, however, somewhat shorter (5–5.5 mm long). Otherwise the plants were intermediate in general appearance, pubescence, and shape and size of floral parts. Seed-surface cells (Fig. 9) were predominantly columnar and elongate to the seed length like those of *L. glandulosa* subsp. *glandulosa* (Fig. 2). Yet few columnar cells were transversely elongate or oblique to the seed length. Some subisodiametric cells characteristic of *L. pilosa* were also present.

Ludwigia pilosa × *L. sphaerocarpa*. The hybrids were intermediate in pubescence (being densely strigillose) and shape and size of floral parts. Seed surface pattern (Figs. 10, 11, 12) was irregular and variable within the same capsule. A small yellow petal was observed in a single flower. Vestigial


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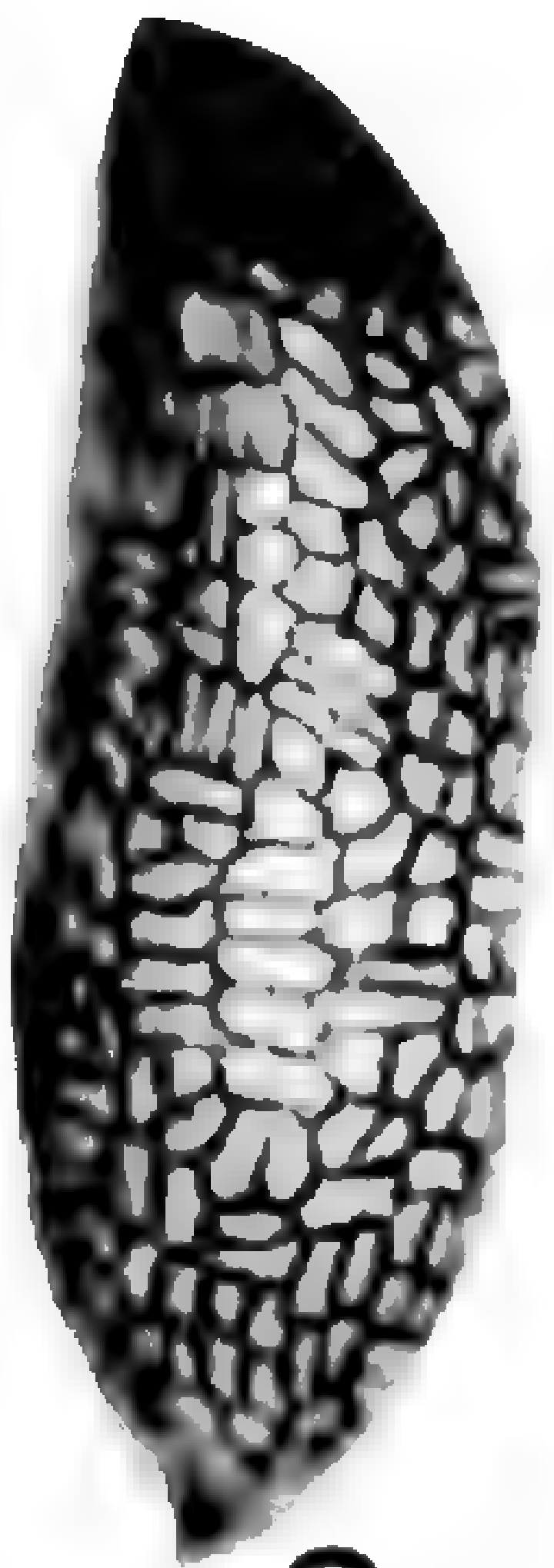
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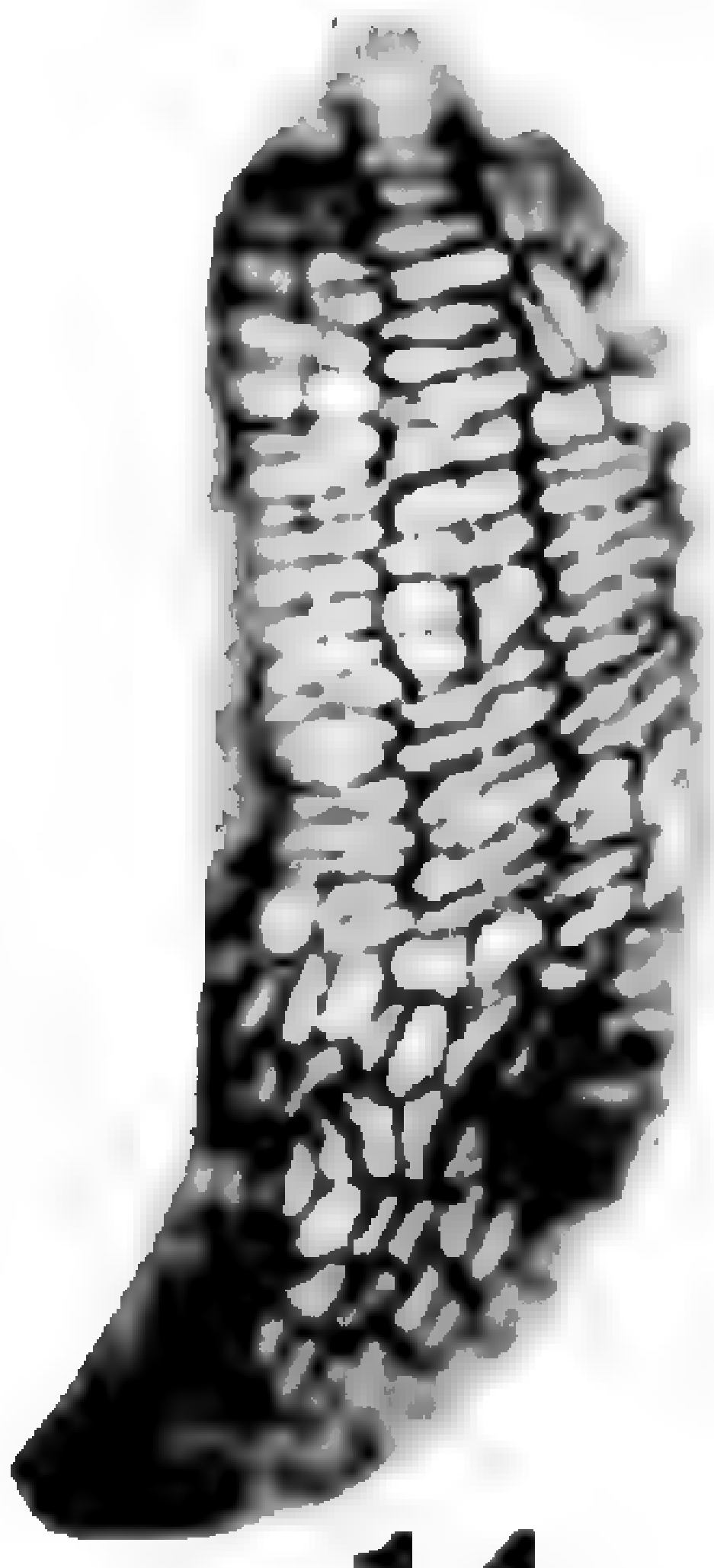
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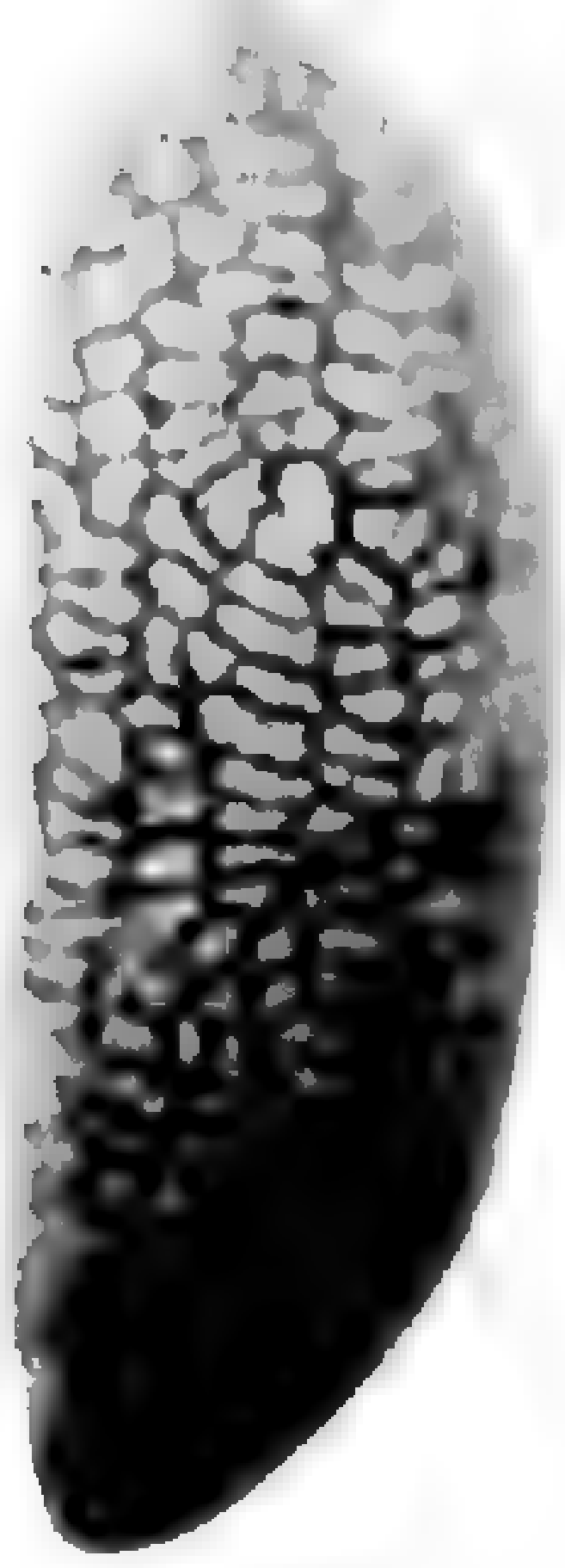
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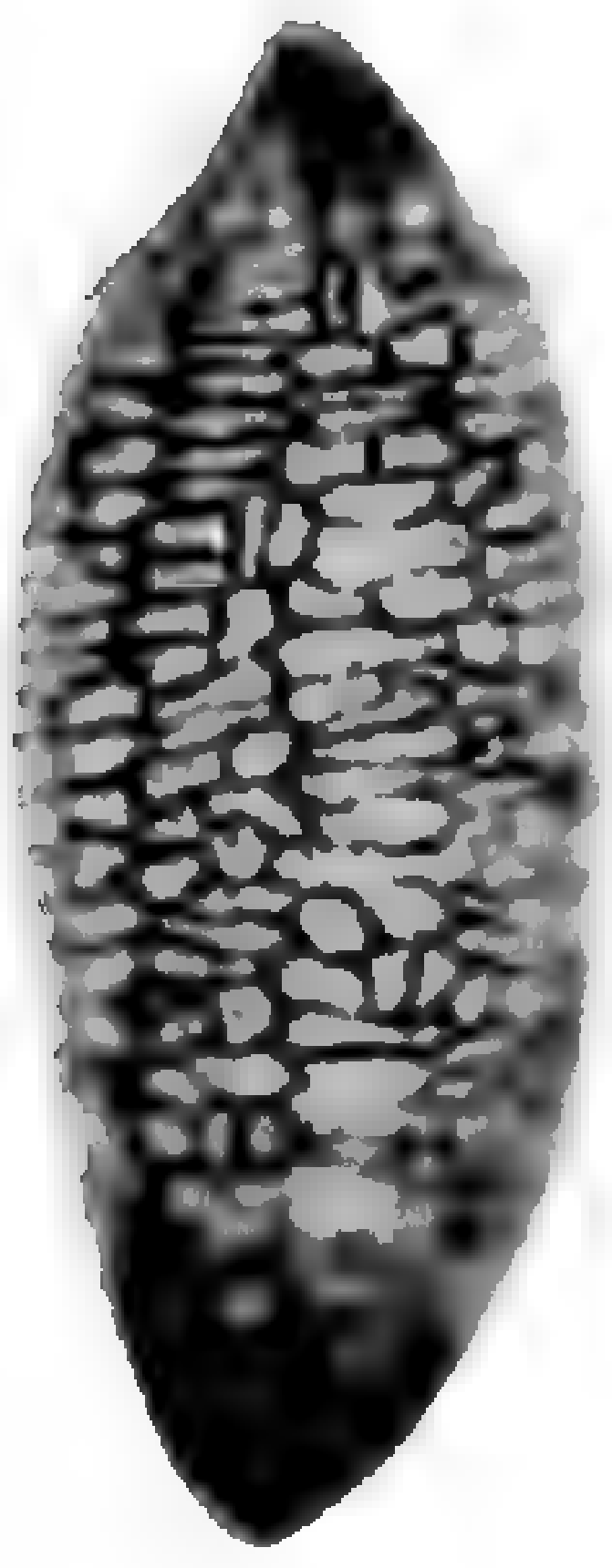
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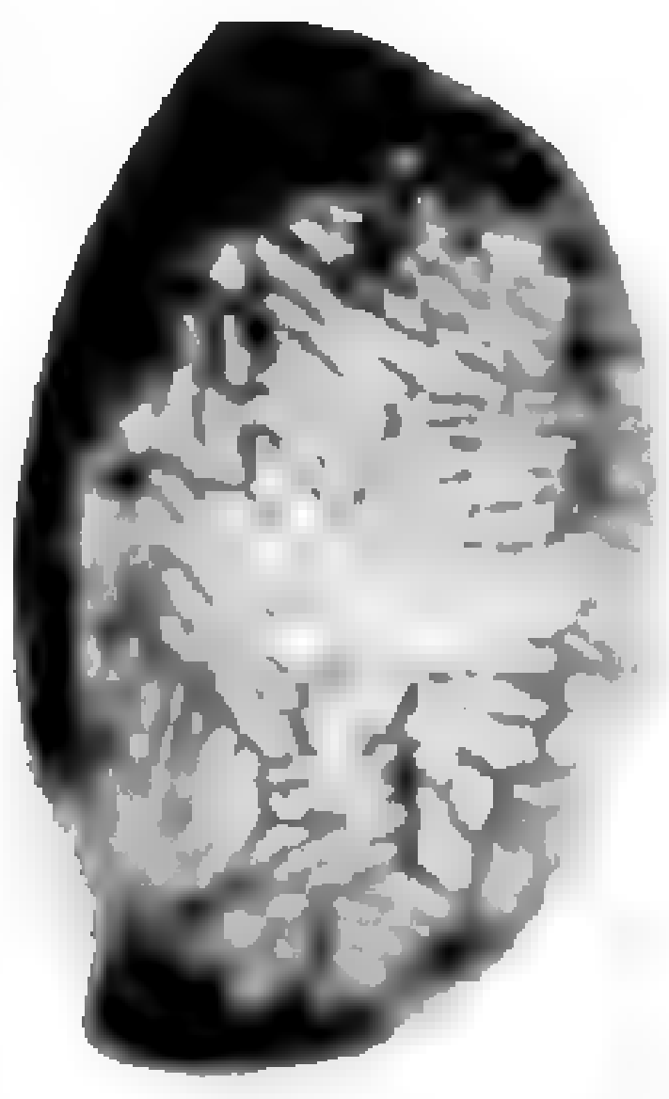
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petals, however, occur occasionally in both parental species.

Ludwigia pilosa × *L. suffruticosa*. The hybrids were intermediate in leaf shape and habit, were similar to *L. pilosa* in being hirtellous, and resembled *L. suffruticosa* in having a congested inflorescence. Fruiting specimens were not studied.

Ludwigia pilosa × *L. glandulosa* subsp. *brachycarpa*. The hybrids were similar to *L. pilosa* × *L. glandulosa* subsp. *glandulosa* in general, although they were less robust and had shorter subcylindric capsules 3–3.5 mm in length. The plants were strigillose. Their seed surface was composed predominantly of columnar cells, which were transversely elongate to the seed length (Fig. 13) as in *L. glandulosa* subsp. *brachycarpa*. Some more or less isodiametric cells typical of *L. pilosa* were also present, however. Also, columnar cells that were either parallel to the seed length or randomly oriented were observed.

Ludwigia polycarpa × *L. pilosa*. Hybrids were morphologically intermediate. Diagnostic features included the overall strigillose pubescence and the cubic-turbinate capsule with long bracteoles. These plants exhibited seed-surface cell patterns similar to those of *L. pilosa* × *L. glandulosa* subsp. *glandulosa* (Fig. 9).

Ludwigia sphaerocarpa × *L. glandulosa* subsp. *glandulosa*. The hybrids were not as vigorous as other hybrid combinations involving members of this group. The plants were reddish and less than 20 cm high. They were glabrous except for the fruits, which were sparsely and minutely strigillose. Only a single individual flowered, which later set plump capsules oblong in outline. Seed-surface cell pattern was basically similar to that of *L. glandulosa* subsp. *glandulosa*, but with some irregularities.

Ludwigia glandulosa subsp. *brachycarpa* × *L. lanceolata*. These hybrids were morphologically intermediate between the parents. The plants were nearly glabrous. The capsules were about 3 mm long, elongate obpyramidal, minutely strigillose on the sepal margins, and weakly winged on the angles. The bracteoles were short (about 1.2–1.5 mm long) and, as in *L. glandulosa* subsp. *brachycarpa*, the seed surface (Fig. 14) consisted mostly of columnar cells elongate transversely to the seed length. Some cells were arranged parallel to the seed length. Isodiametric cells, as characteristic of *L. lanceolata*, were uncommon.

(2) Pentaploid hybrids

Ludwigia alata × *L. glandulosa* subsp. *glandulosa*. These hybrids were similar to *L. alata* in habit, leaf shape, and in having winged capsules. Intermediate characters included capsule shape (elongate obpyramidal) and pollen grains shed singly and as tetrads. The seed surface in the hybrid consisted mainly of columnar cells elongate transversely to the seed length, as in *L. alata*, although the cells were much smaller and were sometimes more nearly isodiametric than on seeds of that species (Fig. 15). Columnar cells elongate parallel to the seed length and similar to those of *L. glandulosa* subsp. *glandulosa* were also observed.

Ludwigia alata × *L. lanceolata*. The parental species were themselves very similar in floral morphology and habit. The hybrids can be identified only by seed surface (Fig. 16), which consists of a mixture of columnar cells elongate transversely to the seed length, as in *L. alata*, and more or less isodiametric cells characteristic of *L. lanceolata*. Pollen grains were shed singly as in *L. alata*.

Ludwigia alata × *L. pilosa*. These hybrids were generally intermediate. They were neither glabrous as in *L. alata* nor hirsute as in *L. pilosa*, but were minutely villous all over. The capsules, like those of *L. alata*, were winged. Seed-surface cell pattern (Fig. 17) was similar to that of *L. alata* × *L. lanceolata*. Pollen grains were shed mostly as tetrads, although single grains were seen occasionally.

Ludwigia alata × *L. polycarpa*. With their winged capsules, the hybrids were more similar to *L. alata* in general appearance. They had the minutely strigillose leaf margins characteristic of *L. polycarpa*, however. Conspicuously intermediate characters include: sepal shape, seed surface

←

FIGURES 6–19. Photographs of seeds obtained from experimental hybrids in *Ludwigia* sect. *Microcarpium*.—6. *L. glandulosa* subsp. *brachycarpa* × *L. glandulosa* subsp. *glandulosa*.—7. *L. lanceolata* × *L. polycarpa*.—8. *L. lanceolata* × *L. sphaerocarpa*.—9. *L. pilosa* × *L. glandulosa* subsp. *glandulosa*.—10–12. *L. pilosa* × *L. sphaerocarpa*.—13. *L. pilosa* × *L. glandulosa* subsp. *brachycarpa*.—14. *L. glandulosa* subsp. *brachycarpa* × *L. lanceolata*.—15. *L. alata* × *L. glandulosa* subsp. *glandulosa*.—16. *L. lanceolata* × *L. alata*.—17. *L. alata* × *L. pilosa*.—18, 19. *L. alata* × *L. polycarpa*. Scale bar = 0.5 mm.

pattern in which columnar cells were randomly oriented (Figs. 18, 19), and pollen grains shed as loose tetrads.

Ludwigia alata × *L. sphaerocarpa*. These hybrids were similar to *L. alata* in habit and in having winged capsules. However, they shed pollen grains as loose tetrads, and their capsules were strigillose, both intermediate character states. Seed-surface cell pattern is not of diagnostic value here, as both parents were similar in this respect.

Ludwigia alata × *L. suffruticosa*. These hybrids generally resembled *L. alata*. The flowers were loosely arranged along the apices of the stems, and the capsules were winged and glabrous. The seed-surface cell pattern was intermediate between that of the two parents, being similar to that shown in Figure 16. The hybrids shed pollen grains singly, as did both parents.

In summary, artificial hybrids between members of the *L. pilosa* group were easily produced and were nearly always vigorous and floriferous. Morphologically, F_1 plants were more or less intermediate between the parents. The only character that exhibited some consistent degree of dominance is the winged capsules of *L. alata*. When tetraploid species with rounded capsules were crossed with *L. alata*, the resultant hybrids invariably had distinctly winged capsules. In contrast, when *L. lanceolata*, a tetraploid with winged capsules, was crossed with tetraploid species having rounded capsules, the F_1 individuals usually exhibited intermediate capsule shape—their capsules were 4-angled or at most slightly winged. Therefore, it seems that in hybrids involving *L. alata*, the apparent dominance of the winged-capsule character may be due to a multiple dose of genetic information received from this hexaploid.

The single most important diagnostic character for hybrids within the *Ludwigia pilosa* group is the shape and size of the capsules. Other diagnostic characters include overall pubescence, seed-surface pattern, and to some extent whether pollen grains are shed singly or as tetrads. This pollen character is of limited value, as most species in the *L. pilosa* group shed pollen as tetrads. When one of the taxa that do shed pollen singly was used as a parent, loose tetrads or a mixture of single and tetrad pollen grains were commonly found in the hybrids. This pattern was also clearly shown by the diploid hybrids *L. microcarpa* × *L. linearis* and *L. microcarpa* × *L. linifolia*. Similarly, hybrids between species that differ in their seed-surface pattern always showed a mixture of cell types or cells with intermediate shapes and/or of random orientation. Likewise, a hybrid resulting from crossing a hirtellous species with a glabrous species always showed minutely villous or strigillose pubescence. Examination of the above-mentioned diagnostic characters permits very accurate determination of the parentage involved in hybrids within the *L. pilosa* group.

HYBRIDS WITHIN THE *LUDWIGIA CURTISSII* COMPLEX

Two species, *L. curtissii* ($n = 32$) and *L. simpsonii* ($n = 24$), are included in this complex. Reciprocal hybridizations (Table 8) between them resulted in vigorous, floriferous F_1 individuals.

Meiotic analysis and pollen stainability

Meiosis was normal in both parental species. Diakinesis and metaphase I cells consistently revealed only bivalents. Multivalents were never observed despite the polyploidy of both parents. The two parents have pollen stainability of 97–100%.

Although reciprocal hybrids were made, meiosis was examined only in F_1s in which *L. curtissii* was the ovulate parent and *L. simpsonii* the pollen parent. Of the seven clear, analyzable cells, three were at diakinensis and four in metaphase I. They consistently showed a configuration of 24 bivalents and 8 univalents. Nearly all of the bivalents in the metaphase I cells were regularly rod-shaped, and were oriented on the equatorial plate. The eight univalents were scattered at random along a continuous bipolar spindle; some were probably lost at anaphase I and II, since micronuclei were observed in many sporads. In spite of the presence of scattered univalents, the hybrids produced 89% stainable pollen grains and a moderate number of viable seeds. Eleven F_2 plants grew up to flower. All of them branched profusely and set abundant fruits and seeds. The reciprocal F_1 hybrid, *L. simpsonii* × *L. curtissii*, had a similar value for stainable pollen (81%).

Morphology of the hybrids

Ludwigia curtissii and *L. simpsonii* are often difficult to distinguish; the only consistent diagnostic character available to separate them is the size of mature capsules. These of *L. simpsonii* are 1.5–2(–2.5) mm long, those of *L. curtissii* (2–) 2.5–4.5 mm long. Artificial hybrids between them had robust, erect stems up to 85 cm high and capsules about 2.5 mm long. Such plants are likely to be identified as *L. curtissii* in the field or the herbarium, although their capsule size is at the

TABLE 8. *Meiotic configurations and pollen stainability of hybrids between members of the* Ludwiga curtissii *complex.*

Hybrid Combination	Modal Meiotic Configuration Observed	Number of Cells with Modal Configuration/ Total Number of Cells Examined	Pollen Stainability (%)
CUR d × SIM d	24II + 8I	7/7	89
SIM e × CUR d			81

lower limit for *L. curtissii*. The hybrid plants set plump capsules with moderate amounts of viable seed.

HYBRIDS BETWEEN THE DIPLOID GROUP AND THE *LUDWIGIA PILOSA* GROUP

Of the 42 hybrid combinations in which reciprocal crossing attempts have been made involving diploid taxa and members of the *L. pilosa* group (Fig. 5, Table 9), only three failed to result in seed set. These crosses involved the small-flowered *L. microcarpa* as pollen parent and one of the larger-flowered species as ovulate parent. Eight of the 39 successful crosses yielded offspring that did not germinate. Of these, 15 resulted in weak F_1 individuals that died soon after germination or remained sterile for the entire season. Only the remaining 15 hybrid combinations flowered successfully, but three of them were weak and died soon after anthesis. The 12 remaining combinations were vigorous and floriferous. Despite this, none of them set any seed. Their ovaries simply turned yellowish and dropped off or were somewhat persistent but shriveled after mechanical self-pollination.

The results of artificially hybridizing the different species of the above two groups ranged from seeds that were unable to germinate to vigorous and floriferous F_1 plants. A few general comments are appropriate here. First, the inability of hybrid seeds to germinate as observed in the present study is not necessarily a reliable indication of reproductive isolation. In some cases, seeds obtained from a particular cross did not germinate the first year, but additional seeds planted the following year did. Seed dormancy, however, is not characteristic of *Ludwigia*, at least of sect. *Microcarpium*. In a few rare cases, hybrid seeds were observed to germinate three or four months after they were sown. These would have been scored as germination failures if the experiments had been terminated after two months, as was generally done.

Second, on several occasions the majority of seeds failed to germinate or produced weak or stunted seedlings, although one or few vigorous and floriferous hybrid individuals grew to maturity. For example, only a single, healthy plant of *L. microcarpa* × *L. alata* was obtained from 18 seeds sown; none of the others germinated. Such failures to germinate are not mentioned in the above discussion, and records were not kept, because the seeds of *Ludwigia* species are very small, and usually 50–200 seeds were sown for each hybrid combination.

Third, weak or sterile hybrids could sometimes be brought to flower if they were grown very carefully or if alternative parental strains were utilized to vary the genetic composition of the hybrids (for examples see Table 9).

Meiotic analysis and pollen stainability

Cytological data are available for ten hybrid combinations. These include seven hybrids resulting from crosses between the tetraploid species and each of the three diploid species, including one reciprocal cross (Table 10), and three hybrids resulting from crosses between *L. alata* (hexaploid) and each of the three diploid species.

(1) Hybrids resulting from crosses between the diploid and tetraploid species

Crosses between diploids and tetraploids would normally be expected to form triploid hybrids. It is most interesting, therefore, that upon sowing 15 seeds resulting from crossing *L. linifolia* ($n = 8$) with *L. lanceolata* ($n = 16$), only 5 plants were obtained, all of which were tetraploid ($2n = 32$). That the diploid *L. linifolia* was used as the ovulate parent suggests that these $2n = 32$ plants were not simply the result of self-pollination in the tetraploid. This chromosome number was apparently produced by the union of an unreduced egg from the diploid *L. linifolia* with a normal sperm nucleus

TABLE 9. *Summary of crossing results between taxa of the diploid group and the* Ludwigia pilosa *group.*

L. linearis as female parent	
LIE b × ALA a	Seeds failed to germinate.
LIE a × LAN a	Plants weak, with reddish leaves, died soon after germination.
LIE a × PIL b	Seeds failed to germinate.
LIE b × POL c	Plants weak, barely flowered; no viable pollen.
LIE a × SPH c	F_1 hybrids vigorous and flowered (see Table 10).
LIE a × SUF b	Low germination percentage; weak plants died when ca. 4 cm high.
L. linearis as male parent	
ALA a × LIE a	F_1 hybrids vigorous and flowered (see Table 11).
BRA × LIE b	Formed a mat in 3-inch pots; remained sterile.
GLA a × LIE a	Plants sterile, about 10–30 cm high.
GLA a × LIE b	Plants sterile, about 5–30 cm high.
GLA a × LIE d	F_1 hybrids vigorous and flowered (see Table 10).
LAN a × LIE a	Died at cotyledon stage.
PIL b × LIE b	Formed 2–4 leaves and died.
POL c × LIE b	Seeds failed to germinate.
SPH c × LIE a	F_1 hybrids vigorous and flowered (see Table 10).
SUF c × LIE b	Some died in cotyledon stage; some produced a few pinkish leaves and soon withered.
L. linifolia as female parent	
LIF b × ALA a	Seeds failed to germinate.
LIF c × ALA b	Seeds failed to germinate.
LIF c × BRA	Cotyledons expanded a month after radicles had protruded; plants weak and died when ca. 1 cm high with 4–6 leaves.
LIF c × GLA c	Seeds failed to germinate.
LIF c × GLA b	Plants weak, mostly died 2–3 cm high; one plant barely flowered and showed 0% stainable pollen.
LIF b × LAN a	F_1 hybrids vigorous and flowered, but with an unexpected chromosome number of $2n = 32$ (see Table 10).
LIF c × PIL b	Very low germination percentage; 3 weak plants obtained, which died when ca. 1 cm high with about 10 leaves.
LIF b × POL c	Seeds failed to germinate.
LIF c × SPH c	Plants weak, sterile, about 5–7 cm high.
LIF b × SUF c	Five out of 20 seeds germinated; all very weak, died soon.
LIF c × SUF a	Numerous seeds germinated, but all died in 4–6-leaved stage.
L. linifolia as male parent	
ALA a × LIF c	F_1 hybrids vigorous and flowered (see Table 11).
BRA × LIF c	Plants remained small, died when ca. 2 cm high.
GLA b × LIF a	Plants weak, with reddish brown leaves, sterile.
LAN a × LIF b	Six out of 30 seeds germinated; all died in seedling stage.
PIL b × LIF b	F_1 hybrids vigorous and flowered (see Table 10).
PIL b × LIF c	Cotyledons reddish, soon withered.
POL c × LIF b	Died in cotyledon stage.
POL c × LIF c	Two weak plants barely flowered and soon died; 0% stainable pollen.
SPH c × LIF c	Plants with pinkish yellow leaves, 10–15 cm high, sterile.
SUF b × LIF b	Seeds failed to germinate.
L. microcarpa as female parent	
MIC a × ALA a	F_1 hybrids vigorous and flowered (see Table 11).
MIC a × GLA b	Plants healthy, flowered when 10–15 cm high.
MIC b × LAN a	Seeds failed to germinate.
MIC a × PIL b	Seeds failed to germinate.
MIC a × POL c	F_1 hybrids vigorous and flowered (see Table 10).
MIC c × SPH c	Plants flowered, but meiosis was not studied; 4% stainable pollen.
L. microcarpa as male parent	
ALA b × MIC a	Crosses failed to set seed.
GLA b × MIC a	F_1 plants healthy and flowered (see Table 10).
LAN b × MIC d	Plants recently grown; healthy, but have not yet flowered.
PIL c × MIC b	Crosses failed to set seed.
SPH a × MIC a	Very low germination rate; soon died.
SUF b × MIC a	Crosses failed to set seed.

TABLE 10. *Meiotic configurations and pollen stainability in seven hybrids resulting from crosses between the diploid with tetraploid species of* Ludwigia *sect.* Microcarpium.

Hybrid Combination	Modal Meiotic Configuration Observed	Number of Cells with Modal Configuration/ Total Number of Cells Examined	Pollen Stainability (%)
L. linearis as one parent			
GLA a × LIE b	(4–7)II + (16–10)I	5/5	2
LIE a × SPH c	(4–7)II + (16–10)I	6/9	1
SPH c × LIE a	(6–7)II + (12–10)I	19/24	1
L. linifolia as one parent			
LIF b × LAN a	8II + 16I[a]	4/8	1
PIL b × LIF b	(6–7)II + (12–10)I	6/6	0
L. microcarpa as one parent			
GLA b × MIC a	(2–6)II + (20–12)I	9/11	0
MIC a × POL c	8II + 8I; 4II + 16I	2/2	13

[a] Hybrids with $2n = 32$, a number apparently produced by the union of an unreduced egg from the diploid (*L. linifolia*) with a normal sperm nucleus from the tetrapoloid (*L. lanceolata*).

from the tetraploid *L. lanceolata*. These plants are, following the terminology of Harlan & deWet (1975), Class I Polyploids. Diakinesis observed in one plant resulting from this cross clearly showed a configuration of 8II + 16I. Configurations at metaphase I, however, ranged from 6II + 20I to 8II + 16I, with two cells each exhibiting a single trivalent. The bivalents were apparently formed between chromosomes of the duplicated *L. linifolia* genome. This unexpected but significant finding suggests strongly that (a) chromosomes in the two genomes in the tetraploid *L. lanceolata* are not homologous and thus remained unpaired; and (b) the genome of *L. linifolia* does not pair with either of the genomes of the tetraploid species when true chromosome homologues are present.

The cytological behavior of all other hybrids generally followed a consistent pattern (Table 10). Although the number of bivalents formed was variable, it never exceeded eight, the haploid chromosome number of the diploid species. The number of bivalents ranged from three to seven in most hybrids, although values ranging from one to six were observed in *L. glandulosa* subsp. *glandulosa* × *L. microcarpa*. The configuration 8II + 8I was observed in only a single cell in *L. microcarpa* × *L. polycarpa*. However, in this metaphase I cell, two of the bivalents are in a somewhat perpendicular orientation to the other six bivalents and appear to be attached univalents. A single trivalent was seen in three of the 33 cells examined of the reciprocal hybrids between *L. linearis* and *L. sphaerocarpa*. One to three heteromorphic bivalents, in which the two chromosomes differed in shape or size, were observed on occasion. Attenuated bivalents and precociously separated bivalents were also seen in some cells. Pseudoassociation resulting from stickiness between two univalents, two bivalents, or one of each, was also observed in a few cases.

It is observed that the two to seven chromosome pairs observed in these diploid × tetraploid hybrids indicate that the diploid genome is homologous with only one of the tetraploid genomes.

The cytological abnormalities and the high proportion of univalents observed in these hybrids are reflected in the low pollen stainability. Six of the seven hybrids had less than 2% stainable pollen; only *L. microcarpa* × *L. polycarpa* had greater than 10% stainable pollen (Table 10), presumably due to chance events. In *L. microcarpa* × *L. polycarpa*, the pollen was shed as single grains and as tetrads, a combination of the characters seen in the two parental taxa. Most stainable pollen, however, was shed as single grains, an observation which cannot be explained at present.

(2) Hybrids resulting from crosses between the diploid and hexaploid species

All hybrids involving diploid and hexaploid taxa were made (Table 11). When *L. alata* was crossed to *L. linearis* and *L. linifolia*, the resulting hybrids typically exhibited a configuration of (1–2)III +

TABLE 11. *Meiotic configurations and pollen stainability in three hybrids resulting from crosses between the diploid and hexaploid species of* Ludwigia *sect.* Microcarpium.

Hybrid Combination	Modal Meiotic Configuration Observed	Number of Cells with Modal Configuration/ Total Number of Cells Examined	Pollen Stainability (%)
ALA b × LIE a	(1–2)III + (4–6)II + (21–16)I	7/12	1
ALA b × LIF c	1III + 6II + 17I	1/6	0
MIC a × ALA b	1IV + (7–10)II + (14–8)I	5/14	15

(4–6)II + (21–16)I in both diakinesis and metaphase I, although a configuration of 8II + 16I was occasionally seen. There is no unequivocal evidence to indicate whether the trivalents represent intergenomic homology in the hexaploid *L. alata* or associations between chromosomes of *L. alata* and those of *L. linearis* or *L. linifolia*. In metaphase I of many cells, one to three bivalents appeared to be attached univalents and were often observed away from the equatorial plate. Other cytological aberrations, including heteromorphic bivalents and elongate, attenuated bivalents, were very common. Normal rod or ring bivalents were infrequent.

In *L. microcarpa* × *L. alata* the modal meiotic configuration was 1IV + (7–10)II + (14–8)I, with maximum pairing of either 1IV + 10II + 8I or 11II + 10I. In the latter case, the quadrivalent was not seen, as it probably separated into two bivalents because of a lack of sufficient chiasmata to hold them together. Rings or chains of four chromosomes were more commonly seen in diakinesis than in metphase I. Trivalents were not noted. It is uncertain whether the quadrivalent indicated that, in addition to the difference in ploidy level, the two species differ by a reciprocal translocation, as the multivalent can also result from associations of one chromosome from *L. microcarpa* and three chromosomes each from one of the three genomes of *L. alata*.

The bivalents observed in the meiotic first metaphase of *L. microcarpa* × *L. alata* were typically normal, being ring- or rod-shaped. Attenuated bivalents were very seldom found. Heteromorphic bivalents or attached univalents were not observed. The reduced occurrence of cytological aberrations and the higher number of chromosome pairings in these hybrids probably account for their higher

TABLE 12. *Summary of crossing results between the diploid species of* Ludwigia *sect.* Microcarpium *and the* L. curtissii *complex.*

L. curtissii as female parent	
CUR a × LIE a	Seeds failed to germinate.
CUR a × LIE b	Most seeds failed to germinate; those that did germinate died at the cotyledon stage.
CUR a × LIE c	Seeds failed to germinate.
CUR e × LIE b	Hybrids stunted at first, vigorous and floriferous eventually.
CUR a × LIF b	Hybrids vigorous and floriferous.
CUR f × MIC a	Hybrids vigorous and floriferous.
L. curtissii as male parent	
LIE b × CUR f	Numerous plants remained in the cotyledon stage and were reddish, four of which flowered ultimately.
LIF b × CUR a	Seeds failed to germinate.
L. simpsonii as female parent	
SIM d × LIE b	Hybrids stunted but flowered.
SIM d × LIF c	Seeds failed to germinate.
SIM e × LIF c	Seeds failed to germinate.
SIM f × LIF c	Seeds failed to germinate.
L. simpsonii as male parent	
LIF c × SIM d	Plants remained small and rosettelike, ca. 10-leaved, 1 cm high 7 months after germination.
MIC d × SIM d	Hybrids vigorous and floriferous.

TABLE 13. *Meiotic configurations and pollen stainability in hybrids resulting from crosses between diploid species of* Ludwigia *sect.* Microcarpium *and the* L. curtissii *complex.*

Hybrid Combination	Modal Meiotic Configuration Observed	Number of Cells with Modal Configuration/ Total Number of Cells Examined	Pollen Stainability (%)
CUR e × LIE b			0
CUR a × LIF b	8II + 24I	13/31	10
CUR a × MIC a	(14–15)II + (12–10)I	5/5	2
LIE b × CUR e			2
MIC b × CUR a			2
MIC d × SIM d			9
SIM d × LIE b			4

pollen stainability (15%) than was observed in *L. alata* × *L. linearis* and the reciprocal hybrids of *L. alata* × *L. linifolia* (0–1%).

Morphology of the hybrids

In diploid species of sect. *Microcarpium*, the presence of petals appears to be dominant over the apetalous condition, judged from the consistent presence of petals in the petalous × apetalous hybrids. It is therefore of interest to examine this character in hybrids resulting from crosses between the petalous diploids and the apetalous polyploids. It was observed that all hybrids between diploids and tetraploids exhibited a variable number (0–4) of vestigial petals on different flowers of the same plant, whereas all hybrids between the diploids and hexaploids lacked petals completely.

When two of the diploid species *L. linearis* or *L. linifolia* were crossed to the tetraploid taxa, the resulting hybrids were somewhat intermediate in overall pubescence, leaf shape, capsule shape and size, sepal shape and size, and bracteole length. However, when *L. microcarpa*, the third diploid, was crossed with tetraploids, the F_1 hybrids were generally similar to their tetraploid parent in aspect but were diminutive in height and in leaf and flower size.

When all three of these diploids were each crossed to the hexaploid, *L. alata*, the resultant F_1 hybrids were more similar to *L. alata*, particularly in exhibiting its characteristic winged capsules. The hybrids *L. alata* × *L. linearis* and *L. alata* × *L. linifolia* resembled each other in their slightly narrower and longer capsules as compared with those of *L. alata*. Neverthelesss, *L. alata* × *L. linearis* had sparsely strigillose capsules, short sepals, and bracteoles shorter than the ovary, whereas *L. alata* × *L. linifolia* was completely glabrous, had elongate acuminate sepals, and had bracteoles longer than the ovary.

Hybrids between *L. microcarpa* and *L. alata* had small leaves and flowers, but were at least as robust and tall as *L. alata*. This is in sharp contrast to the situation in hybrids resulting from crosses between *L. microcarpa* and the tetraploid taxa (see above).

When diploid species (with pollen shed as tetrads) were crossed to hexaploid species (with pollen grains single), the resulting hybrids had single pollen grains only. Hybrids resulting from crosses between diploid species having single grains and tetraploid species having tetrad pollen showed a mixture of tetrad and single pollen in mature anthers. Crosses between diploids and tetraploids that both shed pollen as tetrads yielded hybrids that also produce tetrads. In the hybrid *L. linifolia* × *L. lanceolata*, however, where unreduced gametes of the diploid *L. linifolia* united with normal pollen of the tetraploid *L. lanceolata* to produce tetraploid hybrids, the pollen grains were shed mixed as tetrads and single grains. This result was not expected. In this hybrid, the morphology was intermediate between *L. linifolia* and *L. lanceolata*.

HYBRIDS BETWEEN THE DIPLOID GROUP AND THE *LUDWIGIA CURTISSII* COMPLEX

A summary of the crossing results is shown in Table 12. Some of these data are supplemented by study of natural hybrid populations, as is discussed below.

Meiotic analysis and pollen stainability

Six hybrid combinations were examined to determine percentage of stainable pollen. Two of these were also studied cytologically (Table 13).

TABLE 14. *Summary of crossing results between members of the* L. curtissii *complex and the* L. pilosa *group.*

L. curtissii as female parent	
CUR a × BRA	Only 4 seeds sown, none of which germinated.
CUR a × GLA d	Plants vigorous and floriferous.
CUR a × LAN a	Seeds failed to germinate.
CUR a × PIL b	Seeds failed to germinate.
CUR a × POL c	Plants flowered but were not vigorous.
CUR a × SPH b	Plants very vigorous and floriferous.
CUR a × SUF b	Plants dwarf, but were healthy and flowered.
L. curtissii as male parent	
ALA a × CUR a	Plants with reddish leaves, rosettelike, died when 6-leaved.
LAN a × CUR a	Plants started losing leaves when taller than 10 cm; set a few flowers.
PIL a × CUR f	Plants very vigorous and floriferous.
POL a × CUR a	Plants flowered but were not vigorous.
SPH a × CUR a	Plants very vigorous and floriferous.
L. simpsonii as female parent	
SIM a × ALA a	Plants vigorous and floriferous.
SIM c × LAN a	Seeds failed to germinate.
SIM a × PIL a	Died in cotyledon stage.
SIM a × SUF b	Seeds failed to germinate.
L. simpsonii as male parent	
ALA a × SIM a	Plants weak, leaves drooping, died when 6- or 8-leaved.
GLA b × SIM a	Plants vigorous and floriferous.
LAN a × SIM a	Plants with reddish leaves and much branched below; flowered recently.
TOR × SIM b	Seeds failed to germinate.

Of the 31 analyzable cells in *L. curtissii* ($n = 32$) × *L. linifolia* ($n = 8$), 22 formed strictly bivalents and univalents, ranging from (8–12)II + (24–16)I, with a modal configuration of 8II + 24I; nine cells formed multivalents, in which four cells had a configuration of 1III + (6–9)II + (25–19)I, and five cells showed 1IV + (6–9)II + (22–18)I. An exceptional cell with only 5II + 30I was also observed. In some cells chromosomes were so sticky that cytological analysis was impossible.

In *L. curtissii* × *L. microcarpa* ($n = 8$), only five analyzable cells were studied, the results being (14–15)II + (12–10)I. One or two sticky or precociously disjunct bivalents were noted in two cells.

Pollen stainability in all hybrids examined was very low, ranging 0–10% (Table 13). Despite this problem, a single F_2 individual of *L. curtissii* × *L. linifolia* was raised and another was raised from *L. curtissii* × *L. microcarpa*. The former remained sterile and died, whereas the latter died shortly after anthesis; it had 17% stainable pollen.

Morphology of the hybrids

Reciprocal hybrids of *L. curtissii* × *L. linearis* ($n = 8$) resemble each other. They are erect and branched on the upper stems. The tallest individual reached a height of 65 cm. The plants were extremely similar to *L. curtissii* in aspect, and before anthesis were thought to be selfed progeny of *L. curtissii*. In fact, even their flowers resembled those of *L. curtissii* except that their ovaries were slightly narrower and four-angled and their bracteoles were slightly shorter. Most flowers were apetalous; in a few cases one or two vestigial petals were present. After anthesis, the ovaries turned yellow and fell off. Pollen was shed as loose tetrads and single grains.

Hybrids between *Ludwigia simpsonii* ($n = 24$) and *L. linearis* could not be distinguished from *L. curtissii* × *L. linearis*.

Plants of *L. curtissii* × *L. linifolia* exhibited more morphological intermediacy than those of *L. curtissii* × *L. linearis*, although both resulted from hybridization between an octoploid and a diploid. Plants of *L. curtissii* × *L. linifolia* were smaller than either parent (about 25–30 cm high), much branched, and very floriferous (resembling *L. linifolia*). The flowers commonly had one to four petals (intermediate) and were congested at ends of branches (uncommon in both parents). The leaves were generally similar to those of *L. curtissii* in shape but were slightly smaller. The ovaries were about as long as those of *L. curtissii*, but were not accrescent and were narrower and four-angled. Sepals were intermediate in shape and size. Pollen was shed mostly as tetrads, and with some single grains as well. These hybrids did not usually set

TABLE 15. *Meiotic configurations and pollen stainability in hybrids resulting from crosses between members of the* L. curtissii *complex and the* L. pilosa *group.*

Hybrid Combination	Modal Meiotic Configuration Observed	Number of Cells with Modal Configuration/Total Number of Cells Examined	Pollen Stainability (%)
L. curtissii as one parent			
CUR a × GLA d			5
CUR a × POL c	1III + 4II + 37I	1/1	32
CUR a × SPH b			31
CUR a × SUF b	(11–13)II + (26–22)I	5/5	9
LAN a × CUR f			4
PIL a × CUR a	1III + (10–13)II + (25–19)I	4/16	6
POL a × CUR a	chromosomes very sticky, not analyzable		25
SPH a × CUR f	(1IV) + (1–3)III + (6–13)II + (14–30)I	6/6	17
L. simpsonii as one parent			
GLA b × SIM a			3
LAN a × SIM a	1III + 5II + 27I	1/3	11
SIM a × ALA a			20

seed, although one or two viable seeds were occasionally obtained.

Plants of *L. curtissii* × *L. microcarpa* were very vigorous and floriferous, up to 80 cm high, and much branched. The leaves were similar to those of *L. curtissii*, but smaller. Similarly, all floral parts were reduced and somewhat resembled those of *L. microcarpa*. In the hybrid, however, the nectary discs were always distinctly raised, unlike those of *L. microcarpa*, in which they were nearly flat. The ovaries usually shriveled after anthesis, although in exceptional cases one to three seeds were produced.

Plants of *L. microcarpa* × *L. simpsonii* were also very vigorous. Their floral parts were similar to those of *L. curtissii* × *L. microcarpa*, and their flowers were sterile. These hybrids were smaller (up to 50 cm high) and had slightly broader leaves. As plant height and leaf shape are somewhat variable characters, it is difficult to distinguish between these two hybrids when they occur together in nature.

HYBRIDS BETWEEN THE *LUDWIGIA CURTISSII* COMPLEX AND THE *L. PILOSA* GROUP

As with crosses between the diploid group and the *L. pilosa* group, these crossing results were quite variable, ranging from total failure to germinate to vigorous and floriferous F_1 hybrids (Table 14). None of these F_1 plants were observed to set any seed, however, while most of the hybrids resulted from crosses between the *L. curtisssii* complex and the *L. pilosa* group set at least a few viable seeds. An F_2 family of 12 vigorous plants of *L. simpsonii* × *L. alata* was established.

Meiotic analysis and pollen stainability

In hybrids with *L. simpsonii* as one of the parents, meiosis was studied only in *L. lanceolata* × *L. simpsonii* (Table 15). Only three metaphase I cells were obtained, which had three to five bivalents, most of which were chromosomes connected by a chromatin thread and were aligned randomly. A trivalent was seen in one of the cells.

In hybrids with *L. curtissii* as the male parent, *L. polycarpa* × *L. curtissii* had sticky chromosomes, which rendered study of meiosis difficult.

Four other hybrid combinations were studied cytologically. In *L. curtissii* × *L. polycarpa*, only one first metaphase cell was analyzable; it showed a configuration of 1III + 4II + 37I with two attenuated bivalents in the equatorial plate.

The other three hybrids resulting from crossing *L. curtissii* and the tetraploid species showed significantly higher chromosome associations. A maximum of 13 bivalents were seen in at least some of the cells, and one tetravalent and a maximum of three trivalents were observed in others (Table 15). The meiotic metaphase figures of these hybrids generally consisted of bivalents or multivalents aligned in the equatorial plate with many univalents scattered throughout the cell. The following cytological aberrations were occasionally observed: attenuated bivalents, precociously separated bivalents, attached univalents, and sticky chromosomes.

The pollen stainability was, surprisingly, higher in *Ludwigia curtisii* × *L. polycarpa* (32%), which showed the least chromosome associations, and in *L. polycarpa* × *L. curtissii* (25%), which had stickier chromosomes than in other hybrids known to have higher levels of chromosome pairing. Since in *L. curtissii* × *L. polycarpa* only one meiotic cell was studied, the observed configuration possibly could represent the lower limit of chromosome association in this hybrid. Variability of chromosome pairing is a common phenomenon in species hybrids. The stickiness of meiotic chromosomes of *L. polycarpa* × *L. curtissii*, however, may have a genetic basis, as it was rarely shown by either of the parental species, or the stickiness might be attributable to environmental factors. My unpublished study of meiosis in a sterile natural hybrid between *L. spathulata* and *L. palustris* (both sect. *Dantia*) was not successful in 1979 due to pronounced chromosome stickiness. Nevertheless, very clear chromosomal configurations for the same clone were obtained the next year.

In spite of the prevalence of univalents in meiosis, these hybrids usually set at least a few seeds. They were quite unlike the hybrids between the *L. curtissii* complex and the diploid group, which were completely sterile. This difference is probably attributable to the fact that, when both parents are polyploids, the development of functional pollen and ovules is better able to withstand the random segregation or loss of some chromosomes (as lagging univalents) in meiosis because of genetic redundancy.

Morphology of the hybrids

The hybrids were generally intermediate morphologically. The leaves were characteristically oblanceolate or narrowly oblanceolate. The intermediate nature of the size, shape, and pubesence of the capsules could be diagnostic, although the winged capsules characteristic of *L. alata* and *L. lanceolata* were not taxonomically useful, as the capsules of all the hybrids shriveled to some extent and thus appeared winged. The differences between hybrids with *L. curtissii* and with *L. simpsonii* as one parent were strictly quantitative, with the latter being slightly smaller in their floral features and occasionally in height also. These differences were obvious only when the two hybrids were brought together and compared. When *L. curtissii* and *L. simpsonii*, both of which shed pollen singly, were crossed with species in the *L. pilosa* group, which shed pollen as tetrads, the resultant hybrids consistently produced a mixture of pollen in loose tetrads and single grains.

ECOLOGY AND GEOGRAPHICAL DISTRIBUTION

With the exceptions of *L. stricta*, which is endemic to Cuba, and *L. polycarpa*, which is distributed mainly in the north-central United States, sect. *Microcarpium* is confined primarily to the Coastal Plain of the United States (Fig. 20). The detailed geographical distribution of each taxon in *Ludwigia* sect. *Microcarpium* is presented in a companion taxonomic paper (Peng, in press).

The Coastal Plain is defined geologically as the flat area between the Atlantic and Gulf coasts and the Piedmont, and extending from the Gulf of Mexico to southern New England (Peattie, 1922). The soils of this area are chiefly gray sands and sandy loams, except in the swamps where the prevailing sands are covered by muck or peat (Cooke, 1925). On the Coastal Plain, especially in areas close to the coast, the water table is seldom very far below the surface, and many areas are periodically or permanently flooded (Gleason & Cronquist, 1964). At one end of the Coastal Plain, in southern Texas, the climate is semiarid and the soils are alkaline, containing a high proportion of clay (Hunt, 1974).

In addition to this general distribution of species of sect. *Microcarpium* in North America, several species extend further south. *Ludwigia alata* occurs in Jamaica, *L. simpsonii* in Cuba and Jamaica, and *L. curtissii* in the Bahamas. *L. linifolia* is disjunct to Tabasco, in the Yucatán Peninsula of Mexico, and *L. microcarpa* ranges to the Bahamas, Cuba, and Jamaica. *Ludwigia stricta*, endemic to Cuba, is the only species of the section that does not occur in the United States.

Like *Ludwigia* species occurring in other parts of the world, plants of sect. *Microcarpium* grow in at least seasonally wet habitats. They are commonly found along alluvial ground or in the shallow water of many areas, including ponds, lakes, rivers, streams, lagoons, sloughs, backwaters, swales, wet meadows or prairies, open swamp forests, drainages, and irrigation ditches. All species grow in sandy or occasionally peaty soils.

SYMPATRIC OCCURRENCE AND NATURAL HYBRIDIZATION

The results of experimental hybridizations reveal that vigorous and floriferous hybrid individuals can

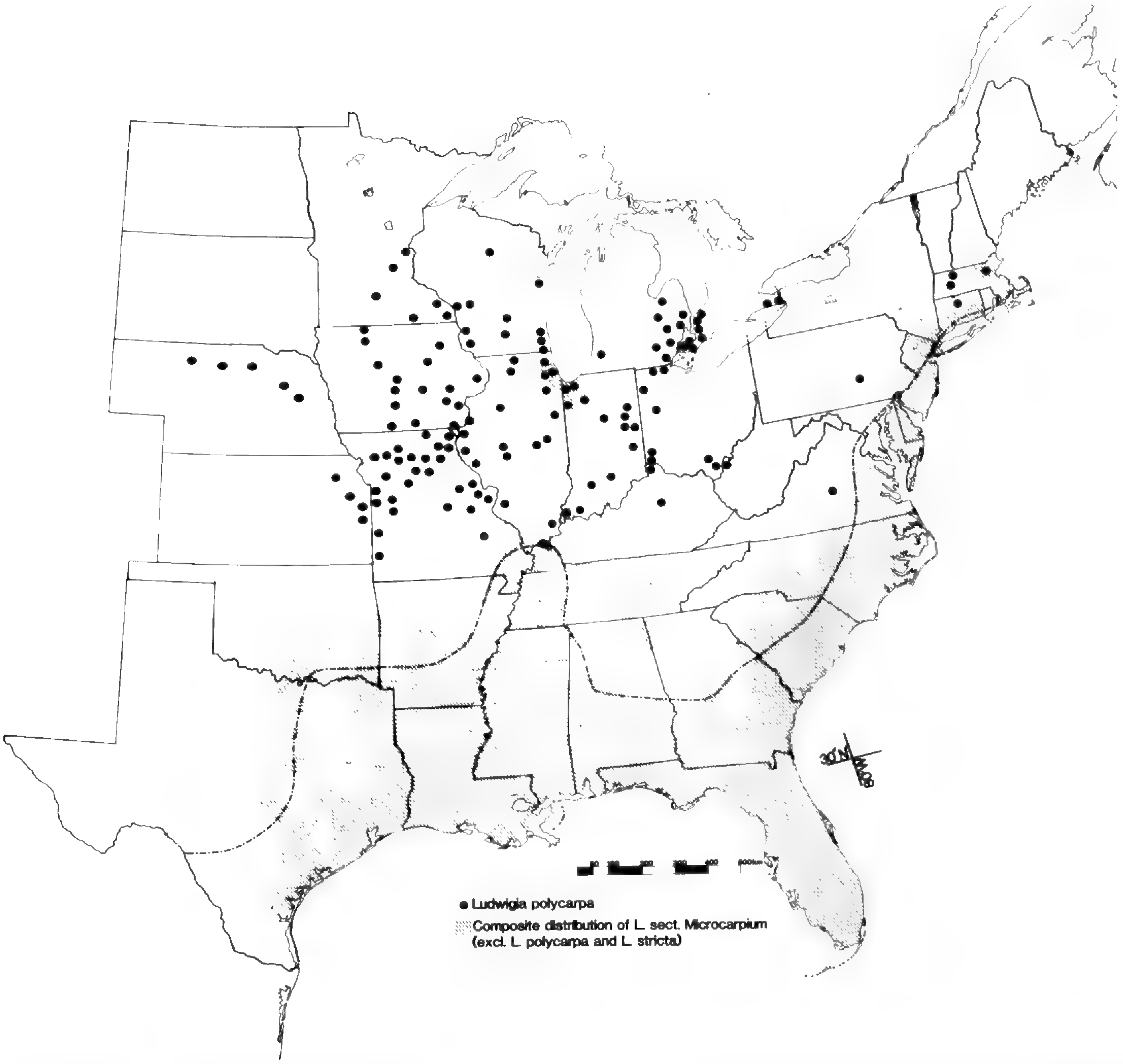
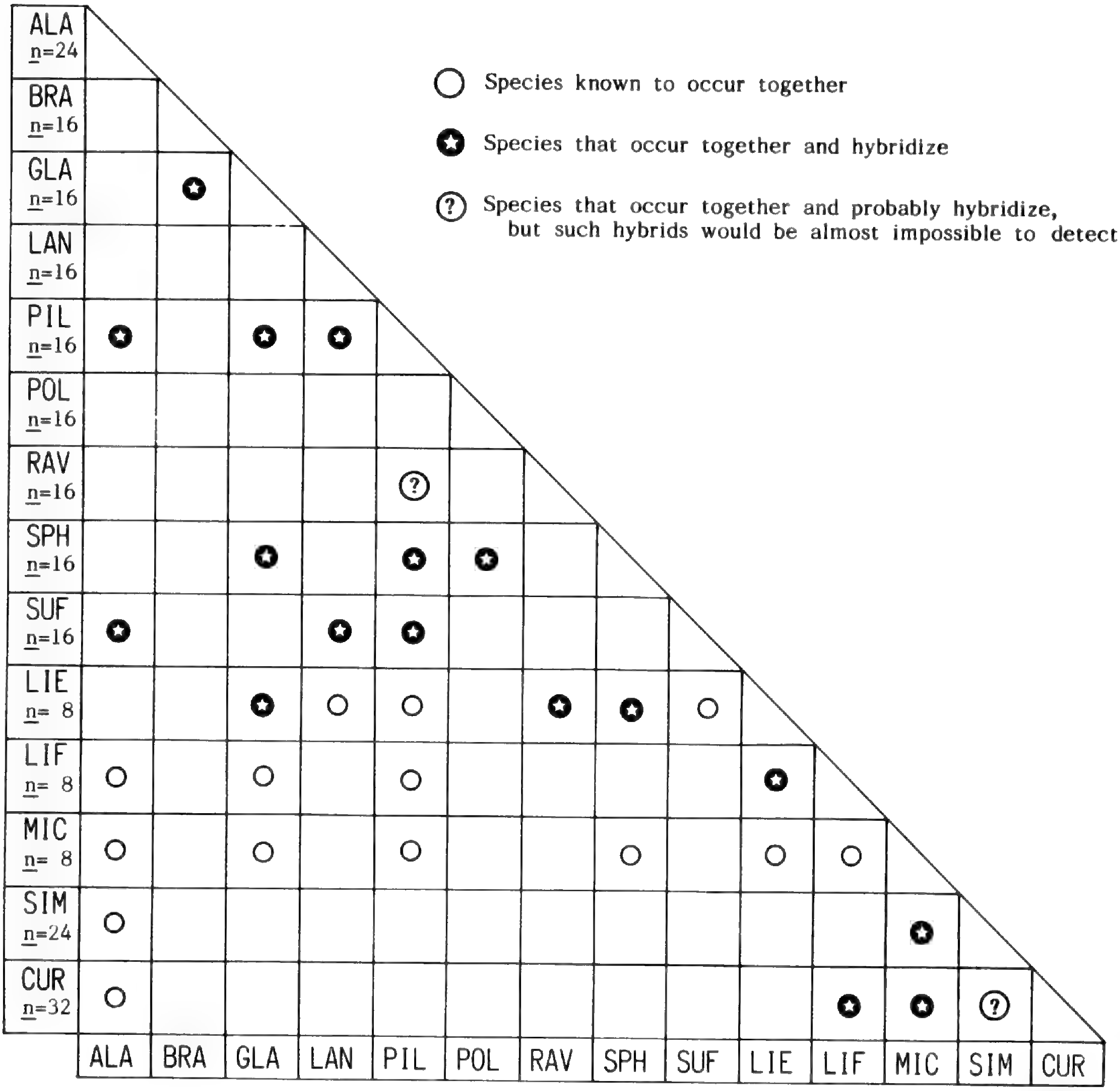


FIGURE 20. Distribution of *Ludwigia* sect. *Microcarpium* in North America, with shading to indicate the combined distribution of all species of this section except *L. polycarpa* and *L. stricta*. Distribution of *L. polycarpa* is indicated by dots; *L. stricta* is endemic to Cuba. Boundary of the Coastal Plain in the United States is marked by dashed line. Other occurrences of several species in the Bahamas, Cuba, Jamaica, and Mexico, and a disjunct population of *L. polycarpa* in Kootenai Co., Idaho, are not mapped.

readily be obtained between most members of sect. *Microcarpium*. Exceptions involved some crosses between members of the *L. pilosa* group (the tetraploid taxa plus the hexaploid *L. alata*) and either the diploid species (*L. linearis*, *L. linifolia*, and *L. microcarpa*) or members of the *L. curtissii* complex (*L. curtissii* and *L. simpsonii*) (Fig. 5). These crosses resulted in seeds that failed to germinate or in inviable hybrids. Even in these instances, if alternative parental strains were utilized to vary the genetic composition of the hybrids, vigorous F_1 individuals could sometimes be obtained. The general lack of postzygotic barriers, in conjunction with the facts that most *Ludwigia* species have overlapping geographic ranges, similar habitat requirements, and similar flowering periods (during the summer), and that they are at least facultatively outcrossing, favor natural hybridization.

Field observations and examination of herbarium specimens suggest that natural interspecific hybridization involving species of sect. *Microcarpium* occurs frequently. Intersectional hybridization is also quite common; at least seven hybrid combinations bridging sect. *Microcarpium* and sect. *Dantia* have been observed.

Observation of individuals exhibiting a combination of characters intermediate between distinct taxa initially suggests the possibility of natural hybridization. However, the members of two species



○ Species known to occur together

✪ Species that occur together and hybridize

(?) Species that occur together and probably hybridize, but such hybrids would be almost impossible to detect

	ALA	BRA	GLA	LAN	PIL	POL	RAV	SPH	SUF	LIE	LIF	MIC	SIM	CUR
ALA n=24														
BRA n=16														
GLA n=16		✪												
LAN n=16														
PIL n=16	✪		✪	✪										
POL n=16														
RAV n=16					(?)									
SPH n=16			✪		✪	✪								
SUF n=16	✪			✪	✪									
LIE n= 8			✪	○	○		✪	✪	○					
LIF n= 8	○		○		○					✪				
MIC n= 8	○		○		○			○		○	○			
SIM n=24	○											✪		
CUR n=32	○										✪	✪	(?)	

FIGURE 21. Sympatric occurrence of species in *Ludwigia* sect. *Microcarpium*. Acronyms are those given in Table 3.

pairs, *L. alata* (*n* = 24)/*L. lanceolata* (*n* = 16) and *L. curtissii* (*n* = 32)/*L. simpsonii* (*n* = 24), are usually so similar in appearance (especially as herbarium specimens) that their hybrids cannot be recognized readily.

As indicated earlier, capsule shape and size are the most important characters for detecting hybrids in sect. *Microcarpium*. Other useful features include overall pubescence, seed-surface cell shape and orientation, presence or absence of petals, whether pollen grains are shed singly or in tetrads, and pollen stainability. Seed-surface pattern is useful only for hybrids within the tetraploid group (including *L. alata*), as these nine taxa are interfertile, yield abundant seeds, and are diverse with respect to this character. Absence of developing fruits and low levels of pollen stainability are characteristic of hybrids resulting from all other interploid crosses, with the exception of *L. curtissii* (*n* = 32) × *L. simpsonii* (*n* = 24). Chromosome number and meiotic chromosome behavior are useful indicators of natural hybrids when the parents involved have different chromosome numbers or differentiated genomes.

Field experience indicates that the occurrence of natural hybrid populations is fairly common wherever two or more species grow together. Hybrids resulting from crosses between members of the *Ludwigia pilosa* group are very common. Also, many hybrid combinations have been observed involving the following species: *L. microcarpa*, *L. curtissii*, *L. simpsonii*, *L. palustris* (*n* = 8; sect. *Dantia*), and *L. repens* (*n* = 24; sect. *Dantia*).

Anderson (1948) suggested that disturbed habitats often afford conditions suitable for establishment of natural hybrids. This does not seem to be the case for *Ludwigia* hybrids, since the parental species themselves nearly always grow with the hybrids. Figure 21 illustrates the sympatric occurrence and known cases of hybridization in nature for all taxa of sect. *Microcarpium* except the Cuban endemic *L. stricta*. Sympatry was determined primarily from personal observation (in 1979, 1980, 1982) and supplemented by field notes of Peter H. Raven and from mixed herbarium collections. Voucher information for the suspected natural hybrids is presented below with comments when appropriate. Chromosome numbers of the parents are indicated in parentheses after their names. The sequence of epithets in each formula is alphabetical.

HYBRIDS INVOLVING MEMBERS OF *LUDWIGIA* SECT. *MICROCARPIUM*

Ludwigia alata (*n* = 24) × **L. pilosa** (*n* = 16). U.S.A. FLORIDA: Franklin Co., 38.8 mi. W of jct. US 98 and US 319, *Peng 4346* (MO). Wakulla Co., 5 mi. S of Sopchoppy on US 319, *Lazor 4984* (FSU, VDB); 1 mi. S of Sopchoppy on US 319, *Morar 29* (FLAS, GH, MSU, USF). Walton Co., Freeport, *Godfrey 57653* (FSU). GEORGIA: Charlton Co., of Folkston, Okefenokee Swamp, Camp Cornelia, *Jones 22996* (GA). MISSISSIPPI: Hancock Co., along Jordan River S of Kiln, *Jones 9539* (MISS).

Notes. *Peng 4346* from Franklin Co., Florida, was found in a very wide roadside drainage ditch (ca. 10–15 m across) at the edge of a pine forest. Hybrids were very abundant and mixed with a large population of *L. alata* and a few individuals of *L. pilosa*. Large populations of *L. linifolia* and *L. microcarpa* were also present. This hybrid exhibited meiotic configurations of 15–16 bivalents and 10–8 univalents. It had 84% stainable pollen.

Ludwigia alata (*n* = 24) × **L. suffruticosa** (*n* = 16). U.S.A. FLORIDA: Hillsborough Co., on E side of FL 581, 2.8 mi. N of FL 582, *Peng 4329* (MO). Lake Co., Tavares, *Biltmore Herbarium 4170*[d] (DS); vicinity of Eustis, *Hitchcock in 1894* (F), *Nash 1154* (NY); 5 mi. SE of Lebanon Station, *Kral 7807* (GA, GH, NCU, US, USF). Taylor Co., N edge of US 27 at Fenholloway River Bridge, *Nelson 667* (USCH); ca. 20 mi. NW of Cross City, *Godfrey & Houk 60296* (FSU, MSU, NCU, SMU).

Notes. More or less congested infloresence and winged capsules are characteristic of this hybrid combination. The hybrids were often identified as *L. alata* when they had lax inflorescences. In these cases, however, reduced levels of stainable pollen and intermediate seed surface cell pattern were useful in revealing the hybrids. *Peng 4329* showed a meiotic configuration of 15 bivalents and 10 univalents.

Ludwigia curtissii (*n* = 32) × **L. linifolia** (*n* = 8). U.S.A. FLORIDA: Monroe Co., Pine Crest, *Moldenke 856*[a] (MO, NY). Pasco Co., 1 mi. E of Gowers Corner off US 41, *Ray et al. 9932* (USF).

Notes. This hybrid is very similar to *L. curtissii* in aspect, but its pollen is not stainable, and its ovaries abort. One putative parent, *L. linifolia* (*Ray et al. 9934*, USF), was collected at the same locality as the hybrid (*Ray et al. 9932*).

Ludwigia curtissii (*n* = 32) × **L. microcarpa** (*n* = 8). U.S.A. FLORIDA: Martin Co., 4.3 mi. E of Okeechobee and Martin Co. line, on FL 710, at Brady Ranch, *Peng 4202* (MO).

Notes. The hybrid population was found in a wide swampy depression between the highway and a railroad, growing with both putative parents. The hybrid had a single analyzable metaphase I cell which showed 8 bivalents and 24 univalents. Pollen stainability was 16%.

Ludwigia glandulosa subsp. **glandulosa** (*n* = 16) × **L. pilosa** (*n* = 16). U.S.A. ALABAMA: Covington Co., along Co. Rd. 42, 15 mi. E of Brooklyn, *Kral 40992* (FLAS, GH, MO, NCU, NY, US, USF, VDB). GEORGIA: Grady Co., 13 air mi. SW of Cairo, 5 air mi. NE of Concord, Florida, with *L. pilosa*, *Anderson 4044* (MO, FSU). MISSISSIPPI: Jackson Co., Ocean Springs, *Demaree 32174* (RSA, SMU); on MS 90, 2 mi. W of US 10 and MS 90, with *L. pilosa*, *Peng 4354-A* (MO). NORTH CAROLINA: Hyde Co., 1.1 mi. N of Scranton Creek on US 264, with both putative parents, *Duke 54-232B* (NCU); 1.2 mi. N of Scranton Creek on US 264, with both putative parents, *Duke 54-276*, *54-277*, and *54-278* (NCU).

Ludwigia glandulosa subsp. **glandulosa** (n = 16) × **L. linearis** (n = 8). U.S.A. GEORGIA: Long Co., 4.2 mi. SW of jct. of US 301 and 25, and GA 99, on US 301 and 25, *Peng 4118* (MO). NORTH CAROLINA: Craven Co., 0.8 mi. N of US 17 on Co. Rd. 1224 (road to Tuscarora), *Boufford et al. 21443* (MO), *Peng 3740* (MO).

Notes. Both hybrid populations were found along with the putative parents. *Peng 3740* from Craven Co., North Carolina, was found in a wet drainage ditch about 60–80 cm wide. The population consisted of ca. 15–20 floriferous individuals, some of which were even more robust than the putative parents, which grew next to and on either side of the hybrid population. The modal meiotic configuration of this hybrid was 3–5 bivalents and 18–14 univalents. Heteromorphic pairs were sometimes observed. A trivalent was seen in one of the 26 cells studied. The pollen stainability was 2%. *Peng 4118*, from Long Co., Georgia, consisted of a few scattered individuals. The putative parents were growing nearby on a grassy roadside shoulder.

Ludwigia glandulosa subsp. **glandulosa** (n = 16) × *L. sphaerocarpa* (n = 16). U.S.A. MISSOURI: Butler Co., swamps, *Eggert in 1893* (MO). SOUTH CAROLINA: Clarendon Co., near shore of Lake Marion, ca. 4.5 mi. SW of St. Paul off US 15, *Bradley & Sears 3561* (BOON, East Carolina Univ., NCU, WCUH).

Notes. Bradley & Sears 3561 is a mixed collection; all four specimens contain a mixture of hybrids and individuals of *L. glandulosa* subsp. *glandulosa*. Although evident hybrids between *L. glandulosa* subsp. *glandulosa* and *L. sphaerocarpa* were found in Butler Co., Missouri, specimens of *L. sphaerocarpa* have not yet been collected from that state.

Ludwigia lanceolata (n = 16) × **L. pilosa** (n = 16) [*Ludwigia* ×*simulata* Small]. U.S.A. FLORIDA: Franklin Co., Apalachicola, *Chapman s.n.* (F, US). Highlands Co., Bear Point, Lake Childs, *Brass 15532* (GH, US). West Florida, *Biltmore Herbarium* (NY, holotype of *Ludwigia* ×*simulata* Small).

Notes. The holotype of *L.* ×*simulata* is characterized by being densely strigillose throughout and having four-angled or slightly winged capsules, isodiametric seed-surface cells, and pollen shed in tight tetrads. Such a combination of characters clearly suggests *L. lanceolata* (which is glabrous, has winged capsules, isodiametric seed surface cells, and pollen shed in tetrads) and *L. pilosa* (which is densely hirsute, has rounded capsules, isodiametric seed-surface cells, and pollen shed in tetrads) as putative parents. Furthermore, *L.* ×*simulata* is comparable to the experimental hybrids obtained from reciprocal crosses between those species.

Ludwigia lanceolata (n = 16) × **L. suffruticosa** (n = 16). U.S.A. FLORIDA: Charlton Co., Okefenokee Swamp, *Harper 1483* (GH, MO, NCU, NY, US). Hillsborough Co., 1.5–1.7 mi. S of FL 674, on E side of Taylor Gill Dr., *Peng 4324, 4328* (MO).

Notes. Both putative parents as well as *L. linearis* were present in the same drainage ditch where *Peng 4324* and *Peng 4328* were collected. *Peng 4324* showed 16 bivalents in diakinesis and metaphase I cells. One precociously separating bivalent was occasionally observed. *Peng 4324* had 85% stainable pollen.

Ludwigia linearis (n = 8) × **L. linifolia** (n = 8). U.S.A. FLORIDA: Palm Beach Co., along the S side of Co. Rd. 74, 1.5 mi. W of the Turnpike, Palm Beach Gardens, *Popenoe 1957* (MO).

Notes. This plant is only 25–30 cm tall and has crowded leaves. It showed features somewhat intermediate between those of *L. linearis* and those of *L. linifolia* in its flowers and capsules. The pollen was shed as tetrads, many of which are unstainable. This plant probably is a hybrid between *L. linearis* and *L. linifolia*, although the experimental hybrids obtained between these taxa have been more robust.

Ludwigia linearis (n = 8) × **L. sphaerocarpa** (n = 16). U.S.A. ALABAMA: Covington Co., Conecuh National Forest, SW Andalusia, *Kral 44732* (ENCB, SMU, VDB).

Notes. The plants are very vigorous and floriferous. One to four vestigial petals are present in most flowers. Seed set is very low or possibly nonexistent.

Ludwigia microcarpa (n = 8) × **L. simpsonii** (n = 24). U.S.A. FLORIDA: Charlotte Co., Punta Gorda City, on US 41, ca. 1 mi. S of jct. of US 17 and 41, *Peng 4297* (MO). Clay Co., 5 mi. W of Penny Farms on FL 16, *Peng 4160* (MO). Collier Co., 4.8 mi. W of Monroe Station, on N side of US 41, *Peng 4263* (MO).

Sumter Co., Cedar Hammock, 1894, *Lewton s.n.* (NY).

Notes. *Peng 4297* from Charlotte Co., Florida, was found intermixed with both parents. Also occurring here were *L. microcarpa*, *L. repens* (sect. *Dantia*), and the intersectional hybrid between them. Of the nine meiotic metaphase I cells examined from *Peng 4297*, seven showed 8 bivalents and 16 univalents, and two showed 9 bivalents and 14 univalents. In the latter, one of the bivalents separated precociously. Pollen stainability was 4%. *Peng 4160*, from Clay Co., Florida, was collected from a large population located in a waterlogged roadside ditch along the margin of a pine woodland. The hybrids were intermixed with one of the putative parents, *L. microcarpa*. Across the highway in the similar habitat was another very large, pure population of *L. microcarpa*. *Peng 4160* had 9% stainable pollen. *Peng 4263*, from Collier Co., Florida, was found in an open palmetto–cypress forest, with both putative parents growing nearby. One somewhat analyzable metaphase I cell from this plant showed 8 bivalents and 16 univalents. Pollen stainability was 24%.

Ludwigia pilosa ($n = 16$) × **L. sphaerocarpa** ($n = 16$).

Before discussing this hybrid combination, a few comments on *L. sphaerocarpa* are appropriate. This species is quite variable and has a widely scattered distribution (Fig. 22). Populations of *L. sphaerocarpa* consist of individuals that are extremely varied in overall pubescence, leaf shape and size, fruit size, and density of fruits on branches. Three varieties (var. *jungens*, var. *macrocarpa*, and var. *deamii*) have been recognized previously within this species (Fernald & Griscom, 1935) based on various combinations of the above characters. Study of numerous herbarium specimens not available to Fernald & Griscom, however, revealed that correlations between these characteristics are not consistent. It is of interest to note that, although seed-surface cell pattern is generally very regular within populations of members of sect. *Microcarpium* (Figs. 1–3), this is not the case for *L. sphaerocarpa* (Fig. 4). The seed surfaces are arranged in columnar cells both transversely elongate and parallel to the seed length, with the former alignment often predominant in the central part of the seeds (Fig. 4). Seeds with variously oriented surface cells are also seen in some populations. A comparison of the irregular seed surface pattern in *L. sphaerocarpa* with that of various artificial hybrid combinations (Figs. 6–19) strongly suggests that earlier hybridizations within the interfertile tetraploid group of sect. *Microcarpium* may have resulted in production of this widespread series of populations that have more or less stabilized in some of their characteristics.

Morphological variation in *L. sphaerocarpa* is further complicated by its frequent natural hybridization with *L. pilosa* (and perhaps with *L. ravenii* as well, although it would be difficult to distinguish these hybrids from those involving *L. pilosa*), which has apparently resulted in many hybrid swarms or introgressed populations. These plants are generally neither typical of *L. pilosa* nor of *L. sphaerocarpa* and exhibit varying degrees of intermediacy between the two species. The diagnostic characters for the hybrids include overall pubescence, leaf shape, bracteole size and location, sepal shape and size, and color of abaxial leaf venation. Examples of populations of such intermediates are too numerous to cite here. Instead they have been mapped (Fig. 22). It is of interest to note that some of the hybrid populations occur in central and southern Florida where typical *L. pilosa* and *L. sphaerocarpa* are absent; this suggests that physiological characteristics, and thereby ecological tolerances, may recombine into novel adaptive combinations in the hybrids also.

Artificial hybrids between *L. pilosa* and *L. sphaerocarpa* were synthesized in an experimental greenhouse. Plants of this hybrid combination showed 15–16 bivalents and exhibited the highest level of stainable pollen (98%) among all the tetraploid hybrids.

Ludwigia pilosa ($n = 16$) × **L. suffruticosa** ($n = 16$) [*L. capitata β pubens* Torrey & A. Gray]. U.S.A. FLORIDA: Citrus Co., 5 mi. S of Homosassa, *Kral 7771* (FLAS, GH, both mixed with *L. suffruticosa*). Gadsden Co., along Old Bainbridge Rd. (Rte. 173); 0.5 mi. NW of Ochlockonee River bridge, NW of Tallahassee, *Anderson 7486* (FSU). Seminole Co., W shore of Prairie Lake, *Schallert 16009, 28652* (S). GEORGIA: McIntosh Co., on Sapelo Isl., ca. 1.4 mi. WNW of S tip of Blackbeard Isl., *Duncan 20445* (DUKE, F, GH, NCU, SMU, TEX, US, USF). Wayne Co., near Jessup, *Biltmore Herbarium 4174*^{c} (US). GEORGIA (?): *Baldwin Herbarium* (NY, holotype of *Ludwigia capitata* Michaux *β pubens* Torrey & A. Gray, mixed with *L. suffruticosa* Walter). SOUTH CAROLINA: Darlington Co., Hartsville, *Smith 44* (NCU). Georgetown Co., North Santee, *Radford 28678* (NCU, NY, VDB).

FIGURE 22. Distribution of *Ludwigia pilosa* (shading), *L. sphaerocarpa* (stippling), and their natural hybrids (dots).

Ludwigia polycarpa (n = 16) × **L. sphaerocarpa** (n = 16). U.S.A. INDIANA: Starke Co., border of Bass Lake, 5 mi. S of Knox, *Kriebel 5715* (SMU); SW corner of Bass Lake, *Friesner 16306* (CAS, NY).

Notes. *Ludwigia polycarpa*, which occurs in the central Midwest (Fig. 20), is effectively isolated geographically from all other species of sect. *Microcarpium*, with the exception of *L. sphaerocarpa*. Where the two species come into contact, hybridization occurs.

The following is a list of collections of hybrids for which the identity of the putative parents is not certain:

?Ludwigia linearis (n = 8) × **L. ravenii** (n = 16). U.S.A. NORTH CAROLINA: Duplin Co., 3 mi. E of Sarecta, *Beal 3674* (NCSC).

Notes. This is a much-branched, densely villous plant with sublinear leaves and small, elongate-pyramidal ovaries that abort after anthesis. The pubescence suggests that either *L. pilosa* or *L. ravenii* is involved in the parentage. The aborted ovaries indicate that hybridization involved one of the above species and a taxon outside of the interfertile *L. pilosa* group. The elongate ovaries and narrow leaves indicate clearly that either *L. linearis* or *L. linifolia* is the other parent. Floral characters as well as geographical distribution of these species, however, indicate that *Beal 3674* from Duplin Co., North Carolina, is probably a hybrid between *L. linearis* and *L. ravenii.*

Ludwigia microcarpa (n = 8) × **L. curtissii** (n = 32)/**L. simpsonii** (n = 24). U.S.A. FLORIDA: Flagler Co., 6 mi. E of Co. line, Hwy. 28 near Andalusia, *West in 1940* (FLAS). Lake Co., 7 mi. SW Okahumpka, *Kral 7611* (FLAS, FSU, GH).

Notes. *Kral 7611* represents a mixture of several species and hybrids. Specimens deposited in GA, GH, US, VDB are *L. microcarpa,* whereas the specimen at FSU contains both the hybrid and either *L. curtissii* or *L. simpsonii,* the separation of which is difficult, since mature capsules are not present.

?Ludwigia pilosa (n = 16) × **L. suffruticosa** (n = 16). U.S.A. FLORIDA: Jackson Co., Ocheesee Lodge Landing S of US 90, near Sneads, *Jones 23569* (GA). Co. unknown, S Florida, *Chapman Herbarium* (NY). GEORGIA: Lee Co., near US 19, ca. 4 mi. S of Smithville, *Moran 2551* (GA).

Notes. These specimens are less pubescent than typical *L. pilosa* × *L. suffruticosa* hybrids. They are for the most part densely strigillose only in the branched and somewhat lax inflorescence and may represent backcrossed populations or segregates of advanced generation of the hybrid *L. pilosa* × *L. suffruticosa.*

HYBRIDS BETWEEN MEMBERS OF *LUDWIGIA* SECTS. *MICROCARPIUM* AND *DANTIA*

Hybrids between members of sects. *Microcarpium* and *Dantia* are easy to recognize; members of sect. *Microcarpium* are erect plants with alternate leaves, whereas plants belonging to sect. *Dantia* are prostrate and have opposite leaves. Intermediacy in these two characters signals hybridization between the two sections.

Ludwigia arcuata (n = 16; sect. *Dantia*) × **L. pilosa** (n = 16). U.S.A. ALABAMA: Mobile Co., Audubon Bird Sanctuary, Dauphin Isl., *Deramus D643* (DS, UNA).

Notes. Hybrids of this combination were synthesized in the experimental greenhouse. They showed a modal meiotic configuration of 12–15 bivalents and 8–2 univalents; 1–2 trivalents were sometimes observed. The high degree of chromosome pairing observed between species of the two sections was quite unexpected. This artificial hybrid, however, had only 38% stainable pollen. Since selfing in the hybrid is physically impossible, as in *L. pilosa,* artificial pollination was attempted in order to investigate seed set. None of the pollination attempts yielded any seed set, even though some seeds were observed in mature capsules of the natural hybrids.

Ludwigia curtissii (n = 32) × **L. repens** (n = 24; sect. *Dantia*). U.S.A. FLORIDA: Glades Co., 4.4 mi. SE of jct. of FL 29 with US 27, with both parents, *Raven 18680* (MO). Lee Co., on US 41, 5 mi. N of Ft. Meyers, with both parents, *Dille & Dille 379* (MO).

Notes. *Ludwigia curtissii* (n = 32) and *L. simpsonii* (n = 24) hybridize with *L. repens* in nature. Unless chromosome numbers are counted, it is unlikely that one would be able to distinguish between these two hybrid combinations morphologically.

Ludwigia curtissii (n = 32)/**L. simpsonii** (n = 24) × **L. repens** (n = 24; sect. *Dantia*). U.S.A. FLORIDA: Charlotte Co., 12 mi. S of Punta Gorda, *Kral 18058* (VDB). Lee Co., 5 mi. S of Bonita Springs, *Crevasse in 1940* (FLAS). Manatee Co., Bradentown, *Cuthbert in 1926* (FLAS). Wakulla Co., between Hwys. 365–367, N of Spring Creek, *Lazor 4561* (NCU).

Ludwigia repens (n = 24; sect. *Dantia*) × **L. simpsonii** (n = 24). U.S.A. FLORIDA: Charlotte Co., Punta Gorda City, on US 41, ca. 1 mi. S of jct. of US 17 and 41, *Peng 4296* (MO).

Notes. This hybrid grew intermixed with both putative parents along a roadside field. It formed 0–1 bivalent(s) and 48–46 univalents in metaphase I cells. This result corroborates an earlier report by Schmidt (1967) [FLORIDA: Glades Co., 8.4 mi. SE of jct. of FL 29 on US 27, *Raven 18849* (DS)].

Ludwigia glandulosa subsp. **glandulosa** (n = 16) × **L. palustris** (n = 8; sect. *Dantia*). U.S.A. ARKANSAS: Clark Co., Okolona, *Demaree 16120* (DS, GA, GH, MO, NY, SMU, TENN). NORTH CAROLINA: Co. unknown, stagnant water just S of Upper Littel River on US 401, *Lloyd in 1962* (MO). Johnston Co., 4.9 mi. W of NC 210 and US 70, on US 70, E of Clinton, *Ahles 59736* (NCU), *61803* (DS, NCU, SMU). OKLAHOMA: Johnston Co., Devil's Den, 4.6 mi. NW of Tishomingo, *Crutchfield 2882* (LL). VIRGINIA: Fluvanna Co., just S of Rt. 696, 1 mi. S of Rt. 250, *Diggs & Diggs 353* (NCU).

Notes. Plants of *Lloyd in 1962* from North Carolina showed 24 univalents in meiosis (Raven, pers. comm.). Schmidt (1967) reported "at most three weakly joined bivalents" in the hybrid plant from North Carolina [Harnet Co., 5.1 mi. S of Lillington, *Lloyd 1022* (DS)]. Artificial hybrids recently synthesized, however, showed higher chromosome associations in meiosis, in the range five to eight bivalents modally.

Ludwigia microcarpa ($n = 8$) × **L. palustris** ($n = 8$; sect *Dantia*). U.S.A. FLORIDA: Franklin Co., 41.7 mi. W of jct. of US 98 and 319, with both putative parents, *Peng 4349* (MO). Hamilton Co., off I-75, ca. 1 mi. N of Columbia Co. line, *Bowers & Wofford 71-550-F* (TENN, a mixture of *L. repens, L. microcarpa*, and *L. microcarpa* × *L. palustris*). Lake Co., 3.7 mi. S of Mascotte city limit, on Co. Rd. 33, with *L. microcarpa* and *L. palustris, Peng 4167* (MO). GEORGIA: Camden Co., 6.6 mi. S of Woodbine on US 17, with *L. microcarpa* and *L. repens, Raven 18704* (MO). NORTH CAROLINA: Jones Co., near NC 41, 0.7 mi. E of Taylor's Corner, *Radford 37152* (NCU).

Notes. Peng 4349 from Franklin Co., Florida, was collected from a large population growing intermixed with both putative parents along a swampy ditch. *Peng 4167* from Lake Co., Florida, was found growing with both putative parents in a narrow ditch. Pollen stainability was 5% in *Peng 4349*. Artificial hybrids of this combination were synthesized and showed 2–5 bivalents and 12–6 univalents in meiotic metaphase I.

Observations from experimental hybridization indicate that hybrid combinations of *L. microcarpa* ($n = 8$) × *L. palustris* ($n = 8$; sect. *Dantia*) and *L. microcarpa* ($n = 8$) × *L. repens* ($n = 24$; sect. *Dantia*) are prostrate herbs with similar leaf shape and minute flowers that abort after anthesis. In *L. microcarpa* × *L. palustris*, the flowers are apetalous as in both parents, and the phyllotaxy is intermediate; the plants have alternate, opposite, and subopposite leaves. By contrast, in *L. microcarpa* × *L. repens* the leaves are always opposite as in *L. repens*, and some of the flowers have one to four vestigial petals. The apparent dominance of the traits of the hexaploid parent over those of the diploid parent is probably due to a multiple dosage of genetic information from the hexaploid.

In two instances, *Bowers & Wofford* (VDB) and *Raven 18704* (MO), the hybrids were collected along with *L. microcarpa* and *L. repens*; *L. palustris* was not observed locally. Although these plants, which have aborted ovaries, might have been considered as hybrids between *L. microcarpa* and *L. repens* on this basis, detailed examination of their flowers and leaves reveals that they are *L. microcarpa* × *L. palustris*.

Ludwigia polycarpa ($n = 16$) × **L. palustris** ($n = 8$; sect. *Dantia*). U.S.A. KENTUCKY: Ballard Co., at intersection of Kelley Branch Creek Rd. and KY 473, *Athey 1158* (NCU, NY, VDB). OHIO: Erie Co., in bottom of South Quarry at N edge of town on Kelley's Isl., *Stuckey 7400* (PH).

Notes. Although one of the putative parents, *L. polycarpa*, has not been recorded from Ballard Co. in extreme southwest Kentucky, it was collected from adjacent Massac Co., Illinois. *Ludwigia palustris* is common in Ballard Co., Kentucky. Plants of *Athey 1158* are comparable to artificial hybrids between these species synthesized in an experimental greenhouse.

In summary, geographical isolation and self-pollination are the primary factors limiting natural hybridization in species of sect. *Microcarpium*. For example, *L. microcarpa*, an extreme selfer, has been hybridized successfully with most species of sect. *Microcarpium* in the greenhouse, and the resulting hybrids were vigorous. It grows sympatrically with many other species (Fig. 21), but natural hybrids have been found only with *L. simpsonii, L. curtissii*, and members of sect. *Dantia*.

In general, however, natural hybrids in sect. *Microcarpium* are frequently found wherever two species occur together. This is particularly so for plants in the tetraploid group (including the hexaploid *L. alata*; Fig. 21), which were often found intermixed with their putative parents.

Especially evident in *L. pilosa* and hybrid populations involving *L. sphaerocarpa* were the effects of backcrossing and introgression, which may provide the hybrid populations with increased evolutionary flexibility, thus enabling them to grow in areas where neither of the parents are found.

As outlined above, natural hybridization is not limited to species within sect. *Microcarpium*. At least seven hybrid combinations, some of which occur commonly in nature, have been found between members of sect. *Microcarpium* and sect. *Dantia.* Most of these have also been synthesized in the experimental greenhouse. Most intersectional hybrids, however, do not set seed, although they are usually very vigorous and appear to compete well with their parents. Once established, these sterile hybrids may be able to persist in a given location due to their perennial habit. New colonies may be established vegetatively if entire parents or fragments are transported to suitable habitats, most likely by water.

SPECIES RELATIONSHIPS AND EVOLUTION

Among the four diploid species, *L. microcarpa* is quite distinct from *L. linearis, L. linifolia,* and *L. stricta.* Plants of *L. microcarpa* are small herbs with spatulate or obovate-spatulate leaves, minute apetalous flowers from which the pollen is shed singly, and short, tiny capsules; whereas the other three species have linear leaves, somewhat showy flowers with four petals from which the pollen is shed in tetrads, and elongate capsules. They appear to be relatively closely related to one another.

All eight taxa in the tetraploid ($n = 16$) group, including *L. alata* ($n = 24$), are apetalous. Their leaves range from linear-lanceolate to lanceolate, elliptic, or oblanceolate. They differ from each other in a number of characters, including capsule morphology, seed-surface pattern, pubescence, and the way in which pollen is shed.

Although *L. alata* and *L. simpsonii* are both hexaploids ($n = 24$), morphological characters suggest that they are not closely related. *Ludwigia alata,* which has winged capsules, is most similar to *L. lanceolata* of the tetraploid group, although it can be distinguished by having pollen shed singly, seed surfaces consisting of columnar cells elongate transversely to the seed length (Fig. 3), and by being modally outcrossing. *Ludwigia lanceolata* sheds its pollen in tetrads, has isodiametric seed-surface cells (Fig. 1), and is autogamous.

By contrast, hexaploid *Ludwigia simpsonii* resembles octoploid *L. curtissii* ($n = 32$). These two species can be distinguished relatively consistently only by the size of their mature capsules, although even this character is not always reliable. Both exhibit a specialized type of capsular dehiscence unique in sect. *Microcarpium.* Moreover, *L. simpsonii* and *L. curtissii,* along with the diploid *L. microcarpa,* are the only species in the section with spatulate or obovate-spatulate cauline leaves. There appears to be a close relationship between *L. microcarpa* and the *L. curtissii* complex.

Results from the crossing program and chromosome analysis of the artificial and natural hybrids confirm these general observations and provide additional evidence for some of the evolutionary relationships discussed below.

RELATIONSHIPS AMONG THE DIPLOID SPECIES (*L. LINEARIS, L. LINIFOLIA, L. STRICTA, L. MICROCARPA*)

The presence of a quadrivalent during meiosis of reciprocal hybrids of *L. linearis* × *L. linifolia* indicates that the genomes of the strains hybridized differ by a reciprocal translocation. Although reciprocal translocations are very frequent in the tribe Onagreae, they are rare in the remainder of the family; their presence here indicates that chromosomal repatterning has occurred between the strains hybridized. The artificially produced F_1 hybrids were very vigorous and set abundant seeds, although many of the F_2 plants were either weak or inviable. Presumably *L. stricta* will show a comparable degree of differentiation.

The hybrids between *L. microcarpa* and either *L. linearis* or *L. linifolia* showed very few (0–3) bivalents in meiosis. The bivalents sometimes appeared to be held together by matrix connections rather than by chiasmata; some of them were heteromorphic, and the chromosomes did not always line up in the equatorial plane. Taken together, these phenomena indicate that *L. microcarpa* has a diploid genome essentially different from that of either *L. linearis* or *L. linifolia,* and presumably *L. stricta* as well.

RELATIONSHIPS AMONG THE TETRAPLOID TAXA (*L. GLANDULOSA* SUBSP. *GLANDULOSA, L. GLANDULOSA* SUBSP. *BRACHYCARPA, L. LANCEOLATA, L. PILOSA, L. POLYCARPA, L. RAVENII, L. SPHAEROCARPA,* AND *L. SUFFRUTICOSA*)

This is a group of eight diverse and morphologically well-delimited taxa. Artificial hybridization between any two species nearly always resulted in vigorously growing individuals with nearly complete chromosome pairing, high levels of stainable pollen, and abundant seeds. Many vigorous F_2 plants were raised that exhibited various degrees of intermediacy between the parents. This group is interpreted as representing an assemblage of interfertile tetraploid species that have two genomes in common and thus represents a homogamic complex.

ORIGIN OF THE TWO GENOMES IN THE TETRAPLOID SPECIES

Most of the tetraploid species have been crossed with each of the three diploid species included in this study in order to assess whether one or more of the extant diploid species has been involved in their formation. *Ludwigia linearis* and *L. linifolia* were shown to share a similar genome that has undergone some chromosomal repatterning. Hybrids between either of these diploid species and any tetraploid species produced 3–7 bivalents in meiosis. Hybrids between *L. microcarpa* and the tetraploid species showed 1–6 bivalents in meiosis. Two lines of evidence suggest that the chromosomal pairing in these hybrids is the result of pairing of chromosomes between the diploid and the tetraploid rather than pairing between the two genomes present in the tetraploid. First, hybrids between *L. linifolia* (♀; $n = 8$) and *L. lanceolata* (♂; $n = 16$) were themselves tetraploid, modally forming 8 bivalents and 16 univalents in meiosis. This tetraploid chromosome number apparently resulted from the union of an unreduced egg from the diploid parent with a normal sperm nucleus from the tetraploid. This unexpected result strongly suggests that the 8 bivalents observed represent paired chromosomes from the duplicated *L. linifolia* genomes, while the 16 univalents are the chromosomes from the two genomes of the tetraploid parent, which are sufficiently different to remain unpaired. Pairing between chromosomes of *L. linifolia* and those of the tetraploids is evidently precluded by preferential pairing between the two sets of chromosomes derived from *L. linifolia*.

Second, when *L. glandulosa* ($n = 16$) was crossed with *L. alternifolia* ($n = 8$), a less closely related species belonging to sect. *Ludwigia*, the resulting hybrids exhibited 0–1 bivalent(s) in meiosis; the one bivalent that was occasionally observed was only loosely associated. This lack of pairing also suggests that the tetraploid species are alloploids with two unlike genomes.

As noted earlier, two distinct genomes appear to be represented among the diploid species; one shared by *L. linearis*, *L. linifolia*, and probably *L. stricta*, and another found in *L. microcarpa*.

Hybridization between any of these species and the tetraploid taxa consistently results in F_1 offspring that show only about 2–7 bivalents, some of them heteromorphic, in meiosis. This strongly suggests that neither of the two genomes present in the tetraploids was derived from an existing diploid.

ORIGIN OF GENOMES IN THE HEXAPLOID *LUDWIGIA ALATA*

Nearly all of the reciprocal hybrids between the hexaploid *L. alata* and the tetraploid species exhibited a modal meiotic configuration of 16 bivalents and 8 univalents. This suggests that they share two genomes: the 16 chromosomes of the tetraploid species pair with their homologues present in the genome of the hexaploid species, while the additional eight chromosomes in *L. alata* remain unpaired and appear to represent a third genome present in *L. alata*.

Ludwigia alata was also crossed with the diploid species in an attempt to assess whether this "third genome" is in fact homologous to one of those present in the existent diploid taxa. Hybrids between *L. alata* and either *L. linearis* or *L. linifolia* typically exhibit a configuration of 1–2 trivalents and 4–6 bivalents with the rest of the chromosomes univalents. Again, heteromorphic pairs are common here. These results are similar to those observed in hybrids between *L. linearis* and *L. linifolia* and the tetraploid taxa. Since the two genomes of the tetraploid species appear to be present in *L. alata*, it is presumed that the bivalents are formed between chromosomes derived from the parental taxa. By contrast, meiosis in hybrids between *L. microcarpa* and *L. alata* shows a high degree of chromosome pairing, with a modal configuration of one quadrivalent, 7–10 bivalents, and a corresponding number of univalents. The maximum amount of pairing seen was 11II + 10I or 1III + 10II + 8I. These chromosome associations involve bivalents of normal appearance, either rings or rods, a situation that contrasts with the sorts of loosely associated bivalents characteristic of hybrids between *L. microcarpa* and the tetraploid taxa. The higher level of chromosome pairing (more than eight bivalents) and the normal appearance of the pairs suggest that the hexaploid *L. alata* may have been derived following hybridization between *L. microcarpa* and one of the tetraploids. Indeed *L. alata* is similar to *L. microcarpa* in that (1) its seed surface consists of columnar cells transversely elongate to the seed length, and (2) its pollen grains are shed singly. These characters are rarely found among members of the tetraploid species group, with which *L. alata* shares two genomes.

ORIGIN OF GENOMES IN THE *LUDWIGIA CURTISSII* COMPLEX

The *L. curtissii* complex consists of *L. simpsonii* ($n = 24$) and *L. curtissii* ($n = 32$). Hybrids between the two species consistently reveal 24 bivalents and 8 univalents in meiosis. This indicates that chromosomes of the three genomes in *L. simpsonii* pair with homologues in *L. curtissii*, leaving the eight additional chromosomes in this species unpaired. Naturally occurring intersectional hybrids between *L. repens* ($n = 24$; sect. *Dantia*) and *L. simpsonii* produce a meiotic configuration of 48 univalents or 46 univalents and two loosely associated chromosomes. This strongly suggests that the three genomes in *L. simpsonii* are distinct from each other and not homologous with any of the genomes present in *L. repens*.

For ease of discussion, letters will be used to designate distinct, nonhomologous genomes. Since the five genomes present in *Ludwigia* sect. *Dantia* have been designated as A, B, C, D, and E (Schmidt, 1967), the genomic formula GGHHII will be used for *L. simpsonii* and FFGGHHII for *L. curtissii*.

The natural hybrid *L. microcarpa* × *L. simpsonii* has a meiotic configuration of 8 bivalents and 16 univalents. The eight chromosomes of *L. microcarpa* thus have 8 homologues in *L. simpsonii*, and its genome is designated as GG.

A configuration of 8 bivalents and 24 univalents is expected in meiotic cells of the hybrid *L. curtissii* (FFGGHHII) × *L. microcarpa* (GG). In a natural hybrid of this combination, the single analyzable cell did indeed show this configuration. In an artificial hybrid, however, more than 8 bivalents have been observed: five cells exhibited 14–15 bivalents and 12–10 univalents. Some intergenomic interaction must have led to the observed configurations.

In the meiosis of *L. curtissii* (FFGGHHII) × *L. linifolia* ($n = 8$), a modal configuration of 8 bivalents and 24 univalents was observed. The genome common to *L. linearis* and *L. linifolia* is designated FF, since it differs from that present in *L. microcarpa* (GG). As in the case of *L. curtissii* × *L. microcarpa*, however, a few meiotic cells in *L. curtissii* × *L. linifolia* exhibited more than 8 bivalents; up to 12 have been observed.

Figure 23 summarizes the chromosomal homologies in the *L. curtissii* complex. The hexaploid *L. simpsonii* appears to have been derived from three different diploid lines. Morphological as well as chromosome pairing data indicate that the diploid *L. microcarpa* has been involved in the formation of *L. simpsonii*. Based on morphology, it seems unlikely that a member of the *L. linifolia*/*L. linearis* lineage could have been a parent of *L. simpsonii*. Nevertheless, it will be necessary to examine meiosis in the artificial hybrid between *L. simpsonii* and *L. linearis* or *L. linifolia*. Although plants of *L. simpsonii* × *L. linearis* were available, my attempts to study meiosis in them were unsuccessful. The octoploid *L. curtissii* was probably derived following hybridization between a diploid similar to *L. linearis* or *L. linifolia* with the hexaploid *L. simpsonii*, based on morphological data and crossing relationships.

To study the genetic relationships among plants from the tetraploid group (including the hexaploid *L. alata*) and the *L. curtissii* complex, 11 artificial hybrids were produced, 5 of which have been studied cytologically. The number of bivalents observed ranged from 4 to 13; a few trivalents and quadrivalents were also frequently seen (Table 15). Chromosome associations between the polyploids of the tetraploid group and the three diploid species, on the one hand, and those observed between the *L. curtissii* group and the diploid species, on the other hand, are consistent with these results.

Following the differentiation of diploid species of sect. *Microcarpium*, some have evidently become extinct. Natural hybridization between the diploid lineages followed by polyploidy has played a major role in the evolution of this group. Postzygotic genetic barriers do not exist between most of the extant species in the section. Rather, the major limiting factor to natural hybridization appears to be the modally autogamous breeding system of most species. Geographical isolation is important only with respect to *L. polycarpa*, which is distributed well to the north of nearly all the other taxa.

Natural hybridization is prevalent within sect. *Microcarpium*, and hybrids often occur in more or less undisturbed habitats where the parental taxa also grow. All interploid hybrids are sterile except for crosses between *L. alata* ($n = 24$) and the tetraploid species ($n = 16$), and crosses between *L. curtissii* ($n = 32$) and *L. simpsonii* ($n = 24$). Even sterile hybrids can persist and form large colonies, at least locally, and compete effectively with their parents, because of strong vegetative reproduction by means of stolons. Natural hybrids are especially common among members of the tetraploid group (including *L. alata*) and are nearly always vigorous and fertile.

Particularly complex is the pattern of variation in the tetraploid *L. sphaerocarpa*, which is apparently comprised largely of widespread stabilized

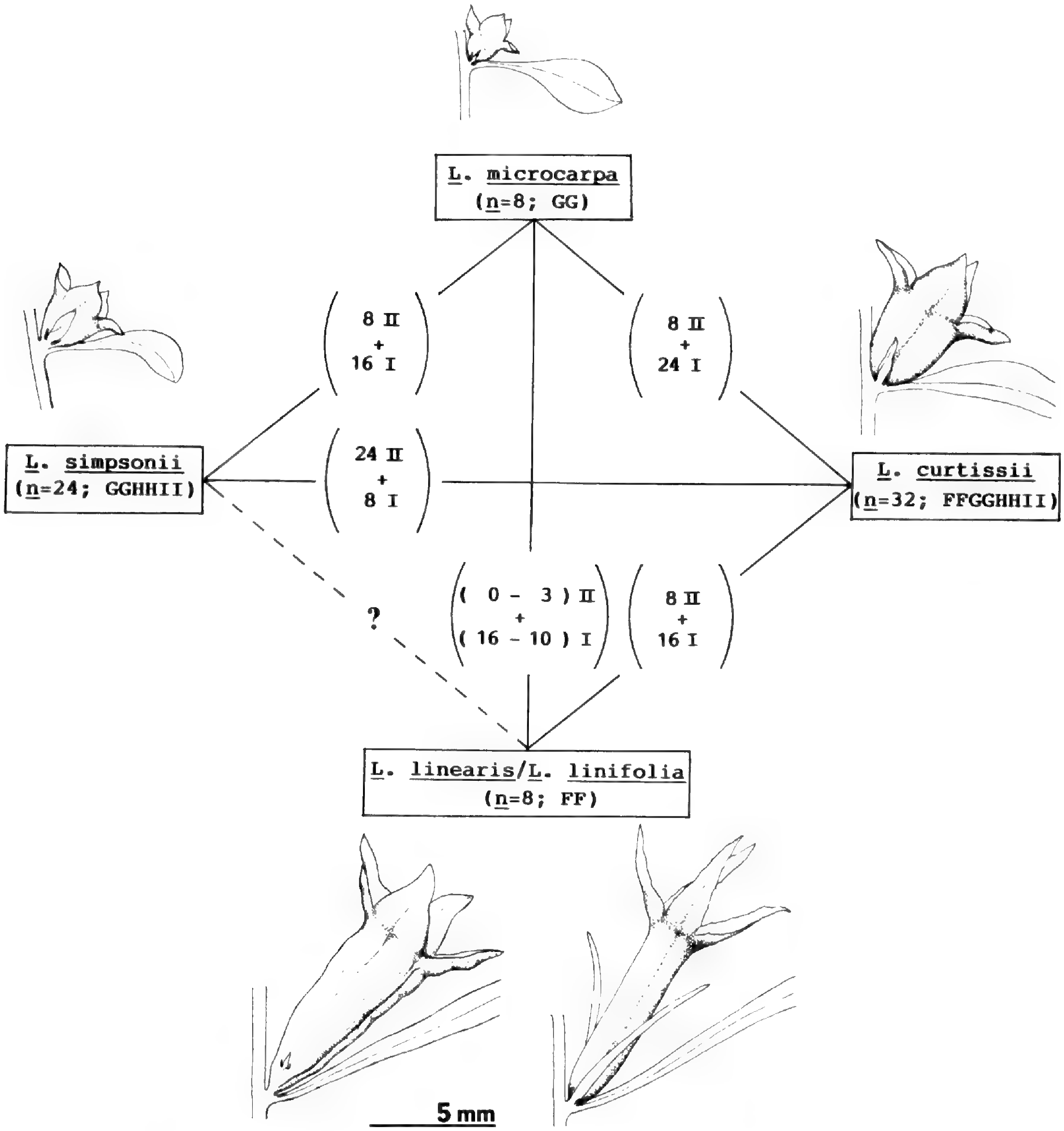


FIGURE 23. Chromosomal homologies in the *Ludwigia curtissii* complex. Dotted line indicates artificial hybrids were obtained, but meiotic analysis was not successful. Illustrations of the plants are drawn to scale.

hybrid populations that exhibit a combination of characters distinguishing them from other taxa. As in the evolution of *Epilobium* in New Zealand (Raven & Raven, 1976), recombination of genetic information from somewhat differentiated populations followed by maintenance of well-adapted genetic strains by a combination of autogamy and vegetative reproduction appears to have played a central role in the evolution of the polyploid members of *Ludwigia* sect. *Microcarpium*.

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RECONSTRUCTIONS OF SELECTED SEED FERNS[1]

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This Paper is Dedicated to the Memory of
Sergei V. Meyen

ABSTRACT

Seed ferns (pteridosperms) make up a heterogeneous group of broadleaf gymnosperms. Our attempts to reconstruct these extinct plants here summarize research over many years on the best-known seed ferns. We have named each reconstructed plant after its best-preserved ovulate fructifications, because these are the most reliable parts for identification of seed plants. We envisage Early Carboniferous (about 352 million years ago) Stamnostoma huttonense *as a large tree, foresting elevated terraces and other well-drained areas of coastal plains. Swampy lagoon margins of the same coast probably were wooded with lycopods and small shrubby seed ferns such as* Lyrasperma scotica. *Of comparable age, but on well-drained ashy soils flanking inland volcanoes, was the early successional* Calathospermum fimbriatum. *Unlike these other plants, which were probably pollinated and dispersed by wind and water, arthropods may have played a role in the reproduction of* C. fimbriatum. *Earliest Late Carboniferous (about 320 million years old)* Lagenostoma lomaxii *is reconstructed as a bushy understory shrub in swamps of arborescent lycopods. Latest Late Carboniferous (about 296 million years old)* Pachytesta illinoensis *was a tree probably growing on elevated and nutrient-rich areas in and around permanently waterlogged swamps of marattiaceous tree ferns.* Pachytesta illinoensis *had large prepollen probably dispersed by insects. Its fleshy ovules may have been dispersed by large amphibians, reptiles, or fish. Another seed fern of these latest Carboniferous swamps,* Callospermarion pusillum, *is reconstructed as an early successional scrambling vine. Its pollen probably was dispersed by wind, and its numerous small seeds scattered widely by wind and water. In contrast to these Euramerican plants of tropical and subtropical climates, Late Permian (about 245 to 253 million years old)* Dictyopteridium sporiferum *was a dominant tree of cool temperate swamp woodlands of intermontane valleys in the southern hemisphere. Large air chambers in its roots enabled it to grow in waterlogged soils. Woodlands of southern hemisphere mid-continental lowlands during Late Triassic time (225 to 230 million years ago) included abundant trees of* Umkomasia granulata, *and a shrubby understory including* Peltaspermum thomasii. *Middle Jurassic (175 to 183 million years old)* Caytonia nathorstii *is reconstructed as a tree of lowland mixed conifer–broadleaf forest in a subtropical, seasonally wet paleoclimate. Its ovules were enclosed in berrylike cupules, which may have been pollinated and dispersed by small animals. From these examples, it is apparent that seed ferns were exceptionally diverse broadleaf plants which occupied a variety of niches now occupied by angiosperms.*

Reconstructions of extinct plants from dispersed fossil organs have not been attempted to the same extent as restoration of vertebrate fossils. Presumably this is because of the modular construction of plants, because of their various deciduous organs, and because of the variety of ways and places in which fossil plants are preserved. Nevertheless, many hypotheses have been published concerning which parts of fossil plants belong together. The drawings presented here are visual expressions of some of these hypotheses for especially well-known seed ferns. We intend these drawings to be working hypotheses of reconstruction in the same way as the written accounts on which they are based. Hypotheses expressed in this way are understood more readily than pages of scientific text. By the same token, however, such drawings also make mistakes of interpretation more obvious. A further

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[1] *These reconstructions have been assembled over so many years and with such varied assistance in the field, with collections and with ideas, that it is not possible to thank adequately all those who have helped. We especially have valued and enjoyed the assistance of Drs. W. D. Dimichele (Smithsonian Institution, Washington), J. A. Doyle (University of California, Davis), R. E. Gould (Quest Ltd., Brisbane), T. M. Harris (University of Reading, England), C. R. Hill (British Museum Natural History, London), S. V. Meyen (Geological Institute, Moscow), G. W. Rothwell (Ohio University, Athens), and T. N. Taylor (Ohio State University, Columbus). Research and publication was funded by N.S.F. Grants DEB7910720 and BSR8516657 to D.L.D. and EAR8206183 to G.J.R.*

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difference between written and illustrated reconstructions of fossil plants is the difficulty of expressing uncertainty and presenting detail in a drawing. With special regard to this problem, the poses of various organs have been selected carefully, and enlargements and insets have been used liberally both to reveal detail and obscure uncertainties.

The plants reconstructed here are those regarded traditionally as "seed ferns," a group of plants being increasingly recognized as an evolutionary grade rather than a clade. This is not to say that the terms "seed fern" or "pteridosperm" should be abandoned, any more than the term "dinosaur," another often loosely defined assemblage, should be discontinued. The discovery that these fernlike fossil leaves belonged to seed-bearing plants reshaped understanding of the evolutionary relationships between seed plants and pteridophytes (Potonié, 1899; Oliver & Scott, 1904), and their importance to understanding vascular plant evolution has remained undiminished. The first seed plant and the ancestors of many other gymnosperms were probably seed ferns (Rothwell, 1982). Seed ferns or allied plants remain most likely ancestors of angiosperms (Dilcher, 1979; Retallack & Dilcher, 1981; Doyle & Donoghue, 1986).

The various organs and preservational styles of each of these fossils have separate botanical names, following accepted paleobotanical nomenclature. Our gathering together of various organs and names for different parts of the same plant should not be construed to mean that each part is equally definitive of the whole plant. A fossil species of root, for example, may have belonged to several different species distinguishable among reproductive structures. It is likely that different organs of plants have evolved at different rates. In gathering together these names we merely imply that there once existed a plant for which each of these names is appropriate for its various fossilized parts.

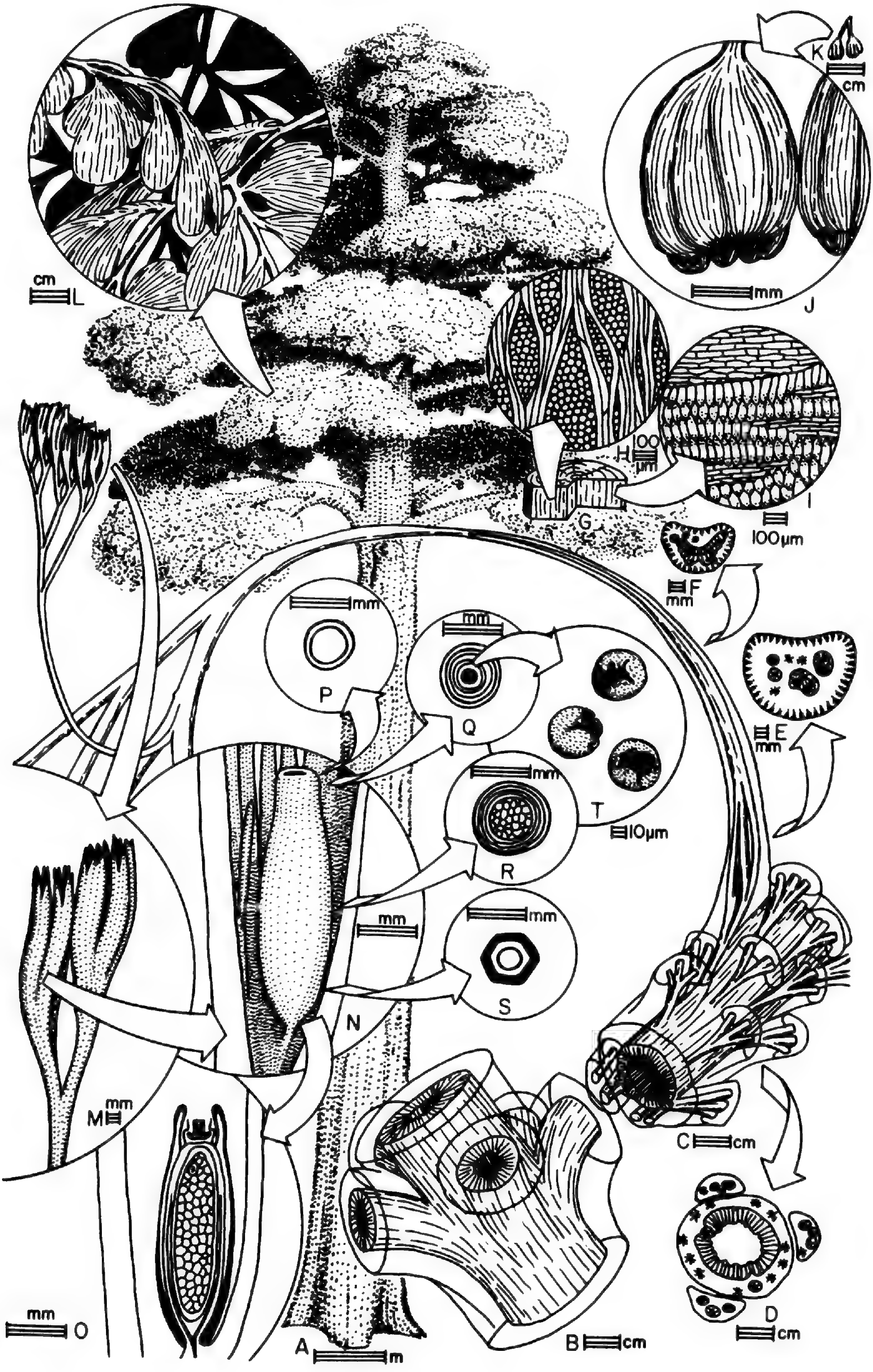
Our choice of a single name for each reconstructed plant does not follow the *International Code of Botanical Nomenclature* (Stafleu, 1978) in its rules of priority, because there are indications in the code that these do not apply between form genera for different kinds of plant parts. In the case of the present compilation, strict adherence to priority would result in naming eight of the plants reconstructed here from leaves, one from wood, and one from a root. Instead, we use the name of the best-preserved ovular fructifications consistently as the name for these reconstructed seed plants (following Retallack, 1980a, and Anderson & Anderson, 1985). Modern seed plants are classified mostly according to their ovulate fructifications, and a new suprageneric classification of seed plants based on ovular fructifications has recently been proposed by Meyen (1984). We do not agree with all of the criteria for his classification, but it is a welcome replacement for the preexisting miscellany of suprageneric taxa based on wood for Carboniferous groups, leaves for Permian groups, and ovular fructifications for Mesozoic groups.

Meyen (1984) outlined a new botanical nomenclature for seed plants, but here we use well-established terms such as sporophyll (phyllosperm of Meyen), sporoclad (branching polysperm), head (ultimate segment of cladosperm), and cupule (also used by Meyen). The word ovule is used here in the strict sense for unfertilized integumented megasporangia. In most gymnosperms, seeds represent dispersed propagules, whereas ovules are found in place in reproductive organs. Thus the word ovule appears in this account of reproductive organs more frequently than the word seed. In much paleobotanical writing, the latter term being understood more easily in general English usage, is used loosely for ovule or seed. We have also used the term prepollen for the microspores of very early seed ferns. Prepollen look more like spores of pteridophytes than pollen of seed plants, and, like spores, prepollen germinate from the side of the grain originally oriented within the parent tetrad (Chaloner, 1976).

We have examined type material of all the seed ferns reconstructed here and a good deal of additional material. One of us (G.J.R.) also has visited the type or comparable localities of these fossil plants in order to assess and obtain new evidence for their geological occurrence. In addition to the drawings, we have written an interpretive summary as an introduction to each plant. The remainder of each account details both evidence and arguments for and against various aspects of our reconstruction. The plants are discussed in order of geological age.

STAMNOSTOMA HUTTONENSE

Hypothetical reconstruction. We envisage this plant as a tall forest tree (Fig. 1) with coniferlike wood (*Pitus primaeva* Witham, 1833). It was a prominent tree of well-drained soils of elevated river terraces surrounding lagoons of a broad coastal plain to the south of a hilly and volcanic region now forming the Southern Uplands of Scotland. During the Early Carboniferous (late Tournaisian or about 352 million years ago) the climate of this region probably was subtropical, with a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pronounced dry season. During this season, the pinnules of its large fronds (*Aneimites acadica* Dawson, 1860) may have been deciduous. In some ways these fronds resembled the plagiotropic short shoot systems of progymnosperms, but the petiole of the plant (*Lyginorachis papilio* Kidston, 1923) was dorsiventrally differentiated and its vascular structure like that of true leaves. Stalks arising from within the dichotomy of the rachis of the frond terminated in cupules (*Calathiops* sp.) bearing ovules (*Stamnostoma huttonense* Long, 1960a). The prepollen organ (*Telangium* sp. when petrified and *Telangiopsis* sp. in compression) probably was borne in a similar manner. It consisted of a copiously branched aggregate of clusters of elongate pollen sacs. The fernlike prepollen grains (*Colatisporites decorus* (Bharadwaj & Venkatachala) Williams in Neves et al., 1973) were released through an elongate dehiscence slit. These plants may have been wind pollinated at a stage when the ovules were immature. The prepollen was sealed in an apical chamber of the ovule (lagenostome) at the base of a trumpetlike opening (salpinx) by the upward and outward growth of a central plug of tissue. There it waited as the multicellular gametophyte and archegonia developed. Once fertilization was achieved, perhaps after shedding and wind dispersal of the ovule, there appears to have been little interruption in the rotting of the seed integuments and germination of the embryo.

Evidence for reconstruction. The main locality for our reconstruction is the quarries in the steep eastern banks of the Crooked Burn west of Newton Farm, near Foulden, Berwickshire, southern Scotland (Wood & Rolfe, 1985; Scott & Meyer-Berthaud, 1985). This is in the lower Cementstone Group of the Calciferous Sandstone Series, of Early Carboniferous age (late Tournaisian, or late Courceyan in the regional stratigraphic scheme; Scott et al., 1984; Clayton, 1985) or 352 million years old (following Palmer, 1983). The attribution of these various remains to a single plant is based on anatomical similarity of petrified petioles and small branches; on attachment of petrified stalks within the dichotomy of petioles as in other fertile seed ferns; on the similarity of pollen found in pollen sacs, in ovules, and dispersed; and on the association of both petrified and compressed remains at the same localities, often with few other associated plants (Long, 1960a, 1962, 1963, 1979a; Neves et al., 1973; Wood & Rolfe, 1985; Scott & Meyer-Berthaud, 1985).

Most of this evidence has been presented by Long (1979a), but we doubt that the leaf type, *Sphenopteris affinis*, or petrified stem, *Tristichia ovensii*, belonged to this plant, for the following reasons. *Aneimites acadica* is a very common leaf at the main locality for this plant (Newton Farm), where it is represented by abundant isolated pinnules, which were probably deciduous. The overall frond morphology thus remains poorly known, and Long's (1979a) objections on this basis against this being the foliage of the petrified petioles have little substance. There are several problems with Long's view that *Sphenopteris affinis* was the leaf of the plant in question. *Sphenopteris affinis* was probably a shrubby plant growing in quite different waterlogged soils (of the Oil Shales: Andrews, 1948). Only one very poorly preserved fragment (British Museum of Natural History specimen 16865) of *S. affinis* has been found at the main locality for our reconstruction (Newton Farm) of *Stamnostoma huttonense*, and this equally could be a badly lacerated specimen of *Aneimites acadica* or a ragged specimen of *Sphenopteridium pachyrrachis*, also reconstructed here as part of *Lyrasperma scotica*. In addition, the prepollen of *Telangium affine* found in association and attached to *Sphenopteris affinis* in the Oil Shales has a clear ornament and trilete mark (Kidston, 1924), quite different from the almost featureless prepollen found in the prepollen chambers of ovules and in prepollen organs attributed to *Stamnostoma huttonense* (Long, 1962, 1979a). Further, the prepollen of *Sphenopteris affinis* is somewhat smaller (52 μm according to Kidston, 1923) than that of the reconstructed plant (54–69 μm according to Long, 1979a). This would have been a more substantial difference if the prepollen grains of *Stamnostoma huttonense* are lacking their outer wall, as Long suspected.

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FIGURE 1. *A reconstruction of* Stamnostoma huttonense *of Early Carboniferous (Tournaisian) age, from Newton Farm, near Foulden, Berwickshire, Scotland.—A. Habit as a large tree of well-drained soils.—B, C. Xylem model of branches, petiole, and cupule.—D–F. Schematic cross sections of branches and petioles, showing primary xylem (black dots), secondary xylem (surrounding areas), sclerotic nests (asterisks), and mechanical cortex (radial shading).—G–I. Cellular structure in tangential and radial (respectively) sections of wood.—J, K. Prepollen organ.—L. Detail of leaf.—M. Ovulate cupule.—N. Ovule.—O–S. Sections of ovule, revealing multicellular megagametophyte and an archegonium.—T. Prepollen.*

Scott & Meyer-Berthaud (1985) reinterpreted *Tristichia ovensii* from the main locality for our reconstruction (Newton Farm) as a separate small seed fern with *Rhodea*-like leaves, "small uncupulate seeds," and "small, lateral, pedunculate male organs." They also questioned whether the specimens of *Tristichia ovensii* between the fork of *Lyginorachis papilio* and aligned with *Stamnostoma huttonense* (Long, 1963) are really attached. We accept their reconstruction of this other plant but see little reason to question the attachments described by Long, especially in view of the very generalized anatomy of *T. ovensii*. Very small axes of several species of seed ferns may have been comparably anatomically simple.

Habit. *Stamnostoma huttonense* was a large tree, with trunks up to 25 m long and 1.4 m in diameter (Long, 1979a). On some of the petrified trunks, branches and petioles have been found attached in a closely spaced helix, whereas other axes lack branches for considerable lengths. This is a common branching pattern in modern forest trees (Rauh's model of Hallé et al., 1978). This plant also had the long and short shoot organization found in many modern conifers, such as Scots pine (*Pinus sylvestris*).

Unlike the leaves of most conifers, its leaves were fernlike. These fossil trees were superficially similar to extinct progymnosperms such as *Archaeopteris ovata* (see Beck, 1981). These had leaves similar to the pinnules of *Aneimites acadica*, although these were arranged in large dorsoventrally planated shoot systems quite different from the true leaves of *A. acadica* (Kidston, 1924).

Ovules were attached on stalklike structures which formed the central axis of a trichotomy of the rachis of the frond. A petrified terete stalk with a triarch stele has been found in the dichotomy of a petrified petiole (Long, 1962). This was a common mode of attachment of ovular and pollen-bearing structures, seen in other Early Carboniferous compression fossils, such as *Sphenopteris affinis* (Kidston, 1924), *Sphenopteris bifida* (Long, 1979a), and *Diplopteridium teilianum* (Walton, 1926, 1931). Compared with modern gymnosperms in which axillary branching and clear differentiation of stem and leaf are the rule, this epiphyllous sporoclad is peculiar. Presumably this arrangement was inherited from progymnosperm ancestors that lacked consistently axillary branching (as shown by Scheckler, 1976, 1978).

The sporoclads of *Stamnostoma huttonense* may have been erect. Their stalks are terete and gently curved, rather than the dorsiventrally planated and flexuous as in pendent fructifications. Niklas (1981) has shown that an erect orientation would have been more effective for pollination, because the rachides of the fronds would have remained in the way of pendent ovules even if all the pinnules were abscised at the time of pollination. Long (1965) and Walton (1964) argued that cupules of other species were pendent because this would protect the pollination drop from rain. However, the open form of this particular cupule would have been a rain guide, rather than protection.

Reproduction. The life cycle of this plant was probably similar in general outline to that of a number of associated Early Carboniferous seed ferns (Rothwell, 1986). Irregularly branching cupulate structures of other species sometimes are found with poorly developed ovules or prepollen sacs (Long, 1969, 1975, 1977a, 1979b). We interpret these as fructifications at the stage of pollination or earlier, analogous to modern fructifications of cycads (*Dioon edule*) and maidenhair trees (*Ginkgo biloba*) at this stage in their development (Chamberlain, 1935). The smooth prepollen were produced in great quantity. These are features of modern wind-pollinated plants (Faegri & van der Pijl, 1966; Whitehead, 1969). The size of the prepollen (54–69 μm in diameter) approaches that of modern insect-dispersed pollen, but their aid in pollination is unlikely in view of other features of the prepollen. At pollination stage the funnellike nucellar apex (salpinx) may have retained a pollination drop for entrapment and withdrawal of prepollen (Walton, 1964) as in some modern conifers.

The best-preserved fossils of mature ovules have a central column filling much of the salpinx and a multicellular megagametophyte, occasionally with one to three apical archegonia (Long, 1960a). These may have been ovules during the long period after pollination and before or shortly after fertilization. Judging from the abundance of remains of this stage, this was a long period in the life cycle, perhaps taking several months, as in modern cycads and *Ginkgo* (Chamberlain, 1935). Even mature ovules have three small cutinized megaspore remnants at the apical end, representing aborted spores of the parent tetrad (Long, 1975). This feature, presumably a legacy of heterosporous progymnosperm ancestors, is no longer seen in modern seed plants.

Mature seeds were small (up to 3.75 mm long by 1.5 mm wide) and had a thin, dense seed coat. Compared with modern seeds (Van der Pijl, 1972), they were unspecialized and possibly scattered by

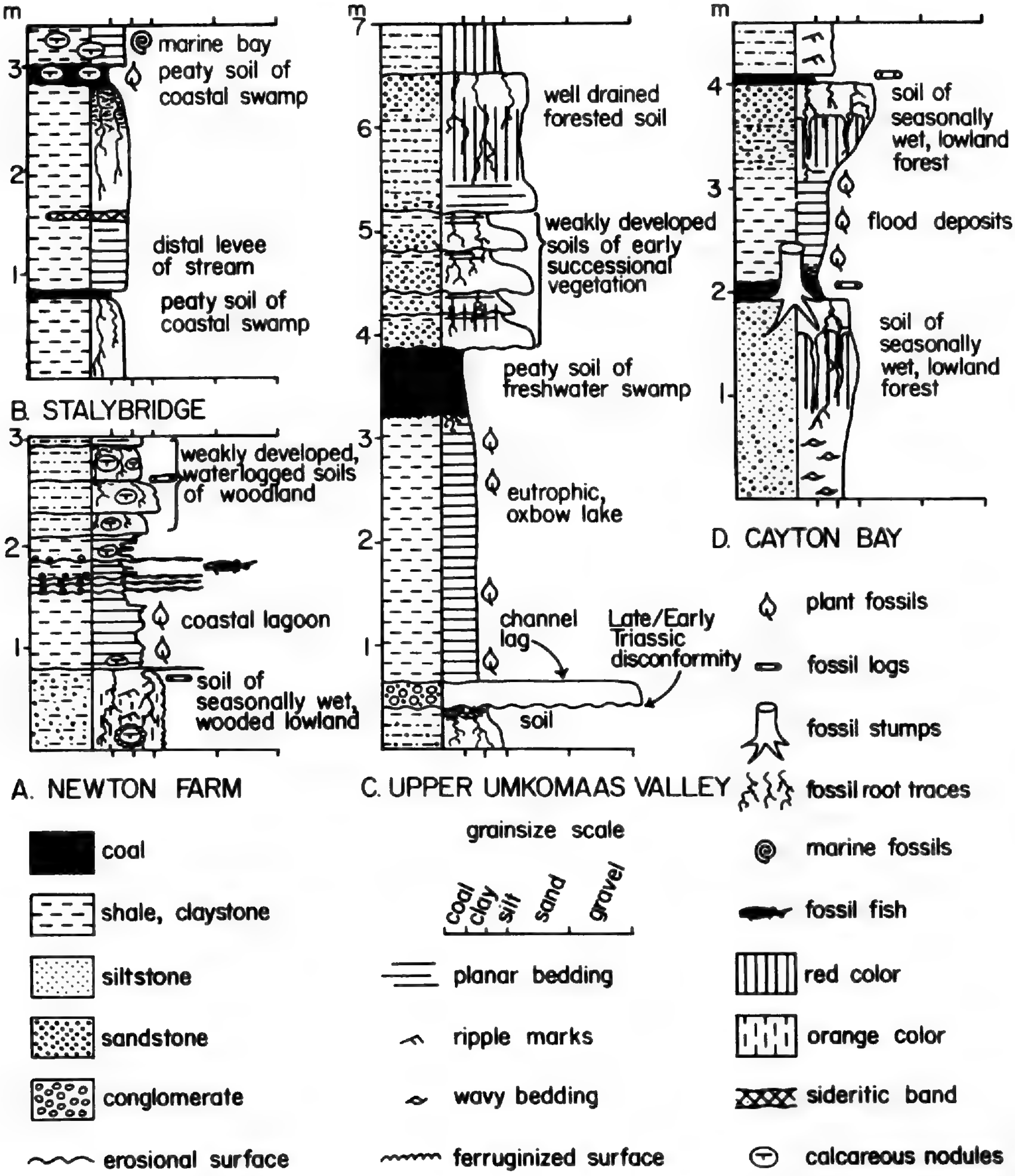


FIGURE 2. *Stratigraphic sections and interpreted paleoenvironments of fossil localities at:—A. Newton Farm, near Foulden, Scotland (for* Stamnostoma huttonense *and* Lyrasperma scotica*).—B. Hough Hill Colliery, near Stalybridge, Cheshire, England (for* Lagenostoma lomaxii*).—C. Near Vergelegen Nature Reserve, upper Umkomaas Valley, Natal, South Africa (for* Peltaspermum thomasii *and* Umkomasia granulata*).—D. Southern Cayton Bay, Yorkshire, England (for* Caytonia nathorstii*). Sections were measured in the field by G.J.R., except for B, which was compiled from sections described by Stopes & Watson (1909) and Tonks et al. (1931).*

shaking from the cupules, followed by wind and water dispersal.

No seeds with embryos have been found among many examined in Early Carboniferous rocks. Those few possible seed fern embryos found have two seed leaves and are free of their seed integuments (Long, 1975). It is likely that germination followed rapidly after fertilization, again as in modern cycads and *Ginkgo* (Chamberlain, 1935). If most embryos grew without pause into small seedlings, this would explain their rarity.

Habitat. The gray shales at Newton Farm (Fig. 2A) have yielded a variety of fossil sharks, palaeoniscid and acanthodian fish, crustaceans, bivalves, and plants (White, 1927; Long, 1960a, 1962, 1964; Wood & Rolfe, 1985; Scott & Meyer-Berthaud, 1985). Apart from arborescent lycopods and rare sphenopsids, the best-known plants from here are the seed ferns reconstructed as *Stamnostoma huttonense* and *Lyrasperma scotica*, and a small plant with *Rhodea*-like foliage. Remains of all these plants have been found mixed together in shales of what was once a large brackish-to-freshwater coastal lagoonal system (Clarkson, 1985).

Several fossil soils (paleosols) in this sequence allow more precise understanding of where *Stamnostoma huttonense* grew. Overlying the lagoonal shales are sequential, thin, waterlogged paleosols (gleyed Inceptisols of Soil Survey Staff, 1975). The size and nonanastomosing cortical striations of fossil root traces in these are most like those of *Lyrasperma scotica*, also reconstructed here. A better-drained paleosol containing larger and more deeply penetrating root traces underlies the lagoonal shales. *Stamnostoma huttonense* probably grew in such well-drained soils, considering the deeply penetrating roots under its fossil stumps, its well-cuticularized seeds, and the growth rings in its wood, not seen in coeval arborescent lycopods of swamps (Gordon, 1935).

The well-drained paleosol thought to have supported *Stamnostoma huttonense* has a carbonaceous surface horizon: an indication that it was not always entirely dry. Its subsurface zone of iron-staining and deep (60 cm) horizon of calcareous nodules (caliche) mark the minimum usual depth of the water table. It was a young soil (probably formed in only hundreds of years before covered), because development did not proceed to the extent that the original bedding was entirely destroyed. It probably formed on an alluvial terrace, a meter or so above the level of the nearby lagoonal system.

Additional evidence of Early Carboniferous forests of *Stamnostoma huttonense* can be seen at other British localities. Along the King Water between Spadeadam and Gilsland in Cumbria, northern England, there are ten petrified stumps of *Pitus primaeva* preserved in growth position within 200 m of outcrop (Long, 1979a). Considering the likely canopy of these trees and the size of the stumps, they would have dominated a forest with closed canopy.

In addition to forests of *Stamnostoma huttonense* and swamp woodlands of *Lepidodendron* and shrubby *Lyrasperma scotica*, documented at Newton Farm, seed ferns lived in a variety of other habitats in southern Scotland during Early Carboniferous time. The oil shale north of Cove Harbour (Craig, 1975) contains abundant *Sphenopteris affinis*, as well as narrow, shallowly penetrating root traces. This was a weakly developed, waterlogged paleosol (Aquent of Soil Survey Staff, 1975), supporting scrubby vegetation similar to modern fen carr. Other seed ferns are now preserved in calcareous nodules (caliche) of paleosols (Inceptisols of Soil Survey Staff, 1975) flanking deposits of a small (about 10 m wide) creek in the Cementstone Group deposits exposed in the southern sea cliffs of Oxroad Bay, south of Tantallon Castle, East Lothian (Long, 1976, 1979b; Barnard & Long, 1973, 1975; Matten et al., 1980; Scott et al., 1984). This fossil assemblage, including *Calathospermum fimbriatum* reconstructed here, appears to have been in large part scrubby, early successional vegetation on the well-drained, ashy soils of a nearby volcano. Even at this early time in the geological history of seed ferns, they appear to have been varied in habit and habitat, and included stately forest trees such as *Stamnostoma huttonense*.

Paleogeographic setting. This plant and its various parts are widely distributed in the lower Cementstone Group of Early Carboniferous age southern Scotland. At this time, the Cementstone Group accumulated in a coastal plain south of a hilly region including basaltic and rhyolitic volcanoes, and north of a shallow marine shelf, a few large islands, and open equatorial ocean (Anderton et al., 1979). Southern Scotland enjoyed a warm tropical climate, in which corals and large fusuline foraminifera flourished. Statistical analysis of palynological data provides evidence of dry climate at this time (van der Zwan et al., 1985). Calcareous nodules in paleosols of the Cementstone Group (Fig. 2A) are evidence of a climate at least as dry as subhumid, and probably seasonally dry. A dry season is also apparent from growth rings in fossil wood of this sequence (Long, 1979a; Creber & Chaloner, 1984) and the development of marine evaporites in tropical seas to the south (Ramsbottom, 1973). Although close to the equator, this area was in the rain shadow of large mountain ranges to the west (Bambach et al., 1980).

LYRASPERMA SCOTICA

Hypothesized reconstruction. *Lyrasperma scotica* is reconstructed as a small bush, with stiff, coriaceous, fernlike leaves (Fig. 3). It probably formed a shrubby understory to swamp woodland of arborescent lycopods around coastal lagoons of the same age and areas already described for *Stamnostoma huttonense*. Its leaves (*Sphenopteridium pachyrrachis* (Goeppert) Potonié, 1899) were strengthened by a thick cuticle and, in the rachis and petiole, by a cortical mechanical tissue (dictyoxylon cortex), formed by radially arranged blades of sclerenchyma. Their petioles (*Kalymma tuediana* Calder, 1938) had a pulvinus and numerous vascular strands. They were borne stiffly and horizontally, in a well-spaced helix on slender erect stems (*Stenomyelon tuedianum* Kidston in Scott, 1909). The stems were smooth and barkless, with an outer dictyoxylon cortex and an inner parenchymatous cortex, and a soft, mixed pith within the central cylinder of secondary xylem. The prepollen organs of this plant are not known, but some ovules were found containing prepollen (*Colatisporites denticulatus* Neville in Neves et al., 1973). The ovules (*Lyrasperma scotica* (Calder) Long, 1960b, when petrified, and *Samaropsis bicaudata* (Kidston) Kidston, 1902, in compression) were lenticular and had two prominent horns on either side of the apex. Ovules only have been found isolated. They may have been enclosed within epiphyllous cupules (*Alcicornopteris convoluta* Kidston, 1887). Like other Early Carboniferous seed ferns, pollination was presumably by wind, and dispersal by wind and water. The distinctive large horns of the ovule may have aided dispersal over water.

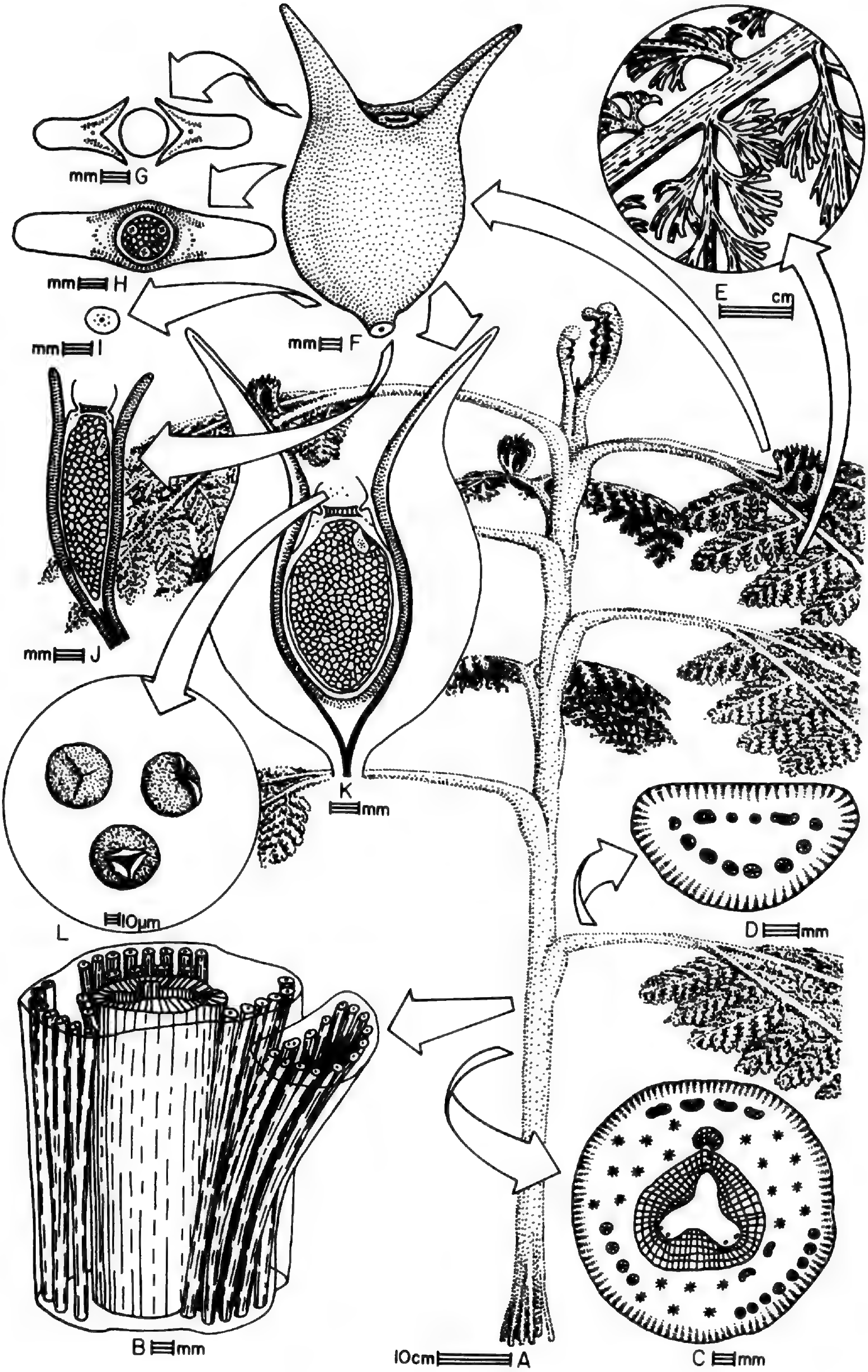
Evidence for reconstruction. Our reconstruction of this plant is based on the same Early Carboniferous (Tournaisian) locality near Newton Farm, southeastern Scotland, already discussed for *Stamnostoma huttonense* (Wood & Rolfe, 1985; Scott & Meyer-Berthaud, 1985). The attribution of these various remains to one plant is based on the similarity of dispersed prepollen to that found in the ovule; attachment of petrified petioles to petrified stems; the similar size, shape, stelar arrangement, long internodes, evidence of sclerotic nests, and nonanastomosing woody cortex in petrified and compressed petiole-bearing stems; the similar size and shape of petrified and compressed ovules; and consistent association at the same localities (Long, 1960b, 1964). A most important specimen for our reconstruction is the large compressed trunk with attached leaves excavated by Long (1964). Although pinnae associated with this compressed trunk agree with *Sphenopteridium pachyrrachis*, the petioles of the specimen lack the pinnae below the fork and the rough transverse bars usually found in that species (Long, 1964). Comparably anomalous compression fossil leaves were referred to the same species by Walton (1931), and it is uncertain whether this is part of the natural variation of this species or represents a distinct new form.

Habit. This plant had an unbranched erect trunk (Corner's architectural model of Hallé et al., 1978). Its stems were quite succulent, as they had a wide parenchymatous cortex, a mixed pith, and inflated petiole bases (Seward, 1917: 184). Compression of soft tissues in some specimens has given the misleading appearance of "multicellular projections" (Taylor, 1981: 363). These slender stems were strengthened by an outer zone of woody mechanical tissue—bands of sclerenchyma forming a dictyoxylon cortex, which in this plant was not anastomosing. There is no indication of bark, and the stem probably was smooth.

The leaves were coriaceous and strengthened by sclerenchyma within their petioles. The base of the petiole was expanded into a broad, fleshy, pulvinuslike structure. Attached leaves were arranged stiffly and horizontally on the stem.

The arrangement of ovules in this plant is uncertain because they only are known isolated. In similar Late Carboniferous plants described by Delevoryas & Taylor (1969) and Corsin (1928), synangia and ovules were borne bipinnately on what appears to be a fertile frond, in a similar fashion to our reconstruction of *Lagenostoma lomaxii*. In contrast, Long (1977a) has argued that the ovules of *Lyrasperma scotica* were borne in complexly branched cupules, similar to our reconstruction of *Stamnostoma huttonense*. Long's argument is based mainly on the widespread association of ovules (*Samaropsis bicaudata*) and cupules (*Alcicornopteris convoluta*), the very similar anatomy (especially of the lagenostome) of other ovules (*Eurystoma angulare, E. burnense*, and *Hydrasperma longii*) known to be borne in cupules (Long, 1965, 1969, 1975, 1979b; Matten et al., 1980), and the existence of compressed fronds (of *Sphenopteridium pachyrrachis*) showing a trichotomy of the rachis (Kidston, 1923, pl. 39, fig. 5; Long, 1960b). It is most likely that the ovules, and perhaps also sporangia, of this plant were borne within infolded cupules as in *Alcicornopteris*. We regard many of Long's *Alcicornopteris*-like specimens of *Hydrasperma longii* (Matten et al., 1980) as immature and have modeled our reconstruction of the cupule after that of *Eurystoma angulare* (Long, 1969). As in the generalized reconstruction of similar plants by Camp & Hubbard (1963), the cupule is shown erect on the frond for reasons similar to those given for our reconstruction of *Stamnostoma huttonense*.

Reproduction. The early development and pollination of *Lyrasperma scotica* was probably similar to that of *Stamnostoma huttonense*. *Lyrasperma scotica* had a wide, shallow salpinx, un-


mm G
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10cm A
C mm

like many other Early Carboniferous seed ferns. The mechanism of sealing the pollen chamber after pollination could not have been by upward growth of a plug of tissue, as envisaged for *Stamnostoma huttonense* or *Lagenostoma lomaxii*. It may have been by lateral growth of the central column or buckling of the central column by growth of the tent pole.

The prominent horns of the ovule are somewhat reminiscent of those in the living water chestnut (*Trapa natans*), in which barbed spines may serve as floats during dispersal over water and deter consumption by fish or other aquatic vertebrates. The fossil ovule does not have an especially woody or fleshy integument of the kind found in modern fish-dispersed seeds (Gottsberger, 1978).

Habitat. A lowland habitat is indicated by the occurrence of *Lyrasperma scotica* at the same locality on Newton Farm (Fig. 2A) already discussed for *Stamnostoma huttonense* (Wood & Rolfe, 1985; Scott & Meyer-Berthaud, 1985). Here seed fern roots with nonanastomosing striations, like those of this plant, as well as poorly preserved lycopod cones, have been found in paleosols overlying the lagoonal shale. These paleosols lack coal, and fossil root traces penetrate them more deeply than usual for permanently waterlogged soils. Nor do they have the reddish oxidized minerals of well-drained soils or the prominent relict bedding of very young soils. They were weakly developed, periodically waterlogged, clayey lowland soils (gleyed Inceptisols of Soil Survey Staff, 1975), probably marginal to the lagoon. Fossil fish and shrimp in the underlying lagoonal deposits (Clarkson, 1985) are evidence that this was a brackish-to-freshwater inland part of a large coastal lagoonal system, connected to the ocean. *Lyrasperma scotica* may have formed a shrubby understory to this lagoon-margin woodland.

The suggested succulence and thick leaf cuticles of this fossil plant could be considered indications of a locally or regionally arid climate, but considering geological evidence for its habitat, these features more likely allowed its growth in salty or nutrient-poor, stagnant groundwater. This interpretation is also compatible with the elaborate, fleshy, open-mouthed seeds of this plant, which would have required moist but not necessarily nutrient-rich conditions for germination and early seedling growth.

Paleogeographic setting. This plant is found at several localities in the Cementstone Group of Early Carboniferous age in southern Scotland, in the same region and time as *Stamnostoma huttonense* (Wood & Rolfe, 1985; Scott & Meyer-Berthaud, 1985).

CALATHOSPERMUM FIMBRIATUM

Hypothesized reconstruction. Also of Early Carboniferous age (Tournaisian or 352 million years old), this small herbaceous-to-shrubby plant was possibly an early successional colonizer of the banks of gullies and ephemeral creeks in ash at the foot of volcanoes within a large rift valley, now the Midland Valley of Scotland (Fig. 4). Its leaves (*Sphenopteridium capillare* Walton, 1931) were dichotomously forked, and the pinnae copiously divided into terete and filiform segments. The stem (*Calathopteris heterophylla* Long, 1976) had a wide cortex with narrow medullated rings of secondary xylem. Ovules were borne within large cupulate structures (*Calathospermum fimbriatum* Barnard, 1960), which had a series of pinnae on the petiole like those of ordinary foliage leaves. Within the cupule were about 16 erect-growing, elongate ovules (*Salpingostoma dasu* Gordon, 1941). The prepollen organ (not yet known) may have been attached to the central stalk of a trichotomously divided leaf rachis. It may have been a copiously branched structure with numerous elongate sporangia, as in allied seed ferns. The prepollen of this plant (*Perotriletes tessellatus* (Staplin) Neville in Neves et al., 1973) were so large (104 μm in diameter) that this plant may have been pollinated by small animals. The long integumented ovules may have been shaken from the cupules by wind.

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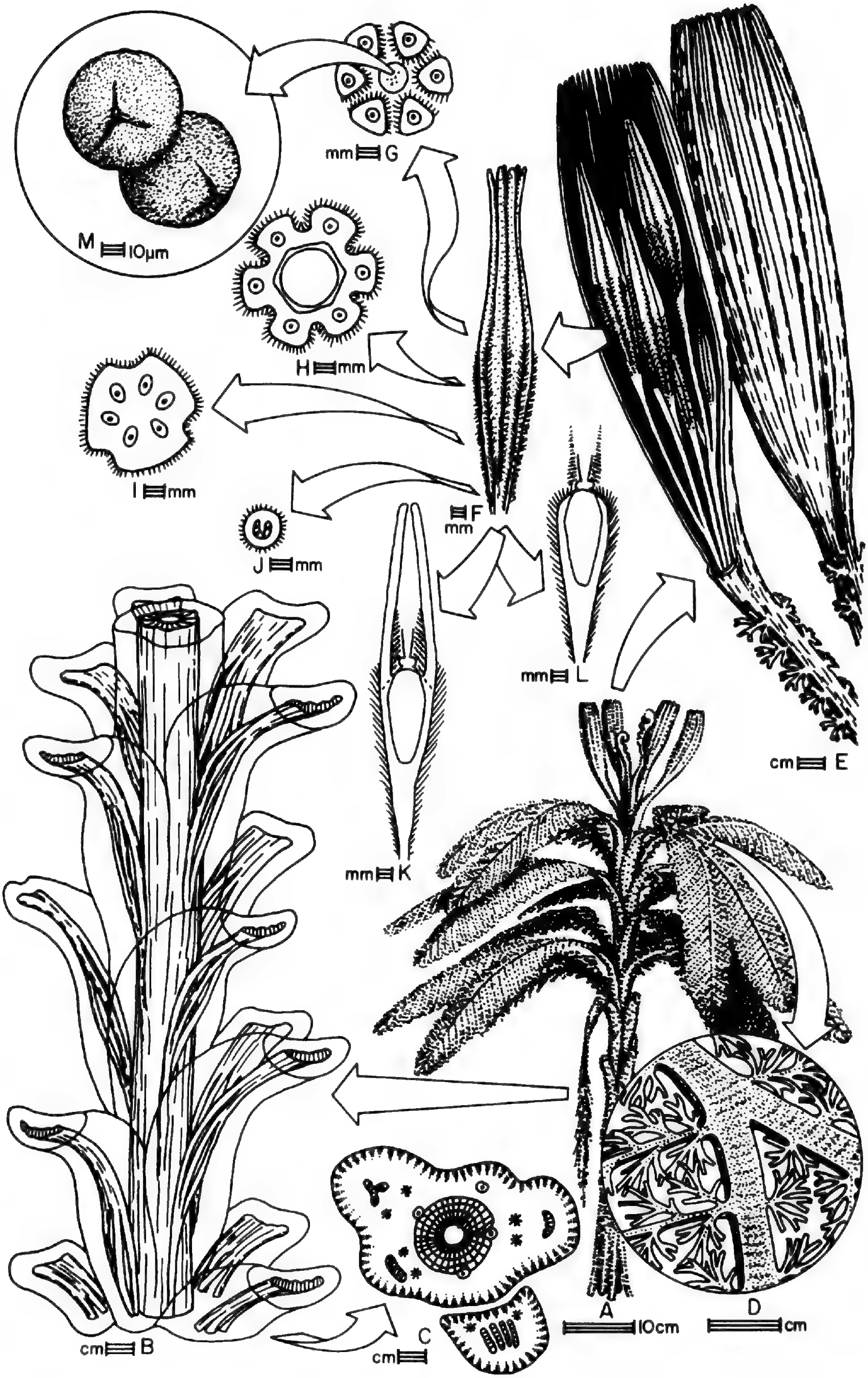
FIGURE 3. *A reconstruction of* Lyrasperma scotica *of Early Carboniferous (Tournaisian) age, from Newton Farm, near Foulden, Berwickshire, Scotland.—A. Habit as a shrub of coastal swampland.—B. Xylem model of stem and petioles.—C, D. Schematic cross section of stem and petiole (respectively), showing primary xylem (black points), secondary xylem (surrounding cellular pattern), sclerotic nests (asterisks), and mechanical cortex (radial shading).—E. Detail of leaf.—F. Ovule.—G–K. Transverse and longitudinal sections of ovule, showing vascularization (heavy lines), woody integumentary layer (stipple), megagametophyte (cellular pattern), and archegonium (circle with stippled center).—L. Prepollen.*


M 10µm
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cm E
A 10cm
D cm
cm B
C cm

Evidence for reconstruction. The various parts of *Calathospermum fimbriatum* have been put together from similarities in anatomy and hairs between isolated ovules and cupules; from the similar anatomy of petioles of petrified cupules and petioles of petrified stems; and from close association at one especially well-studied locality (Barnard, 1960; Long, 1976; Scott et al., 1984). These are the calcareous, nodular layers of a buried creeklike feature in sea cliffs south of Tantallon Castle, in Oxroad Bay, East Lothian, Scotland (Long, 1976). This is part of the Cementstone Group, Calciferous Sandstone Series, of Early Carboniferous age (late Tournaisian or Courceyan of Scott et al., 1984), or 352 million years ago (following Palmer, 1983).

The prepollen of this plant have been found in petrified ovules (Long, 1976) and are similar to a common type of dispersed grain (Neves et al., 1973). Similar prepollen are found in a fructification of another closely allied species (*Staphylotheca kilpatrickensis* Smith, 1962) from another Scottish locality of comparable age (Loch Humphrey Burn). The prepollen organ of *Calathospermum fimbriatum* may have been similar in some respects but remains unknown. Only the petioles likely to have borne the prepollen organ of *Calathospermum fimbriatum* are known.

No compression fossils have been found in association with the petrified remains, but the petrified pinnae below the fork of the cupule agree in all respects with *Sphenopteridium capillare* (G.J.R., pers. obs.), a leaf known from other localities in Fife, Scotland (Walton's, 1931, material from Burntisland; British Museum (Natural History) specimen v31831 from Ardross). Unlike Oxroad Bay, these Fife localities are within the Oil Shale Group or its equivalents (MacGregor, 1968) and are slightly younger (Visean) within Early Carboniferous time (equivalent or older than Pettycur fossils from this area; Scott et al., 1984).

Other kinds of fronds are unlikely to have belonged to this plant, as they are thought to have had quite different fructifications (*Stamnostoma huttonense* and *Lyrasperma scotica*, as reconstructed here, and fertile *Sphenopteris bifida* of Long, 1979b), or they differ in having few (*Sphenopteris affinis*: see Kidston, 1924, pl. 100, fig. 1) or no pinnae below the fork (*Adiantites machanekii*, *Diplotmema bermudensiforme* and *Spathulopteris ettingshausenii* of Walton, 1931). The other common kind of leaves of this age (*Rhacopteris* spp.) were unforked, although their microsporangiate axes were forked (Walton, 1926). Compression fossils showing these leaves attached to stems (Walton, 1926) are very similar in size, phyllotaxy, angle of attachment of petioles, and spacing of pinnules to petrified plant remains (referred to Buteoxylaceae by Barnard & Long, 1973, 1975), different from the plant reconstructed here.

Habit. From a distance these plants probably looked like umbelliferous weeds, such as hemlock (*Conium maculatum*) and anise (*Pimpinella anisum*). The stem of *Calathospermum fimbriatum* was weak, with medullated secondary wood (Long, 1976). No growth rings were seen. The single stem found was densely clothed in leaves and showed no branches within its 17 cm length (Long, 1976). It was not a copiously branched plant and had much weaker wood than seed ferns such as *Stamnostoma huttonense*. We have reconstructed it as a small shrub, but the available specimen may have been a young plant of a species usually more complex in architecture (G. W. Rothwell, pers. comm., 1985).

Reproduction. The enlargement and differentiation of the megagametophyte between the time of pollination and fertilization was not synchronous. There are small, poorly developed ovules on short stalks near the base of the cupule, as well as large, mature ovules on long stalks near the mouth of the cupule (Barnard, 1960). Such variation in development is not nearly so marked in other Early Carboniferous seed ferns, although these do include occasional "aborted" ovules (Long, 1960a). "Continuous flowering" of this kind is commonly found in modern plants of disturbed habitats, where opportunities for seedling establishment are unpredictable (Heinrich, 1976).

Several features of this plant suggest a syndrome now associated with pollination by animals (Faegri & van der Pijl, 1966). These features are especially striking in comparison with co-existing wind-polli-

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FIGURE 4. *A reconstruction of* Calathospermum fimbriatum *of Early Carboniferous (Tournaisian) age, in Oxroad Bay, East Lothian, Scotland.—A. Habit as a weedy shrub of inland streamsides.—B. Xylem model of stem and petioles.—C. Schematic cross section showing primary xylem (black points), secondary xylem (surrounding cellular pattern), sclerotic nests (asterisks), and mechanical cortex (radial shading).—D. Detail of leaf.—E. Ovulate cupules.—F. Ovule.—G–L. Transverse and longitudinal sections of ovule.—M. Prepollen.*

nated seed ferns such as *Stamnostoma huttonense* and *Lyrasperma scotica*. The cupules were large and almost radially symmetrical, and so might have been easily recognized by animals. They were borne erect, as can be seen from the kink where the cupule was bent farther upwards (adaxially) on the attached petiole (Barnard, 1960; Long, 1975). The prepollen of this plant were large (104 μm), much larger and heavier than is effective for wind-pollinated plants today (Whitehead, 1969). Finally, the ovules and the interior of the cupule were covered with numerous glandular hairs (Gordon, 1941; Barnard, 1960) of unknown function. They may have offered a nutritional reward to animals or protected the ovules from them.

It is difficult to be certain what kinds of creatures could have been pollinators—few likely terrestrial animal fossils are known from this geological time. There is a poor Late Devonian and Early Carboniferous fossil record of canopy-dwelling spiders and mites. Winged insects are not found as fossils in rocks older than earliest Late Carboniferous (Namurian: Rolfe, 1980).

The propagules of this plant appear to have been individual ovules, because only a few mature ovules are found in any particular cupule, and in some cases cupules contain none. Mature ovules were elongate and of moderate size (6 mm diameter and 5 cm long including nucellar extensions). There were zones of resinous hairs on the inside of the nucellar extensions and between the ribs of the body of the ovule, which was enveloped in a hard sclerotesta. The whole structure is larger, heavier, and more elaborate than propagules usually dispersed by wind or water alone, such as the pappus of modern Compositae which Walton (1964) thought comparable. They were probably shaken loose from the cupule by wind (a "wind ballist" of van der Pijl, 1972). Also possible is dispersal by ground-dwelling spiny millipedes and similar large arthropods (Rolfe, 1980).

Habitat. This fossil plant at Oxroad Bay is found encased in calcareous nodules (caliche) of weakly developed paleosols (Inceptisols of Soil Survey Staff, 1975) on the aggrading banks of a small (10 m wide) creek deposit (Gordon, 1941, pl. 1, fig. 1; Scott et al., 1984). The stabilized banks (rooted calcareous nodules) can be seen to be laterally impersistent, eroded on top, and covered alternately on each side of the creek. The area was well drained and quite near the volcano, as can be seen from the nature of these paleosols and associated bouldery volcanic mudflows. In such well-drained, frequently disturbed soil one would expect small, xeromorphic, and early successional plants.

Such a habitat agrees with several adaptive features of this plant: small size (Long, 1976), dissected pinnae (Walton, 1931; Barnard, 1960), cupular protection of ovules (Barnard, 1960), long extensions of the ovular integument, and hairy coat and woody integument of the ovule (Gordon, 1941). This also is compatible with what is known about the other fossil plants found there (listed by Scott et al., 1984). Lycopods and remains of arborescent plants such as *Stamnostoma huttonense* are rare and fragmentary. Most common are small seed ferns and enigmatic plants (family Buteoxylaceae).

Paleogeographic setting. This reconstruction is based mostly on petrified fossils of Early Carboniferous (late Tournaisian) age, from Oxroad Bay, East Lothian, Scotland (Long, 1976; Scott et al., 1984). Only the basal parts of pinnae are known from Oxroad Bay, and the remainder of the frond is modeled after compressions from Ardross and Burntisland, Fife, Scotland (Walton, 1931; British Museum specimen v31831).

All of these localities were in a large rift valley, now occupied by the Midland Valley of Scotland. This was flanked by the Grampian Highlands to the north and the Southern Uplands to the south, and opened out to the sea toward the southwest (Anderton et al., 1979). It was a volcanic landscape with extensive flows from fissure eruptions and some imposing alkali-basaltic volcanoes (Francis, 1983).

Calathospermum fimbriatum may have lived more inland and at higher elevation than the coastal lagoons colonized by *Stamnostoma huttonense* and *Lyrasperma scotica*, and probably in a similar subtropical and seasonally dry climate. As Gordon (1941) argued, it may have lived in a drier climate than these other plants. It was within the rain shadow of rift valley walls, volcanoes, and the mountain ranges of the Grampian Highlands and contiguous ranges now in North America (Bambach et al., 1980).

LAGENOSTOMA LOMAXII

Hypothesized reconstruction. We envisage *Lagenostoma lomaxii* as a shrub with an irregular crown of large leaves (Fig. 5). It grew in extensive, permanently waterlogged swamps, dominated by arborescent lycopods, on deep peaty soils. During the early part of the Late Carboniferous (early Westphalian A or about 320 million years ago) this area was in the subhumid tropics. The trunk (*Lyginopteris oldhamia* (Binney) Potonié, 1899) was slender (3–4.5 cm diameter) and strengthened by a thick outer zone of sclerenchyma forming an anastomosing system of radially arranged plates (dictyoxylon cortex). The lower part of the stem was anchored by numerous slender prop roots (*Kaloxylon hookeri* Williamson, 1875), which ran directly down from the stem and branches but did not sheath the stem as they do in many modern tree ferns and palms. Its petioles (*Rachiopteris aspera* Williamson, 1874) were flattened and had two vascular strands near the base. The leaves (*Sphenopteris hoeninghausii* Brongniart, 1828) were large and spreading, with a dichotomously forked rachis and numerous small, orbicular, third-order pinnules. The frond rachis and the stems were clothed in prominent stalked glands. Cupulate ovules (*Lagenostoma lomaxii* Williamson in Oliver & Scott, 1903, when petrified, and *Calymmatotheca hoeninghausii* (Brongniart) Stur, 1877, in compression) were borne pinnately, in modified apical parts of fronds. Prepollen organs are not certainly known, and prepollen are represented only by badly corroded specimens within the pollen chamber of the ovules. The cupulate cover to the ovules was liberally studded with stalked glands like those on the stem and leaves.

Evidence for reconstruction. Our reconstruction of *Lagenostoma lomaxii* is based principally on structurally preserved fossils in coal balls from the Hough Hill Colliery, presently abandoned on the south face of the hill 1 km south of Stalybridge, near Manchester, in Cheshire, England (Stopes & Watson, 1909). They come from the "Six Inch Mine Coal" of the uppermost Millstone Grit, of early Late Carboniferous age (early Westphalian A; Tonks et al., 1931; Phillips, 1980) or about 320 million years ago (in time scale of Palmer, 1983). The distinctive stalked glands on these fossil leaves, petioles, stems, and cupules were the main evidence used by Oliver & Scott (1903, 1904) in their reconstruction of this plant, which was the first indication that some gymnosperms included plants with fernlike leaves. There are additional anatomical similarities between the various parts, which are closely associated in coal balls and shales (Benson, 1904; Oliver & Scott, 1903, 1904; Seward, 1917; Jongmans, 1952; van Amerom, 1968).

There has been considerable debate about the likely prepollen organ of this plant. Benson (1904) argued that it was *Telangium scottii*, but *T. scottii* is nonglandular, and so more likely to have belonged with *Lagenostoma ovoides*. Kidston (1905, 1906) thought the prepollen organ was the fossil now known as *Crossotheca kidstonii* (Hemingway) Jongmans (1952) found attached to leaves in siderite nodules of slightly younger geological age (Westphalian B) in the Lancashire Coalfield. However, Jongmans (1952) pointed out that the attached foliage belongs to another species of *Sphenopteris*, lacking the characteristic stalked glands. A third possibility figured by Seward (1917) is a fragment of a petrified pinnule with an attached sporangium on the abaxial side, and a nearby emergence where it appears that another sporangium may have fallen off. A similar specimen with glands and stalks was figured by Kidston (1906, fig. 2). Until this material is studied further, the prepollen also remain poorly known, because those found in the ovules are too badly corroded to be identified with dispersed species.

Habit. Because of the small size of these stems (up to 4.5 cm diameter), this plant has been considered a vine (Phillips, 1981). This was a common habit for some Carboniferous seed ferns such as *Callospermarion pusillum* (reconstructed here). By comparison *Lagenostoma lomaxii* has a much more prominent zone of mechanical tissue in the cortex and a lesser development of secondary xylem, and lacks asymmetric wood. This plant is also very abundant locally (it may comprise up to 38% by volume of some coal balls: Phillips, 1981). It may have grown in waterlogged soils, because there are lacunae within the cortex of the stems (Blanc-Louvel, 1966). It was branched copiously, with some very slender branchlets (Blanc-Louvel, 1966). Both axillary and nonaxillary lateral branching have been observed. For all these reasons we do not think that *Lagenostoma lomaxii* was a vine. Nor do we follow the reconstruction of Scott (1900), showing the plant leaning for support on adjacent trees. Instead, it was probably a shrubby plant with a tangle of prop roots (Attim's model of Hallé et al., 1978).

Reproduction. Judging from compression fossils (Jongmans, 1952) and the anatomy of cupule stalks (Oliver & Scott, 1904), the cupulate ovules were borne pinnately on fertile fronds or parts of fronds. After pollination, the prepollen chamber was occluded by growth of the central column against the overarching sclerotesta of the ovule.

A considerable delay between pollination and fertilization is likely. This would account for the abundance of either ovules or of pollen organs of allied species, but not both, in association with compressed foliage. Jongmans (1952) has argued

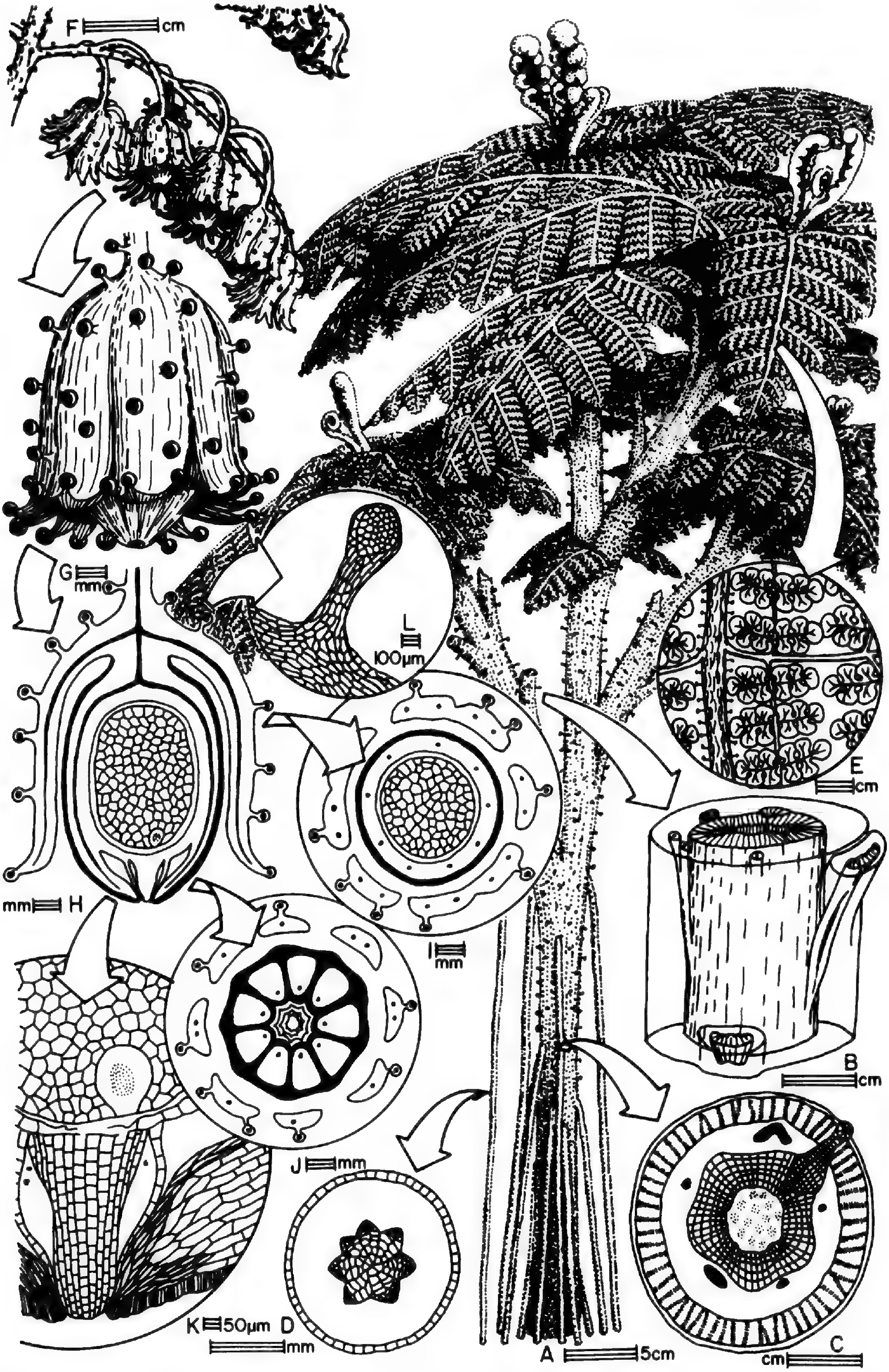

FIGURE 5. *A reconstruction of* Lagenostoma lomaxii *of earliest Late Carboniferous (Westphalian A) age, from Hough Hill Colliery, near Stalybridge, Cheshire, England.—A. Habit as a swampland shrub.—B. Xylem model of stem and petioles.—C, D. Schematic cross sections of stem and of root (respectively), showing mixed pith*

that pollen organs and mature ovules were produced, abscised, and then decayed during different parts of the year. Compressions of conical cupules lacking prominent ovules (Jongmans, 1952; van Amerom, 1968) may have been fertile fronds with immature ovules at or close to the time of pollination. Petrified ovules containing megagametophytes and archegonia are a good deal larger than these remains and set within a bell-shaped cupule with flaring lobes (Oliver & Scott, 1904).

Lagenostoma lomaxii may have been pollinated by insects, considering the large size (averaging 55 by 70 μm) and coarse ornament of the prepollen (Oliver & Scott, 1904), within the range found in modern insect-pollinated plants (Whitehead, 1969). A case also could be made that the capitate glands were insect attractants, but we find this unlikely. The distribution of glands over almost all known parts of the plant is most compatible with interpretation as organs to deter insect herbivory. Winged insects were around in some diversity and abundance by this geological period (Rolfe, 1980).

By the time the ovule was ready for dispersal, it was about 5.5 by 4.5 mm in size (Oliver & Scott, 1904). The cupule appears to have spread open and the capitate glands withered, judging from compression specimens (Benson, 1904; Seward, 1917). Since many of these lacked attached ovules, it is doubtful that the cupule played a role in dispersal.

Habitat. This fossil plant is best known in coal balls from Hough Hill Colliery near Stalybridge, England (Stopes & Watson, 1909). Coal balls are calcareous or dolomitic nodules found within coal seams (Scott & Rex, 1985). Although modified somewhat during burial (Rao, 1985), coal balls developed as the peat accumulated, as a kind of caliche nodule in peaty soils (Retallack, 1986). In most swamps the development of such nodules is limited by acidity. Coals containing coal balls form under fen or carr vegetation of neutral to alkaline wetlands, where acidity is buffered by a subhumid, seasonally dry climate and nearby limestone bedrock.

The coal containing coal balls in Hough Hill Colliery is interpreted here as the less decayed (mor) humus layer of the organic horizon of a peaty paleosol (Histosol) of permanently waterlogged ground (Fig. 2B). It is underlain by a thick zone of carbonaceous claystone (Tonks et al., 1931) representing a more decayed (mull) humus, which may have formed at a time during the development of this soil when it was periodically better drained. Below this dark clay is gray, leached clay with root traces ("fireclay"). A thin zone of siderite ("ironstone") represents a deep gley horizon of this older paleosol (comparable to cases discussed by Retallack, 1976).

This paleosol changes character along strike, and in places the organic horizon (Six Inch Mine Coal) directly overlies levee (Rough Rock Flags) and channel deposits ("massive current bedded grit" of Rough Rocks; Tonks et al., 1931) of a former stream. Clayey soils (Entisols of Soil Survey Staff, 1975) of the stream levee supported vegetation dominated by seed ferns, such as *Alethopteris lonchitica* and *Mariopteris muricata* (Stopes & Watson, 1909, discussed this "flora in shales"), quite different from vegetation of the swamp (the flora in coal balls).

The former stream may have flowed into a lagoon or bay, which ultimately inundated the swamp. The shale overlying the coal contains marine fossils such as goniatites (*Gastrioceras* sp. aff. *G. listeri*) and scallops (*Pterinopecten papyraceus*, ?*Posidonomya insignis* and *Posidoniella* sp.: Tonks et al., 1931) as well as plant fragments (*Lepidodendron lycopodioides*: Stopes & Watson, 1909).

In general, *Lagenostoma lomaxii* is found in coal balls dominated by the remains of arborescent lycopods (more than 90% by volume of the coal ball assemblage: Phillips, 1981) and a variety of understory ferns (Phillips, 1980). We envisage it as a small bush of these lycopod-dominated wetlands. Vegetation of these permanently waterlogged woodlands was distinct from that of streamsides, which were dominated by other seed ferns. There was not any detectable marine influence in these lycopod woodlands, although coastal lagoons may not have been far away.

Paleogeographic setting. *Lagenostoma lomaxii* is best known from coal balls in the uppermost Millstone Grit (Stopes & Watson, 1909; Tonks et al., 1931; Phillips, 1980). The same species is

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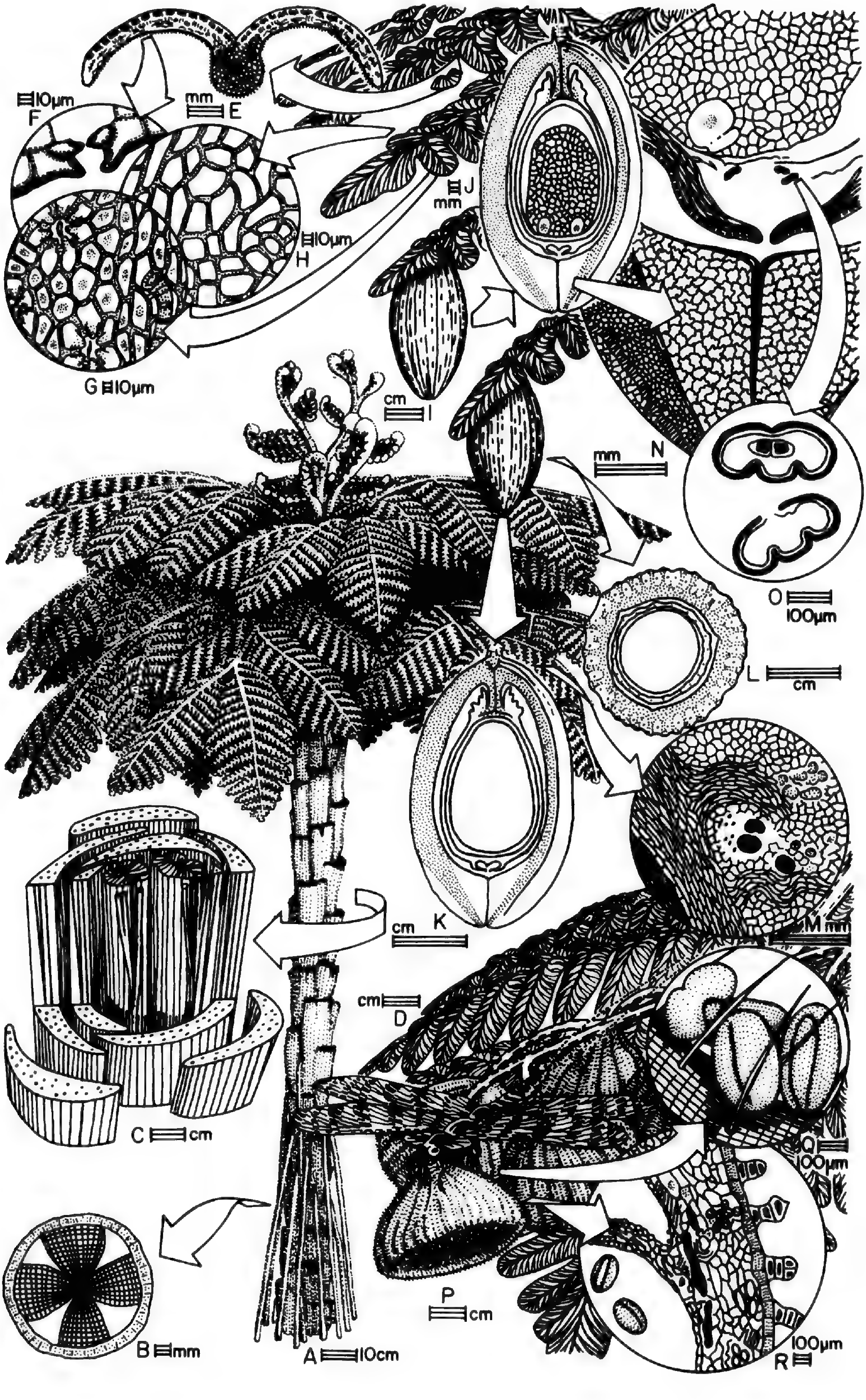
(clumped stipple), primary xylem (black), secondary xylem (cellular pattern), and mechanical cortex (radial shading).—E. Detail of leaf.—F, G. Cupules with ovules.—H–K. Longitudinal and transverse sections of cupulate ovules, showing vascularization (heavy lines), multicellular megagametophyte (cellular pattern) and archegonium (circle with central stipple).—L. Longitudinal section of capitate gland.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found also in shales of about the same age elsewhere in the British Isles and western Europe (Jongmans, 1952).

In Cheshire, the coal accumulated as peat in a coastal swamp on the northern margin of the Wales–Brabant landmass (Anderton et al., 1979), which was a promontory extending west into the mountains of eastern North America (Ziegler et al., 1979). During most of the Late Carboniferous this was a subhumid part of the tropics, in the rain shadow of mountains to the west (Bambach et al., 1980). There were dry periods (perhaps seasonal) and forest fires, which left charcoal in the swamps (Scott, 1979).

PACHYTESTA ILLINOENSIS

Hypothesized reconstruction. *Pachytesta illinoensis* was similar to modern tree ferns in overall appearance (Fig. 6). It probably grew on river and deltaic levees and other open and slightly elevated or disturbed areas of midcontinental North American coastal swamps of late Pennsylvanian (Stephanian) age, about 296 million years ago. By this time the dominant swampland plants were no longer arborescent lycopods but marattiaceous tree ferns. By comparison with these and modern tree ferns, this plant had less copiously divided and more leathery leaves (*Alethopteris lesquereuxii* Wagner, 1964). Its trunk (*Medullosa noei* Steidtmann, 1944) was formed largely of closely adpressed leaf bases. It had a wide fleshy cortex and little woody tissue. Large ovules of this plant (*Pachytesta illinoensis* (Arnold & Steidtmann) Stewart, 1954) hung pendulously from beneath terminal pinnules. Synangiate prepollen organs (*Bernaultia formosa* (Schopf) Rothwell & Eggert, 1986) containing large prepollen (*Schopfipollenites ovatus* (Schopf) Potonié & Kremp, 1954) dangled in pinnate structures replacing parts of fronds. These fructifications were among the largest and most conspicuous of Carboniferous swamps, and the prepollen grains so unusually large and heavy that insect pollination is likely. Among the great variety of Late Carboniferous insects known, Paleodictyoptera such as *Homaloneura dabasinkasi* Carpenter (1964), shown in our reconstruction, were the most likely pollinators of these plants. After pollination, the megagametophyte differentiated and the pollen chamber was sealed by continued growth of the outer integument. The large (2.5 by 4.5 cm) ovules had well-developed fleshy layers of the kind attractive to animal dispersers. Their sclerotesta could have protected them from crushing and acids of the digestive tract. Animals of that time sufficiently large to swallow such ovules included reptiles, amphibians, fish, and sharks. With large food reserves, the young seedlings could grow in the shade and tolerate other adverse influences of competing vegetation. Although this plant is associated with disturbed, nutrient-rich parts of swamps, it was probably not the earliest successional colonizer, but a later species in plant succession.

Evidence for reconstruction. Our reconstruction is based on remains preserved in coal balls from the bed of Sugar Creek 3.7 km northwest of Berryville, Lawrence County, Illinois. Another well-known locality is a tributary of Bonpas Creek 4.5 km east of Calhoun, in nearby Richland County, Illinois. These are both from the Calhoun Coal of the Mattoon Formation in the McLeansboro Group, of Late Pennsylvanian (Stephanian) age (Phillips, 1980), or about 296 million years ago (in time scale of Palmer, 1983). Our reconstruction may also be valid for fossils from coal balls of the Herrin No. 6 coal of slightly older (Westphalian D) Pennsylvanian age, where many of the species gathered together here have been found in association (Phillips & DiMichele, 1981). Because of the probability of mosaic evolution, we do not mean to imply that the whole plant existed in every locality where some small part of it has been found. The attribution of these various remains to one plant is based on the

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FIGURE 6. *A reconstruction of* Pachytesta illinoensis *of Late Pennsylvanian (Late Carboniferous or Stephanian) age, from Berryville, Illinois, U.S.A.—A. Habit as a palmlike tree of well-drained parts of swampland.—B. Schematic cross section of adventitious root, showing secondary xylem (cellular pattern).—C. Cutaway model of xylem and petiole traces of stem.—D. Detail of leaf.—E. Cross section of leaf.—F. Cross section of stomate.—G, H. Lower and upper (respectively) cuticles.—I. Attached ovules.—J–L. Schematic longitudinal and transverse sections of ovule, showing sclerotesta (stipple and rectilinear cellular pattern) and vascular strands (black).—M. Detail of secretory gland, with black resinous contents in transverse section.—N. Detail of prepollen chamber, apical end of megagametophyte and archegonium in longitudinal section. O. Cross section of prepollen, with supposed sperm (black and subtriangular, above).—P. Prepollen organs and a palaeodictyopteran insect.—Q. Prepollen on hairy leg of insect.—R. Cross section of prepollen organ, showing glandular hairs (outer margin) and internal secretory glands (black).*

anatomical similarity of petioles attached to leaves, stems, and prepollen organs (Ramanujam et al., 1974); the similar pollen found in prepollen organs and ovules (Taylor, 1965); and close association of different organs in coal balls (Schopf, 1948; Taylor, 1965; Phillips, 1981).

Although preserved as petrifactions, splitting and degaging of coal balls has revealed the nature of the leaf, which conforms in shape and venation to *Alethopteris lesquereuxii* var. *cerverae* Wagner, 1968 (Stidd, 1981), and has a cuticle (Ramanujam et al., 1974; Oestry-Stidd & Stidd, 1976; Reihmann & Schabilion, 1976, 1978) generally similar to that of the compression species *A. davreuxii* (Barthel, 1962). There are other alethopterid leaves in coal balls at the main locality for this plant (Berryville, Illinois), and these have blunter, shorter, and straighter pinnules, more like the impression species *A. bohemica* and *A. grandinoides* var. *subzeilleri* (Mickle & Rothwell, 1982). Similar impression fossils have been found in nearby Indiana with numerous small ovules attached (Taylor, 1981, figs. 13–18A, B), and it is likely that this second type of frond is the foliage of other small fructifications, such as *Pachytesta berryvillensis* and *Dolerotheca villosa*, also found in Berryville coal balls (Schopf, 1948; Taylor, 1965; Phillips, 1980). There is only one other allied species in these coal balls (*Pachytesta hexangulata*), and this is much rarer than the other two (known from only one specimen: Taylor, 1965).

Habit. Our reconstruction of *Pachytesta illinoensis* follows that of Stewart & Delevoryas (1956), which is drawn as if it were a young plant. Fossil stems of this plant range from 10 to 50 cm in diameter. They probably were about 5 m high and occasionally attained heights of 10 m (Wnuk & Pfefferkorn, 1984). It is a common plant, yet branches have not been found on long stem compressions (Pfefferkorn et al., 1984), so it probably conformed to Corner's architectural model (of Hallé et al., 1978), as do modern tree ferns such as mamaku (*Cyathea medullaris*) of New Zealand. As in modern tree ferns, *Pachytesta illinoensis* probably had a crown of about ten large leaves, oriented so that a good deal of the trunk was visible from the side (Wnuk & Pfefferkorn, 1984). Like these modern plants also, it was perennial, growing slowly by the development of new leaves above the leaf bases of the old crown. The trunks were strengthened somewhat by several bundles of wood. These were not separate steles, but rather a single eustele with secondary xylem and phloem developed in several separate bundles (Basinger et al., 1974; Stewart, 1983; Smoot, 1984b). The base of the plant was invested in adventitious roots, although these did not cover the stem to the same extent as in associated fossil tree ferns, and it was more like New Zealand mamaku in this respect. Like this modern plant also, the fossil trees lacked lacunar spaces in their roots (Phillips, 1981).

The large, hemispherical, compound prepollen organ (microsynangium) included numerous elongated sporangia oriented perpendicularly to the flat side. The pattern of their open ends in this flat (lower) side is almost radial and has been interpreted to be homologous to an infolded stack of bladelike synangia (Rothwell & Eggert, 1982, 1986) and, alternatively, to a branch of pinnately arranged individual sporangia (Dufek & Stidd in Stidd, 1981). By either arrangement and considering the number of vascular strands in its petiole (Ramanujam et al., 1974), each large synangium is the morphological homolog of a primary pinna of a frond. We do not think that prepollen organs were scattered randomly among otherwise sterile fronds, an impression that could be gained from uncritical inspection of the reconstruction of Ramanujam et al. (1974). They were probably borne pinnately in special fertile fronds or parts of fronds. Such an arrangement has been demonstrated for other synangia of closely comparable structure (*Potoneia*), but containing different prepollen (Taylor, 1982, pl. 6, fig. 2).

Ovules of *Pachytesta illinoensis* have not been found attached, but their mode of attachment can be inferred from similar compressions of ovules found attached under the terminal pinnule of the leaves (Crookall, 1959). We do not think that they formed at the end of the pinna (as reconstructed by Darrah, 1939: 95). Close inspection of these specimens often reveals the terminal pinnule twisted into a less-conspicuous upright position beside the heavier and larger ovule (Crookall, 1959: 27, figs. 1–5). Other related species of ovule have been found attached farther back on the rachis of the pinna (Halle, 1929; Wagner, 1968; Zodrow & McCandlish, 1980).

Reproduction. The prepollen of *Pachytesta illinoensis* had an alveolate exine ultrastructure and was so large (300–350 μm long by 200–250 μm wide) and heavy that it would not have been dispersed far by wind. It was more likely dispersed by insects (Taylor, 1978). The glandular hairs of the microsynangium and the resinous internal glands of both the microsynangium and ovules may have produced a nutritional reward for pollinating insects or have deterred their herbivory. Both organs also were enclosed in fleshy tissue, which may have been nutritious.

It is uncertain which among the great variety of Carboniferous insects known could have pollinated this plant, but several circumstantial lines of evidence implicate Paleodictyoptera. These were superficially like modern dragonflies, but, unlike these modern carnivorous insects, had only narrow sucking mouthparts (Kukalova, 1970). The example we have shown in our reconstruction is *Homaloneura dabasinkasi* Carpenter, 1964, known largely from wings with camouflage color-banding in siderite nodules of slightly older Late Carboniferous age (Westphalian D) near Braidwood, Illinois. Paleodictyopterans were active, flying insects, with large compound eyes and hairy legs: all features of modern insect pollinators. Their sucking mouthparts match in size and shape the fine borings seen in petrified microsynangia and ovules (Schopf, 1948). The claim of paleodictyoptera as pollinators of these plants could be regarded as diminished by the discovery of prepollen like that of *Pachytesta illinoensis* lodged in the leg joints of a large fossil millipedelike creature (Scott & Taylor, 1983), but it is unlikely that these extinct arthropods were any more adventurous in the canopy than modern litter-feeding millipedes (Rolfe, 1980). Coprolites containing these prepollen also have been found (Scott, 1977), but these cannot be attributed to any particular animal. A variety of animals probably ate these grains, both in the canopy and on the ground.

As in all the seed ferns considered here, there was a period of time between pollination and fertilization. For ovules with such large megagametophytes this was probably at least a few weeks. Fossil prepollen grains within ovules of *Pachytesta illinoensis* have been found with two large black bodies (Stewart, 1954), which have been compared to the ciliated, motile sperm of modern cycads (Chamberlain, 1935). Such opaque "spots" in petrified cells also could be remains of decayed cytoplasm, as paleobotanists have learned from painful experience in the study of other fossils (Knoll & Barghoorn, 1975). However, there is other possible cytoplasmic material in the medullosan pollen grain in question.

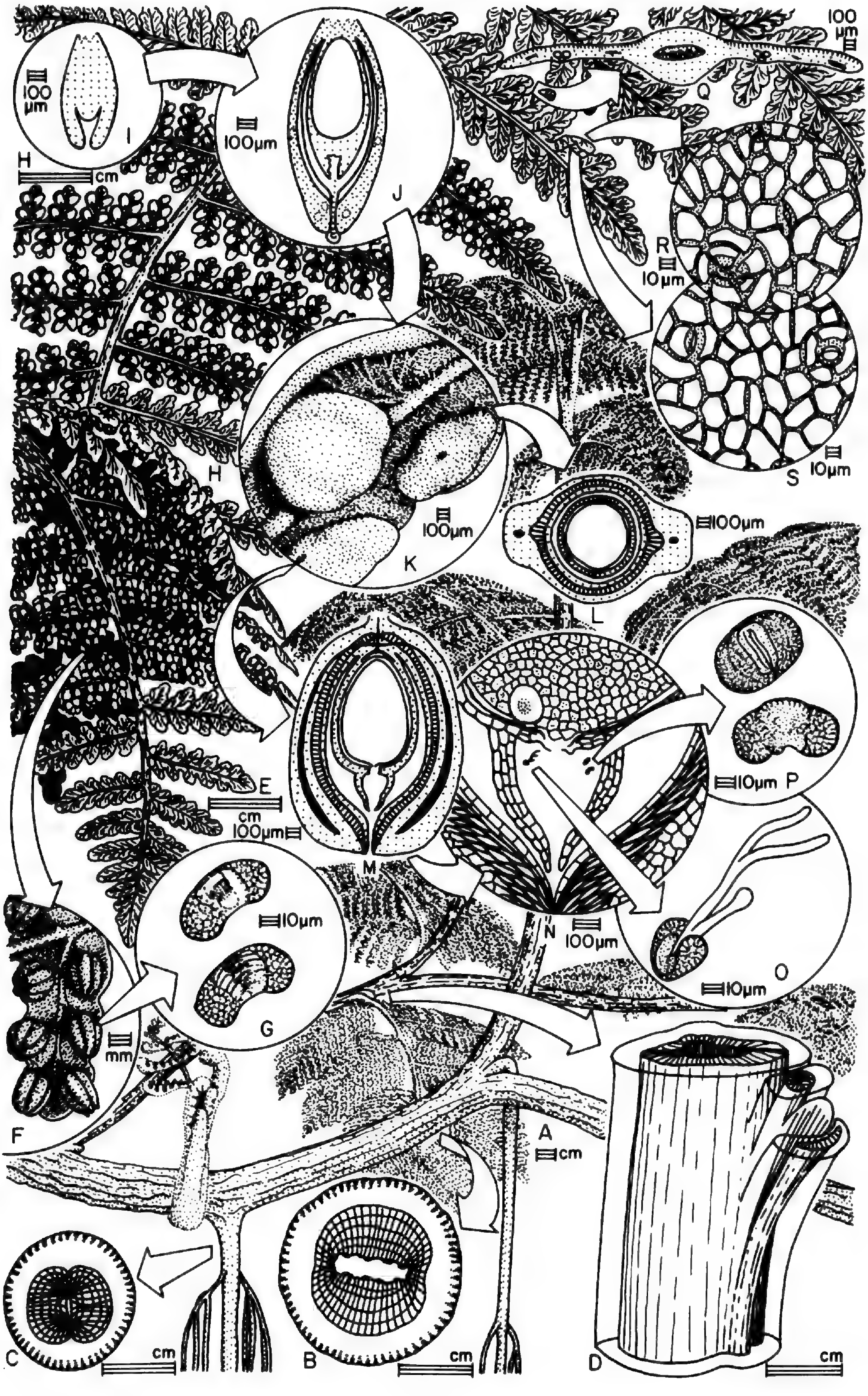
The ovule of *Pachytesta illinoensis* was conspicuous in its large size (about 2.5 cm in diameter and up to 4.5 cm long). Like many modern stone fruits, the fossil ovules had well-differentiated sarcotesta and sclerotesta. The sarcotesta was especially thick near the apex, which was early to decay or be eaten, judging from some specimens (Stewart, 1954). This succulent flesh may have attracted animal dispersers. The sclerotesta can be seen to seal the micropyle in some specimens (Taylor, 1965). Similar stones in modern fruits serve to withstand crushing and acidity during passage through the guts of animals (van der Pijl, 1972). Of the array of known Late Carboniferous reptiles and amphibians (Moodie, 1916; Reisz et al., 1982), edaphosaurs, temnospondyls, and microsaurs were large enough to have been able to swallow a fruit this size. Considering the likely habitat of this plant, the ovules could have been dispersed by fish, as are some modern angiosperm fruits in the varzea swamp forests of Amazonian Brazil today (Gottsberger, 1978). Large palaeoniscid fish and pleuracanth sharks were common within parts of the Late Carboniferous swamps of Illinois (Zangerl & Richardson, 1963; Zangerl & Case, 1973).

Individuals of *Pachytesta illinoensis* and related plants appear to have borne fruit in massive bursts, judging from local accumulations of petrifactions and molds-and-casts of similar large ovules (Seward, 1917, fig. 423; Tonks et al., 1931, pl. II; Taylor, 1965; Jennings, 1974). Such a reproductive effort probably was not begun until after a few years in the life of the plant. In modern angiosperms, copious production of fruit ensures that some remains unmolested by animals and is especially common in trees with large fruits (Janzen, 1978).

Habitat. This plant was preserved in coal balls in the manner already described for *Lagenostoma lomaxii*. Although *Pachytesta illinoensis* grew in and near swamps, it lacked root lacunae usually found in plants of waterlogged ground and thrived in slightly elevated and nutrient-rich parts of the swamp (Phillips, 1981). A similar habitat is indicated by the bundle sheath cells (Krantz anatomy) found around veins within petrified leaves, thought by Baxter & Willhite (1969) to indicate the C_4 photosynthetic pathway for this extinct plant. Like modern plants using this pathway (Chazdon, 1978), *Pachytesta illinoensis* may have been able to endure hotter, sunnier, and drier sites than many associated plants.

Leaves of the plant had thick cuticles, especially on the adaxial surface. Stomates and hairs were confined to the abaxial surface, and each stomate was overhung by papillae borne on the subsidiary cells (Ramanujam et al., 1974; Oestry-Stidd & Stidd, 1976; Reihmann & Schabilion, 1976, 1978). These are all features of sun leaves of plants subject to deficiency of water or nutrients (Mickle & Rothwell, 1982).

Such large ovules would have been able to main-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tain the growth of seedlings, even under the shade and other adverse influences of other plants, as in modern plants of the "competitive strategy" (of Grime, 1979). Although *Pachytesta illinoensis* is geologically associated with disturbed and more-elevated parts of the swamps, it may have been a late species in succession, growing through and then shading out the earliest successional plants. In better-drained areas outside the swamps, similar plants may have formed stable, long-term communities, but within the swamp itself these plants were less persistent than associated tree ferns and lycopods (Phillips & DiMichele, 1981).

Judging from paleobotanical and palynological studies of Calhoun coal balls (Phillips et al., 1974; Phillips, 1980), *Pachytesta illinoensis* formed a minor part of vegetation dominated by marattiaceous tree ferns (with *Psaronius* spp. trunks and *Scolecopteris* spp. and *Asterotheca* spp. fructifications). Lycopods (*Sigillaria ichthyolepis*) and horsetails (*Calamites retangularis*) were moderately common, and the rest of this diverse flora was made up of rare cordaites, other ferns, and seed ferns.

Ecologically, *Pachytesta illinoensis* probably preferred elevated, slightly dryer, nutrient-rich parts of the swamp where there was either sandy or clayey soil or exposed dry, dusty peat. It was not the earliest successional colonizer of such habitats. In shale floras of stream and lake margins (Scott, 1979), calamites and small ferns appear to have occupied that niche. In coal balls of peat swamps, successional patterns are less clear (Phillips & DiMichele, 1981), but weedy plants of erratic occurrence include other seed ferns (such as *Callospermarion pusillum* reconstructed here), and small herbaceous lycopods and horsetails. Nor were *Pachytesta illinoensis* or allied plants part of marine-influenced swamps (mangroves) at this time. This habitat was dominated by cordaites (Raymond & Phillips, 1983).

Paleogeographic setting. The principal locality for our reconstruction of *Pachytesta illinoensis* is in Sugar Creek near Berryville, Illinois, of late Pennsylvanian (Stephanian) age (Phillips, 1980). Illinois was then part of a large central lowland within North America, bordered on the west by mountains in what is now Nevada and Montana, on the north by low hills and limestone plateaus on the Canadian Shield, and on the east by the Appalachian Mountains. These mountains were much more imposing than they are today, and more like the present European Alps (Heckel, 1977). Much of the mid continent was inundated by shallow seas opening out on deep ocean in the area of modern Texas. At the time the Calhoun Coal formed, the sea extended only as far as western Illinois and Missouri. Most of central Illinois was covered by a swamp, dissected by a large stream system draining the granitic shield and carbonate plateau country to the north. This ancient river is usually called the "Michigan River" but is in some senses a forerunner of the Mississippi (Stanley, 1985). To the west in Indiana and Ohio were more swamps and riverine lowlands. The present area of Illinois was about 5° north of the equator at this time, on the margin of the tropical humid and subtropical subhumid belts (Heckel, 1977). Evaporites formed in the dry climate of the present area of the Black Hills of South Dakota. Climate became increasingly humid southeastward toward the equatorial Appalachian Mountains (Schopf, 1975).

CALLOSPERMARION PUSILLUM

Hypothesized reconstruction. We envisage *Callospermarion pusillum* as a scrambling fernlike vine (Fig. 7). It probably formed dense tangles in moist, disturbed sites within and around Late Pennsylvanian swamp forests of tree ferns. Leaves of this plant (*Dicksonites pluckenetii* (Schlotheim)

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FIGURE 7. *A reconstruction of* Callospermarion pusillum *of Late Pennsylvanian (latest Late Carboniferous or Stephanian) age, from near Berryville, Illinois, U.S.A.—A. Habit as a swampland early successional scrambling vine.—B, C. Schematic cross sections of stem and root, showing primary xylem (black), secondary xylem (cellular pattern), and mechanical cortex (radial shading).—D. Xylem model of a node with petiole, bud, and root traces.—E. Fertile pollen-bearing leaf.—F. Pollen organ.—G. Monosaccate pollen with 2- and 4-cell microgametophytes.—H. Fertile ovulate leaf.—I. Longitudinal section of young ovule.—J. Longitudinal section of ovule at pollination time.—K–N. Overview and cross section of mature ovules, showing vascular strands (black) and sclerotesta (hachured), multicellular megagametophyte (equant cellular pattern), and archegonium (circle with central stipple).—O, P. Monosaccate pollen from pollen chamber of ovule, one showing a pollen tube.—Q. Cross section of leaf showing vascular bundles (hachured), secretory cells (open circles), and palisade layer (vertical lines).—R, S. Upper and lower cuticles, both with stomates.*

Sterzel, 1881) had stomates on both sides and little differentiation between the upper and lower surface. The clambering stem (*Callistophyton poroxyloides* Delevoryas & Morgan, 1954) was woody and perennial. In addition to horizontal runners, there were slender erect leafy stems and, at intervals, stout adventitious roots, which arose in the axils of foliage leaves or from within bifurcations of the main axis. Pollen-bearing organs (*Idanothekion callistophytoides* (Stidd & Hall) Rothwell, 1980) and ovules (*Callospermarion pusillum* Eggert & Delevoryas, 1960) were borne in zones on the abaxial surface of foliage leaves otherwise normal in appearance. The numerous pollen organs released abundant small saccate pollen (*Vesicaspora schaubergeri* (Potonié & Klaus) Jizba, 1962). Pollination may have been by wind and possibly occurred before the megagametophyte or pollen chamber was fully differentiated. After fertilization, which may have occurred on the ground, the seeds were already worn back to their sclerotesta. The numerous small seeds were probably dispersed largely by wind and water.

Evidence for reconstruction. This plant is best known at the locality near Berryville, Illinois, already discussed for *Pachytesta illinoensis*, and also is known from nearby coal-ball localities such as the one near Calhoun, Illinois. Reconstruction of *Callospermarion pusillum* was based on the similarity of secretory cavities in stems, sterile foliage, ovules, and microsporophylls; on the occurrence of similar pollen in the pollen organs, in the ovule pollen chamber, and dispersed; and on close association of its parts (Stidd & Hall, 1970a, b; Millay & Taylor, 1974; Rothwell, 1975, 1980, 1981).

Habit. The young stems have a nearly cylindrical mass of secondary xylem, a thin zone of secondary phloem, and a subsurface zone of mechanical tissue formed from anastomosing bands of sclerotic cells (dictyoxylon cortex: Rothwell, 1975; Smoot, 1984a). These were probably erect, leaf-bearing stems. Older stems do not all have such well-developed mechanical tissue, but rather a thick bark and a large central asymmetric mass of secondary xylem. These were probably horizontal runners. Stout adventitious roots arose from these runners, usually in the axils of leaves, but also within the branches of the main axis (Kidston, 1924; Rothwell, 1975). Buds, petioles, and adventitious roots often arise from within the dichotomies of stems and leaves. These are false dichotomies (Kidston, 1924) arising by development of opposite branches with suppression of the terminal meristem. This branching system is similar to Leeuwenberg's architectural model of plants proposed by Hallé et al. (1978), although the two are not strictly comparable because the leaf-borne fructifications of seed ferns are very different from those of most modern plants. A similar architecture is seen in the modern Australian and Southeast Asian fern *Gleichenia dicarpa*.

The synangiate pollen organs were attached on the underside of the leaves in a manner similar to sporangia of marattiaceous ferns (Kidston, 1924; Stidd & Hall, 1970a). They contain, however, monosaccate pollen rather than fern spores. The saccus is laterally expanded, so that it is superficially similar to bisaccate grains (Hall & Stidd, 1971; Millay & Taylor, 1974). As in modern bisaccate grains, the saccus of the fossil pollen formed by detachment and expansion of the sexine from the lamellated nexine. These fossil pollen also were similar to those of modern gymnosperms in germinating through the side of the grain opposite the point of attachment in the original tetrad, unlike the prepollen of the other Carboniferous seed ferns already considered (Eggert & Millay, 1976).

Ovules and their attachment scars are found over large areas of compressed fronds (Grand'Eury, 1905; Kidston, 1924). Ovules were attached at the ends of veins near the abaxial margin of the pinnules, and their micropyles faced inwards toward the pinnule midribs (Loubière, 1929; Rothwell, 1980).

Reproduction. *Callospermarion pusillum* was probably wind pollinated, considering the moderate size (37–54 μm long by 30–49 μm wide: Millay & Taylor, 1974) of its pollen and the large amount of it produced. Saccae sometimes have been considered the "wings" of wind-dispersed pollen, but they are now thought to have served more for orientation and flotation in an inverted pollination drop (Doyle, 1945). Microgametophytes at the two- and four-celled stage have been found in some synangia (Millay & Eggert, 1974), indicating that these were fully formed at the time of pollination.

In some coal balls, ovules have been found which vary considerably in degree of maturity (Rothwell, 1971). Large fructifications of modern weeds of disturbed habitats show comparable "continuous flowering," thus improving chances that some propagules will mature at an appropriate time (Heinrich, 1976). The youngest ovules found are small and weakly differentiated. At what is thought to have been pollination stage, the ovule was small, with an imperfectly differentiated seed coat and no indication of a megagametophyte. A fossilized pollination drop has been reported in a closely related species (*Callospermarion undulatum*: Rothwell, 1977), but it appears rather more resinous than modern pollination drops (described by Doyle & O'Leary, 1935b) and contains spores known to belong to other plants (Rothwell, 1980). It may be an exudate from the micropyle of a partly decaying ovule rather than a pollination drop. Nevertheless, larger ovules than this do contain pollen grains and have a sealed micropyle, thus suggesting that ovules were at this stage of development at the time of pollination. With further growth after pollination, the micropyle was occluded by growth and differentiation of sclerotesta and sarcotesta as the megametophyte developed. In the most mature ovules, presumably already dispersed, there were several archegonia at the apical end of the megagametophyte, and the sarcotesta was abraded away.

A germinated pollen grain with a branched pollen tube has been found in the pollen chamber of an immature ovule of a related species (*C. undulatum*; Rothwell, 1972). It could be that this pollen tube merely served for nutrition and stabilization of the pollen grain during its long wait until fertilization was achieved by motile gametes. Alternatively, this pollen tube, or at least one branch of it, may have delivered nonmotile sperm nuclei to the archegonium (siphonogamy), as in living conifers such as black pine (*Pinus nigra* = *P. laricio* in Chamberlain, 1935). Rothwell (1980) was impressed with the coniferlike development and morphology of this plant's ovules, pollen, and pollen tubes, and thought that siphonogamy was more likely.

The small ovules were dispersed individually, as can be inferred from compressed leaves showing only the attachment scars where ovules had abscised (Kidston, 1923). The ovules were numerous, small, and somewhat flattened, with narrow wings. They were probably dispersed largely by wind and water. The ovules were made in quantity, rather than quality, thus maximizing the chance that at least a few would find places suitable for germination, as in modern weedy plants ("ruderals" of Grime, 1979).

Habitat. This reconstruction is based on specimens from coal balls found in Sugar Creek northeast of Berryville, Illinois (Rothwell, 1975, 1980), and it is known from coal balls of comparable age at several other localities in the mid-continental U.S.A. (Phillips, 1980). This species of compressed leaves (*Dicksonites pluckenetii*) has long been known from compression floras of Britain and France (Grand'Eury, 1905; Kidston, 1923), where allied species of petrified plants have also been found (Loubière, 1929; Rothwell, 1981). Like *Pachytesta illinoensis* reconstructed here, it was locally abundant in swampy lowlands.

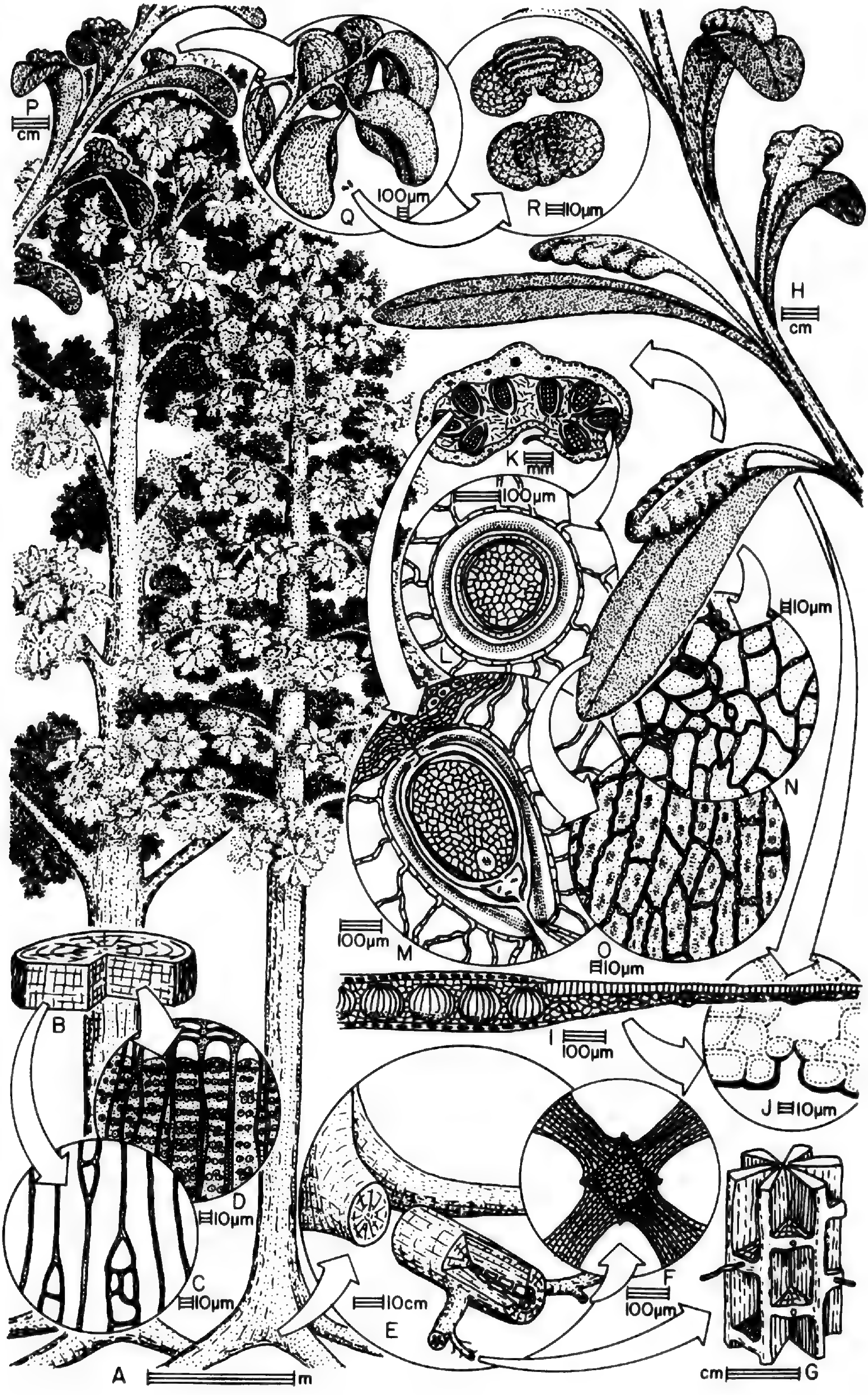
Several features of *Callospermarion pusillum* can be construed as evidence that it was a plant of moist, somewhat shady understory habitats. The pinnules are attached along the middle of the rachis of the frond (Rothwell, 1975), and there is little differentiation between the upper and lower cuticle, both of which are stomatiferous (Barthel, 1962).

Considering this and its weedy reproductive features, we hypothesize that *Callospermarion pusillum* was an early successional plant of disturbed ground. This may have included stream margins, tracts of forest devastated by hurricanes, locally well-drained peat, forest defoliated by fire, or light gaps around fallen trees. It lived among swamp forests dominated by tree ferns during the late Pennsylvanian (Stephanian: Phillips, 1980).

Paleogeographic setting. This plant is known from the locality of *Pachytesta illinoensis* already described. *Callospermarion pusillum* lived in very similar climate and general environment.

DICTYOPTERIDIUM SPORIFERUM

Hypothesized reconstruction. In our view, *Dictyopteridium sporiferum* was a swampland tree, widely distributed in cool-temperate regions of the Gondwana supercontinent during Late Permian time, some 245 to 253 million years ago (Fig. 8). In Queensland and New South Wales, it grew in an extensive system of intermontane valleys west of a volcanic mountain range like that of the modern South American Andes, and east of the plains and hill ranges of inland Australia. Its tongue-shaped leaves (*Glossopteris communis* Feistmantel, 1876) were seasonally deciduous. They had a thick adaxial cuticle and stomates sunken into the abaxial surface. Their venation was reticulate, but not organized into veins of different thickness, as in modern angiosperms. Its wood (*Araucarioxylon bengalense* (Holden) Maheshwari, 1972) was massive and coniferlike, with clear growth rings. Large roots spread out horizontally from the trunk, and the rootlets (*Vertebraria australis* McCoy, 1847) had internal chambers, which may have allowed growth in oxygen-poor, waterlogged, peaty soils. Ovule-bearing (*Dictyopteridium sporiferum* Feistmantel, 1881) and pollen-bearing structures (*Eretmonia* sp. cf. *E. hinjridaensis* Surange & Maheshwari, 1970) were borne on the midrib of leaflike structures. These were arranged helically on fertile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short shoots, but it is not certain whether these shoots were bisexual or unisexual. Pollen sacs (*Arberiella africana* Pant & Nautiyal, 1960) were borne at the ends of slender, copiously branched stalks. They dehisced longitudinally to release numerous bisaccate, striate pollen grains (*Protohaploxypinus limpidus* (Balme & Henelly) Balme & Playford, 1967). These plants were probably wind pollinated. Numerous ovules (*Stephanostoma crystallinum* (Pant) Pant & Nautiyal, 1960) were borne on the underside of a leaflike organ and loosely enclosed by its inrolled margins. The ovules were interconnected by a meshwork of multicellular hairs and probably also a good deal of mucilage. By the time of fertilization the leaflike structure bearing ovules probably was unfurled, shrivelled, and decayed. Seeds were numerous, small, and lightweight. They probably were scattered by wind.

Evidence for reconstruction. This reconstruction is based on petrified material from near the Homevale–Elphinstone road at the southwest property boundary of Homevale Station (or "cattle ranch"), 87 km west-southwest of Mackay, Queensland, Australia (Isbell, 1955; Gould & Delevoryas, 1977). These petrified peats are part of the Fort Cooper Coal Measures, Blackwater Group, of Late Permian age (Jensen, 1975) or about 245 to 253 million years old (in time scale of Palmer, 1983). In these petrified fossils, sterile leaves are anatomically identical to leaflike structures bearing ovules; pollen is present in pollen sacs and in ovules; the same kind of tracheids are found in leaves and trunks; and identical secondary xylem is found in trunks and around large septate roots (Gould & Delevoryas, 1977).

These petrified fossils have not been named but appear identical to several compression fossils from the same region. The petrified fructifications are the same size and elongate shape and enclose numerous wingless ovules of the same size as compression fossils of *Dictyopteridium sporiferum* Feistmantel (1881) from Late Permian coal measures of India (Surange & Chandra, 1975), Queensland (as "*Cistella bowenensis*" of White, 1964, and "*Plumsteadia microsacca*" of Rigby, 1971, 1978), and New South Wales (Holmes, 1974; White, 1978). The petrified material also agrees closely in size and anatomy with compression fossils of ovules and pollen sacs comparable in age from India (Pant & Nautiyal, 1960). The petrified pollen organs have up to 17 pollen sacs in a cluster (Gould & Delevoryas, 1977), more like the compression genus *Eretmonia* than *Glossotheca* (as defined by Surange & Chandra, 1975). Impressions of *Eretmonia* from New South Wales (White, 1978) and a variety of "scale fronds" from Queensland (White, 1964) have a thickened tip, most like *Eretmonia hinjridaensis* Surange & Maheshwari (1970). Most of the pollen from petrified remains (Gould & Delevoryas, 1977) is identical to the broadly defined dispersed species *Protohaploxypinus limpidus* (Balme & Henelly) Balme & Playford, 1967 (Foster, 1975; Rigby & Hekel, 1977).

Impressions of *Dictyopteridium sporiferum* from Queensland have been found attached to leaves of *Glossopteris communis* Feistmantel, 1876 (White, 1964; Rigby, 1971). *Glossopteris communis* is a common fine-meshed leaf, like *G. indica*, *G. linearis*, and *G. angustifolia*. This last-mentioned species also has been considered the leaf of *Dictyopteridium sporiferum*, although on less secure evidence of association and venation density (White, 1964; Maheshwari, 1965). The petrified ovular heads and associated leaves (Gould & Delevoryas, 1977; G.J.R., pers. obs.) were also fine-meshed (veins about 0.2 mm apart), but they have a clearly defined midrib of a size most like that in *Glossopteris communis*. Associated coarse-meshed *Glossopteris* leaves in the Late Permian coal measures of Australia belonged to quite different plants, as shown by their attachment to nearly circular ovulate fructifications bearing winged seeds (Holmes, 1974; White, 1978). The petrified leaves of the

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FIGURE 8. *A reconstruction of* Dictyopteridium sporiferum *of Late Permian age, from near Homevale Station, Queensland, Australia.—A. Habit as a swamp woodland tree.—B–D. Cellular details of wood structure in tangential and radial sections (respectively).—E. Cutaway reconstruction of secondary wood of basal trunk and main roots.—F. Cross section of wood of small root, showing primary xylem at points between arms of secondary wood.—G. Xylem model of small chambered root.—H. Ovulate fertile leafy shoot.—I. Cross sections of leaf, showing vascular bundles of midrib (circles with curved hachure), their sheathing sclerenchyma (black ellipses), upper palisade cells (vertical lines), and spongy mesophyll (irregular pattern).—J. Cross section of stomate, showing cuticle (heavy outline) and cell walls (dotted and broken lines).—K–M. Transverse and longitudinal sections of ovulate fertile structure and ovules, showing vascular traces (black), woody integumentary layer (stipple), multicellular megagametophyte (irregular pattern), and archegonium (circle with central stipple).—N, O. Lower and upper (respectively) cuticles of leaf, with stomates on under side only.—P. Pollen-bearing organs.—Q. Dehiscent sporangia.—R. Striate bisaccate pollen.*

plant reconstructed here are hypostomatic, with low papillae on the abaxial side, similar to the cuticles of the compression species *Glossopteris waltonii* Pant & Gupta (1968), after which our cuticular restoration was modeled.

Petrified wood of this plant, both within trunks and its distinctive chambered roots, includes late wood like *Araucarioxylon arberi* (Seward, 1919) Maheshwari (1972) and early wood like *A. bengalense* (Holden, 1917) Maheshwari, 1972 (Gould, 1975). We have chosen the latter name for our reconstruction on the grounds of priority.

There have been some nomenclatural problems also with the name for the root of this plant, which Schopf (1982) decided should be *Vertebraria australis* McCoy (1847). Only one species of *Vertebraria* is recognized. This fossil species probably includes remains of what were roots of numerous species of glossopterid plants recognized from their reproductive structures.

Habit. The overall habit of the plant has been reconstructed from specimens of trunks showing alternate and whorled branching (Gould & Delevoryas, 1977). The whorled specimen conforms to Rauh's architectural model of modern trees (Hallé et al., 1978). The other trunks may represent other growth forms but also could be old or damaged trunks. Regularly whorled young trees and extensively repaired and irregular old trees are characteristic of many living conifers, of *Ginkgo biloba*, and some angiosperms (Hallé et al., 1978; Retallack & Dilcher, 1981). The wood of this plant was like that of modern softwoods, with very narrow unicellular rays and abundant pitting in the cross field. It was a kind of wood apparently conservative in gymnosperms and still found in many conifers and in *Ginkgo biloba* (Beck, 1971).

Leaves were arranged in close helices on short shoots, which in turn were arranged on long shoots (Pant & Singh, 1974). The venation of the leaves was a fine mesh, with a zone of much narrower meshes and a sclerenchyma sheath forming a midrib. There is a good deal of evidence that these plants were seasonally deciduous: the noncoriaceous nature of the leaves compared with those of associated and presumably evergreen conifers, well-developed abscission scars at the bases of the petioles, and well-marked growth rings in its fossil wood (Gould & Delevoryas, 1977; G.J.R., pers. obs.). A variety of triangular scalelike leaves have been found in association with these fossils (Walkom, 1922; White, 1964, 1978). Some of these were fertile scales, but others may have been young leaves or protective scales of dormant winter buds.

Fertile structures were attached to leaflike organs arranged in a closely spaced helix (Pant & Singh, 1974). Fertile scales arranged on the same short shoot as sterile leaves would have formed distinct clusters (White, 1978). On some short shoots there were up to three kinds of scales or leaves (White, 1978), but there is no evidence that any of these shoots were bisexual.

Pollen sacs were borne at the end of copiously dichotomizing stalks arising from the midrib of a scale leaf. Although much reduced, this epiphyllous structure is similar to that found in seed ferns such as *Telangium affine* (Kidston, 1923) and *Diplopteridium teilianum* (Walton, 1926, 1931). In many of these Early Carboniferous plants, the sporangia were fused into bell-like synangia, but in *Dictyopteridium sporiferum* the sporangia were free, as in other enigmatic Early Carboniferous plants (Skog & Gensel, 1980) and Late Devonian progymnosperms (Beck, 1981). The walls of each pollen sac were only one cell thick (Gould & Delevoryas, 1977). They opened by way of a long, sinuous slit (Pant & Nautiyal, 1960), which presumably developed because of diagonal stresses arising during drying.

Ovules were borne on the underside of an infolded leaflike structure which was attached by a long stalk to the midrib of the adaxial side of what looks like an ordinary foliage leaf. This epiphyllous structure also can be compared with fructifications of Early Carboniferous seed ferns, such as *Sphenopteris bifida* (Long, 1979b). The structure of these fossils was anticipated in some studies of impression fossils (Schopf, 1976) but did not become clear until well-preserved petrified fossils were studied (Gould & Delevoryas, 1977). In earlier studies of impressions, they were thought to have been bivalved cupules (Plumstead, 1958a) or bracteate cones (Surange & Chandra, 1975). The first view is now thought incorrect, but the second interpretation has gained some support from experimental compaction of model structures (Rex, 1986) and from cuticular studies of compressed specimens (Chandra & Surange, 1976). In our view, however, the three separate cuticles can be explained as (1) a central abaxial hair-bearing cuticle with holes marking positions of ovule attachment; as (2) a peripheral abaxial stomatiferous cuticle with hair bases; and as (3) an adaxial thick nonstomatiferous cuticle. A comparison of experimentally deformed structures with compression fossils indicates that some real biological diversity may be reflected in the large number of generic names for glossopterid fructifications (reviewed by Rigby, 1978), but some of them may be merely different developmental and preservational states of the same kinds of fructifications (Gould & Delevoryas, 1977).

Reproduction. Each pollen sac contained numerous pollen grains. The combined release of pollen from a stand of trees could have produced clouds of yellow dustlike grains. Considering the amount of pollen produced and its moderate size (32–46 μm in breadth and 14–26 μm in corpus diameter: Gould & Delevoryas, 1977), this plant was probably wind pollinated. As in *Callospermarion pusillum,* the saccae may have served to orient and float the grains in a pollination drop. Stout striae on the body of the pollen grain also may have functional significance, because similar striate bisaccate grains were also produced by apparently unrelated seed ferns in Permian coal swamps of Siberia (Meyen, 1984). Mormon tea (*Ephedra* spp.) has pollen with bands that strengthen the grain against stresses arising from desiccation in a dry climate (Hughes, 1976). Striae on the pollen of *Dictyopteridium sporiferum* may have served to withstand stresses associated with moisture losses during wind pollination.

At the time of pollination the ovule-bearing head was infolded to enclose the ovules and an interovular mesh of unicellular hairs. Rigby (1978) has suggested that these filaments were fungal hyphae, from decay of the fossil. This seems unlikely considering their radiation from the micropyles of the ovules without plugging them, the apparent lack of damage tissue in petrified specimens (Gould & Delevoryas, 1977), and the cuticularized hair bases seen in macerated preparations (Pant & Nautiyal, 1960; Chandra & Surange, 1976). The filamentous meshwork may have produced or trapped fluid which bulged from the gaping lips of the underside of the ovule-bearing structure, like pollination droplets. Pollen of *Dictyopteridium sporiferum* entrapped in this material and floated and oriented by their inflated saccae would have been pulled into the micropyles of the ovules inside as the fluid dried back along the guiding filaments.

Ovule-bearing heads have been found withered and open, partly or wholly naked of ovules (Gould & Delevoryas, 1977). The seeds of this plant lacked wings or fleshy layers found in associated fossil plants (Walkom, 1922; Holmes, 1974; Plumstead, 1963). They were numerous, small (0.8–1.5 mm long: Gould & Delevoryas, 1977), and possibly were shaken from the fructifications by swaying in the wind (a "wind ballist" of van der Pijl, 1972), then dispersed widely by wind and water. The hair bases appear to have been quite persistent on dispersed seeds (Pant & Nautiyal, 1960) and may have aided dispersal.

Habitat. Leaves of this plant are abundant in roof shales and clastic partings within coal seams, and its roots riddle the drab underclays to coal seams (Jensen, 1975; Retallack, 1980b). These plants lived in waterlogged muds, silts, and sands (gleyed Entisols of Soil Survey Staff, 1975), as well as in peaty organic substrates (Histosols of Soil Survey Staff, 1975).

Trunks of this plant (Jensen, 1975, fig. 45; Gould, 1975) and of glossopterids in general (David, 1907; Plumstead, 1958b) had shallow root systems. This kind of tabular root system is commonly found in modern plants of waterlogged habitats (Jenik, 1978). Such a habitat also may explain the peculiar construction of the roots of these plants, in which xylem is restricted to narrow radial arms and transverse platforms that enclose empty spaces within the root. There has been some concern whether these spaces were filled with parenchyma, but calluslike groups of parenchyma cells on the walls of mature examples is evidence that they were originally empty (Gould, 1975). They may have served for aeration of the root in oxygen-poor ground, as in living crack willow (*Salix fragilis*: Kawase & Whitmoyer, 1980).

The texture of the leaves, with an adaxial thick cuticle and an abaxial stomatiferous and papillate cuticle (Gould & Delevoryas, 1977) is similar to sun leaves of modern angiospermous trees (Salisbury, 1927). This, together with the abundance of these leaves, is an indication that these probably were dominant canopy trees.

Modern riverside weed trees such as sycamore (*Platanus occidentalis*) and sheoak (*Casuarina cunninghamiana*) produce seeds in comparable numbers and sizes to those of *Dictyopteridium sporiferum.* Associated fossil seeds of other glossopterid plants (Walkom, 1922) are generally larger and more elaborate, thus supporting the view that *D. sporiferum* was weedy in comparison. Judging from their sedimentary context, the earliest successional plants were horsetails (*Phyllotheca* spp.) and lycopods (*Selaginella harrisii*). Other species of glossopterids were probably the dominant plants of stable swamp woodlands. Associated osmundalean tree ferns (Gould, 1970) may have formed understory shrubs and small trees. In contrast to those of *Glossopteris,* the leaves of these tree ferns were delicate, like those of shade plants. Higher land to the west, and perhaps also the volcanic highlands to the east, were forested by conifers (*Walkomiella australis*: Retallack, 1980b).

Paleogeographic setting. Dictyopteridium sporiferum is exquisitely preserved in Late Permian silicified peat near Homevale Station and is found as compression fossils in shales elsewhere in the northeastern Bowen Basin (Jensen, 1975). This

FIGURE 9. *A reconstruction of* Peltaspermum thomasii *of Late Triassic (Carnian) age, from the upper Umkomaas Valley, Natal, South Africa.—A. Habit as a shrub of seasonally wet bottomlands.—B. Abscission scar and leaf traces of petiole base.—C. Leafy shoot.—D, E. Upper and lower (respectively) leaf cuticles, with*

basin is continuous to the south with the Sydney Basin of New South Wales. Coal measures in the Sydney–Bowen Basin accumulated in a broad intermontane depression between the plains and hill ranges of inland Australia to the west and a volcanic, Andean-style mountain range to the east (Jensen, 1975).

The eastern Australian part of the Gondwana supercontinent was at very high paleolatitudes during the Late Permian (Herbert, 1980). There is no clear evidence of glaciation in the Bowen Basin at this time, but there were probably alpine glaciers on high mountains to the east. There are several lines of evidence for a seasonal, cool temperate climate throughout these lowlands. Growth rings are seen not only on fossil wood (Rigby, 1971) but also in the shells of marine shellfish, which were much less diverse in this region of the world during Late Permian time than in other formerly tropical regions (Runnegar & McClung, 1975). Varved lacustrine shales have been found with rafts of leaves at the very top of the silty layer, overlain by the thin shaley layer of the varve. This may be explained as coarse material washed out by brisk spring runoff and summer storms, followed by autumn leaf fall and slow winter accumulation of clay (Retallack, 1980b). Winters were not harsh by this time, because osmundalean tree ferns were widespread. They are represented by silicified trunks and foliage in the Bowen Basin (Gould, 1970).

PELTASPERMUM THOMASII

Hypothesized reconstruction. This plant is thought to have been a low-growing perennial shrub, vegetating stream, pond, and lake margins within temperate mesophytic woodlands and forests of South Africa and other southern continents during Late Triassic (Carnian) time, about 225 to 230 million years ago (Fig. 9). Its leaves (*Lepidopteris stormbergensis* (Seward) Townrow, 1956) were coriaceous, stiff, and fernlike. They varied from pinnatifid to bipinnatifid and in the proportion of stomates on either side of the leaf. This and the blisterlike hydathodes covering the frond rachis and the stem are features found in some modern waterside plants. Leaves had clear abscission scars, so it probably was a long-lived, perennial plant and may have been seasonally deciduous. The pollen-bearing (*Antevsia extans* (Frenguelli) Townrow, 1960) and ovulate organs (*Peltaspermum thomasii* Harris, 1937) were pinnately arranged, and each frondlike structure formed a large paniclelike fructification. Pollen (*Monosulcites minimus* Cookson, 1947) was moderately sized (23–40 μm) and produced in great quantity: both features of modern wind-pollinated plants. The reconstructed plants may have had a pseudostigmatic kind of pollination, in which pollen adhered to the ovule or head and only pollen tubes entered the micropyle, as in modern conifers with relatively inaccessible ovules and nonsaccate pollen. Seeds of the fossil plant probably were dispersed mainly by water.

Evidence for reconstruction. This reconstruction is based largely on fossil compressions from the black shales of "Burnera Waterfall," where a tributary creek of the Umkomaas River drops over a scarp of the basal Molteno Formation, 4 km southeast of Vergelegen Nature Reserve, Natal, South Africa (our Fig. 2C; locality Umk 111 of Anderson & Anderson, 1983). These shales form the base of the Molteno Formation and are Late Triassic in age (*Yabeiella* oppel-zone of Retallack, 1977; or Carnian in the marine time scale), which is about 225 to 230 million years old (in time scale of Palmer, 1983). The various fossil organs attributed to this species have also been found in association at other localities in South Africa, South America, and New South Wales (Retallack, 1977; Anderson & Anderson, 1983). The remains discussed were attributed to one plant by Townrow (1960) for several reasons: the close similarity of the cuticles of leaves, microsporophylls, and megasporophylls; pollen found dispersed and in microsporophylls; and close association at several localities.

Habit. This plant is mainly known from coriaceous, bipinnatifid to pinnatifid leaves. Unipinnate leaves also have been included in the genus (Townrow, 1960). These have identical cuticle and may be closely allied plants but are now placed in the genus *Pachydermophyllum* (Retallack, 1981). Also variable is the distribution of stomates on both sides of the leaf in *Lepidopteris stormbergensis.* They are usually more numerous on the abaxial side but occasionally are more common on the adaxial side, which can be distinguished because

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stomates overhung by papillae.—F. Cross section of stomate.—G. Blisterlike structure on cuticle of petiole.—H, I. Ovulate fructification.—J. Reconstructed longitudinal section of ovule, showing vascularization (heavy lines) and resinous glands (black ellipses).—K, L. Pollen-bearing organ.—M. Monocolpate pollen.

of its thicker cuticle and less-bulging venation. Such a stomatal distribution is found in leaves of understory shrubs (Salisbury, 1927) and of waterside herbs (Townrow, 1960). The peculiar blisterlike swellings under hair bases on the stem and rachis of this plant are similar to hydathodes in waterside herbs such as water dock (*Rumex hydrolapathum*: Townrow, 1960). A waterside understory habitat seems likely, but we reconstruct this plant as a small, much-branched, perennial woody shrub for the following reasons. The leaves have thick cuticles and were probably stiff and coriaceous. Leaf bases with clear abscission scars and two leaf traces have been found (Townrow, 1960). These were abscised, perhaps seasonally. Slender stems of this plant have also been found which have stomates and blisters like those of the leaves (Townrow, 1960). Such stems are unlikely to have been the main stem of a plant with a single palmlike stem. It is more likely that these were short shoots of a branched plant.

Pollen sacs and ovules were arranged radially on more or less laminar organs, which were arranged pinnately. These pinnate structures formed large, lax, paniclelike structures (Anderson & Anderson, 1983, pl. 23, and possibly also their "female cone gen. C. sp. A." of pl. 26).

Reproduction. Wind pollination of this plant may be indicated by its copious production of smooth, moderately sized (23–40 μm) pollen. However, its large (5 mm long by 2 mm wide) pollen sacs, with glandular bumps and borne in groups of four, are distinct from the more numerous, nonglandular, smaller pollen sacs of other Mesozoic seed ferns usually regarded as wind pollinated, such as *Umkomasia granulata* (also reconstructed here).

Ovulate fructifications have been found in several different stages of maturation. The least-developed examples have only bumps rather than obvious ovules underneath the ovular head (Retallack et al., 1977). These may be remains at or close to the time of pollination, when the ovules and their elongate micropyles were not as obvious as in other remains with ovules attached (Townrow, 1960).

Pollination by means of a pollination drop is unlikely, considering the nature of the pollen grains. Unlike the bisaccate pollen of related peltasperm seed ferns such as *Pteroma* (Harris, 1964) and *Townrovia* (Retallack, 1981), *Peltaspermum thomasii* had nonsaccate pollen grains. This is also true of some modern conifers such as western hemlock (*Tsuga heterophylla*) and Prince Albert's yew (*Saxegothaea conspicua*), compared with closely allied conifers with bisaccate pollen (Doyle, 1945). These modern conifers with nonsaccate pollen have pseudostigmatic pollination, in which pollen grains adhere to parts of the plant near ovules, and long pollen tubes enter the ovules. The time between pollination and fertilization in these conifers is no less brief, compared with other conifers such as pines (Doyle & O'Leary, 1935b), because the tip of the pollen tube overwinters in the nucellus of the ovule (Doyle & O'Leary, 1935a, c).

The largest ovules seen are attached singly or in pairs to fructifications with abscission scars indicating a former complement of about six ovules (Townrow, 1960). The most complete remains lack ovules, and the most common remains are of isolated ovular heads only rarely with attached ovules (Anderson & Anderson, 1983). Even at these stages, associated ovules lack differentiation of woody and fleshy integuments to the degree seen in associated seeds, such as those of *Umkomasia granulata.* Neither the ovular heads, which may have been dispersal units, nor the ovules were adapted to specialized modes of dispersal, and they probably were scattered by wind and water.

Habitat. The black shale in the Umkomaas Valley (Umk 111 of Anderson & Anderson, 1983) is the deposit of a poorly oxygenated lake. The lacustrine shale overlies a thin conglomerate, which disconformably overlies floodplain deposits of the Katberg Formation, of Early Triassic age (*Lystrosaurus* zone). Such conglomerates at the base of a shale are found often in abandoned channels (oxbow lakes) of meandering streams (McDonnell, 1974).

At the Umkomaas Valley locality the shales are overlain by a variety of paleosols in which the plants may have lived (Fig. 2C). The so-called "oil shale" overlying the black shales is a coal (du Toit, 1954) and was probably a peaty soil (Histosol of Soil Survey Staff, 1975) fringing the Oxbow Lake. Overlying this are some very weakly developed fossil soils (Entisols of Soil Survey Staff, 1975), consisting of little-modified alluvium riddled with fossil root traces. These are interpreted as early successional soils of river levees. Above these are red, clayey, noncalcareous paleosols with slightly sandier surface horizons (probably Alfisols or Ultisols). Their root traces, profile differentiation, and degree of oxidation are typical for well-drained forested soils.

Of these various possible habitats, we think that *Peltaspermum thomasii* preferred the peaty lakeside soils. Unlike other associated fossil plants, this species lived very close to the lake, because it is equally abundant through the entire thickness of the lacustrine shales (Townrow, 1960). There also are reasons for regarding it as a waterside plant (as already discussed). *Peltaspermum thomasii* has been found in place in the organic layer and immediately overlying carbonaceous shales of waterlogged, peaty paleosols at other localities, such as Konings Kroon, South Africa (Kon 111 of Anderson & Anderson, 1983; G.J.R., pers. obs.) and in Nymboida Open Cut Mine, New South Wales, Australia (Retallack, 1977). In all of these localities *Peltaspermum thomasii* is associated with *Umkomasia granulata.*

Although a waterside and lowland plant, there are indications that it could tolerate deficiencies of water or nutrients. The stomates, for example, are overarched by papillae on the subsidiary cells. The blisters on the stems and leaves are comparable to water control structures (Townrow, 1960), such as salt glands or hydathodes (discussed by Esau, 1977). Judging from its geological occurrence, it is more likely that these peculiar features of the plant reflect growth in nutrient-deficient habitats rather than lack of water. It may have been suited to siliceous, nutrient-poor, streamside sands of point bars, or acidic swampy lowlands.

The other local habitats revealed by paleosols at the Umkomaas Valley locality seem less likely for this plant, because there is evidence from other localities that they were vegetated by other plants. Entisols of streamsides may have been colonized by broad-leaved conifers (*Heidiphyllum*) in drier, sandy, and elevated areas, and by ferns (*Cladophlebis* sterile, or *Asterotheca* when fertile) and horsetails (*Neocalamites*) in wetter places. Alfisols and Ultisols of well-drained floodplain forests and woodlands in contrast were dominated by other seed ferns (*Dicroidium elongatum* and *D. coriaceum*) and a variety of plants with ginkgolike leaves (Retallack, 1977). Within this mosaic of vegetation, *Peltaspermum thomasii* is envisaged as an understory plant of woodlands dominated by *Umkomasia granulata* in periodically waterlogged lowlands.

Paleogeographic setting. During Late Triassic time the Molteno Formation formed an extensive lowland piedmont north of the mountainous Cape Fold Belt (Turner, 1978). The lower part of the formation in the Umkomaas Valley lies disconformably on older alluvial rocks, which may have formed low hills flanking low ranges of much older (Precambrian), resistant rocks to the north, west, and east. This far north of the mountains, streams laid down sequences of sediment of a type formed in loosely sinuous modern streams transporting a mixed load of clay and sand (Turner, 1978; compare general models of Schumm, 1981).

Climate in this region was humid and cool temperate, perhaps seasonally snowy. This can be inferred from the high paleolatitude of this part of Gondwana (Anderson & Schwyzer, 1977). Late Triassic fossil wood from South Africa (Walton, 1923) has well-marked growth rings, an indication of strong seasonality. A humid climate is indicated by the quartz-rich composition of Molteno sandstones (Dingle et al., 1983) from which most of the easily weathered minerals have been lost. High rainfall probably also accounts for noncalcareous fossil soils and the dearth of vertebrate fossils in the Molteno Formation (G.J.R., pers. obs., following general models of Retallack, 1984).

UMKOMASIA GRANULATA

Hypothesized reconstruction. This was probably a woodland tree which dominated seasonally waterlogged floodplains of extensive lowlands north of mountains in the Cape region of South Africa, and of other humid regions of Gondwana during Late Triassic time, some 225–230 million years ago (Fig. 10). The leaves of this plant (*Dicroidium odontopteroides* (Morris) Gothan, 1912) had callused abscission scars, so probably were deciduous. Its wood (*Rhexoxylon tetrapteridoides* Walton, 1923) was coniferlike, but with exceptionally wide rays. Ovulate (*Umkomasia granulata* Thomas, 1933) and pollen-bearing structures (*Pteruchus johnstonii* (Feistmantel) Townrow, 1962b) of this plant were pinnately organized, and the pinnate structures were arranged helically in large paniculate fructifications. The copious production of moderately sized (corpus averaging 46 by 32 μm), bisaccate pollen (*Alisporites australis* de Jersey, 1962) is compatible with pollination by wind and possibly with a pollination drop. At ovulation, the ovules were weakly developed, and their bifid, elongate micropyles extended out below the margin of the cupulate head that enclosed their inverted bases. During subsequent development the ovule elongated well below the cupule margin and gained a sclerotesta with three broad ribs as the formerly elongate micropyle withered away. Seeds were released as their stalk abscised and the bivalved cupule spread open. The moderately-sized (3.7–7 mm × 2.2–5 mm) seeds were produced in great numbers and protected by a sclerotesta from desiccation or damage during possible ingestion. They probably were dispersed in a variety of ways, mainly by wind and water.

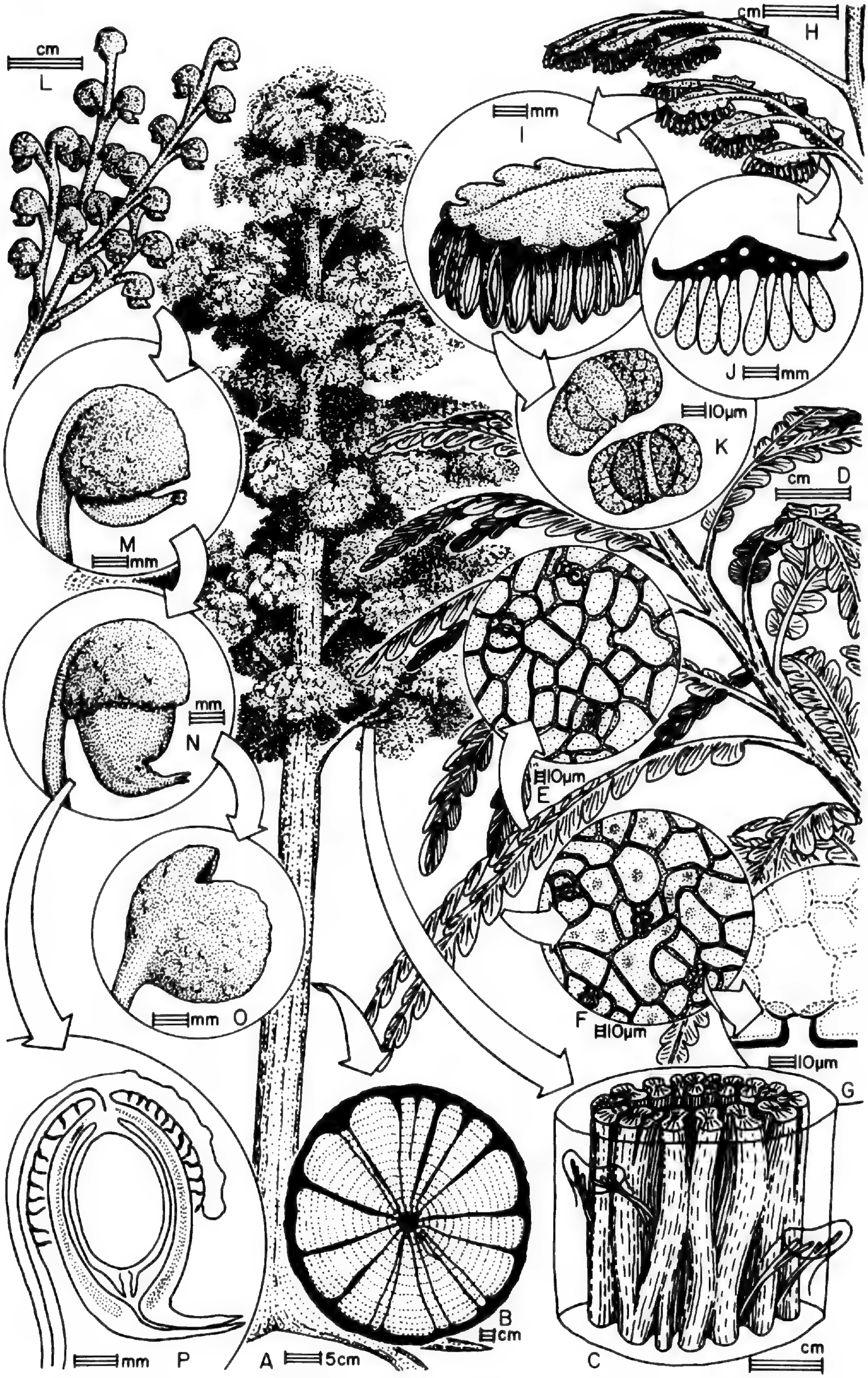

FIGURE 10. *A reconstruction of* Umkomasia granulata *of Late Triassic (Carnian) age from the upper Umkomaas Valley, Natal, South Africa.—A. Habit as a tree of seasonally wet bottomlands.—B. Diagrammatic cross section*

Evidence for reconstruction. This plant has been put together on the basis of compressed remains of leaves, ovulate and pollen-bearing organs with similar cuticle, and similar pollen grains in pollen sacs and ovules (Thomas, 1933; Townrow, 1962a–c). These remains were first demonstrated to be closely associated in the same locality (in the Umkomaas Valley, South Africa) that also serves as a basis for our reconstruction of *Peltaspermum thomasii*. The association of these fructifications and leaves is now known at most localities where it is found in South Africa, South America, Australia, and New Zealand (Retallack, 1977, 1980c).

Evidence that this plant was a tree of deciduous woodlands and forests includes associated fossil trunks, root traces, and the callused abscission scar at the base of its leaves. Other lines of evidence have been used in support of the idea that its wood, at least in South Africa, was *Rhexoxylon tetrapteridoides* Walton (1923). There is a close association of *Dicroidium* with petrified wood of *Rhexoxylon pianitskyi* at two localities in Argentina (Archangelsky, 1968). Of the two species of *Rhexoxylon* found in South Africa, *R. tetrapteridoides* is the only one found in the Molteno Formation near, but not at, the same localities (such as the Umkomaas Valley; Walton, 1923; Anderson & Anderson, 1983) from which our reconstructions of *Umkomasia granulata* and *Peltaspermum thomasii* came. A petrified leafy shoot of *Rhexoxylon pianitskyi* from Argentina (Archangelsky & Brett, 1961) formed the basis for our reconstruction of *R. tetrapteridoides* here, which we have assumed also to have six vascular traces leading into the petioles of the leaves. Because of this, *Rhexoxylon* could not be the wood of associated conifer (such as *Rissikia* or *Heidiphyllum*) or ginkgolike foliage (such as *Sphenobaiera*), which had only one or two vascular strands in their petioles. Nor does *Rhexoxylon* show the girdling leaf traces or intimately admixed parenchyma and xylem seen in the wood of cycads and cycadeoids, which presumably produced associated foliage of *Pseudoctenis* and *Taeniopteris*. Among associated seed ferns in South Africa, *Peltaspermum thomasii* (as reconstructed here) had only two leaf traces in the petiole (Townrow, 1960) and is here reconstructed as an understory shrub. *Glossopteris verticillata* is a rare element with multistranded petioles of this Triassic fossil flora, but it has been found attached to stems in a much closer helix than apparent for petrified *Rhexoxylon pianitskyi* or natural groups of impressions of *Dicroidium odontopteroides* leaves (du Toit, 1927; Thomas, 1952; Anderson & Anderson, 1983).

Thomas's (1933) numerous species of pollen organs have been revised and reduced in number by Townrow (1962a, b). This task has not yet been completed for ovulate organs, although most of these remains have been transferred to the genus *Umkomasia* (Holmes, 1987). From our examination of Thomas's specimens and preparations (in the British Museum of Natural History), we think that there are probably only three species. The type species of Thomas's three genera can be taken as representative of these species, which can be recognized by deeply incised cupular lobes (*Umkomasia macleanii*), weakly lobed cupule margins (*Umkomasia sewardii*), and smooth, bivalved cupule margins (*Umkomasia granulata*). These three taxa also show cuticular differences comparable to those found in the three associated species of *Pteruchus* by Townrow (1962a). Thus, the species name *Umkomasia granulata* is used broadly here to include several other named species ("*Pilophorosperma*" *costulatum*, "*P.*" *geminatum*, "*P.*" *paucipartitum*, "*P.*" *burnerense*, "*P.*" *natalense*, "*P.*" sp. type A, "*P.*" sp. type B, and "*P.*" sp. type C), which we regard as different stages of development and different parts of a large fructification. In the case of one of these species ("*P.*" *geminatum*), Thomas (1933, 1934, fig. 12F) thought that it had paired cupules, back to back. From comparison of the branching pattern of this specimen with the others, as well as our examination of its cuticular preparations, we interpret this as a dehisced, bivalved cupule. The branching pattern and small bractlike organs were regarded by Thomas (1933) as evidence that these fructifications were stalked, like the flowers of angiosperms. We prefer Townrow's (1962a) interpretation, developed for the pollen organ, that each

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of wood showing wide parenchymatous rays (black) and secondary wood (concentric dotted lines).—C. Xylem model of a small shoot and petioles.—D. Leafy shoot.—E, F. Upper and lower (respectively) cuticles of leaf, both with stomates.—G. Cross section of stomate.—H, I. Pollen organ.—J. Cross section of head of pollen organ, showing vascular traces (white circles) and pollen sacs (stipple).—K. Bisaccate pollen.—L. Ovulate organ.—M. Cupulate ovule at time of pollination.—N. Cupulate ovule at time of fertilization.—O. Dehisced cupule.—P. Longitudinal section of cupulate ovule, showing hairy inner side of cupules (irregular extensions) and sclerotesta (stipple).

cupule is a homolog of a pinna, each "bracteole" a sterile pinna, and the whole pinnate structure homologous with a frond. This structure is in some ways similar to the ovule-bearing cupule arising from the dichotomy of a frond in early Carboniferous seed ferns such as *Sphenopteris bifida* (Long, 1979b).

Habit. Judging from the trunks of *Rhexoxylon tetrapteridoides* found (up to about 16 cm in diameter), this plant was a woodland tree (Archangelsky & Brett, 1961; Petriella, 1985). A trunk showing branch scars (Walton, 1923) provides evidence that the large branches were arranged in tiers that were not quite whorled. Like *Dictyopteridium sporiferum* reconstructed here, *Umkomasia granulata* probably had tiered branching which became more irregular with old age. This, and a long shoot and short shoot organization apparent from small petrified leafy stems and leaf groups, is very similar to our envisaged habit of *Dictyopteridium sporiferum.*

The leaves of this plant were variable in morphology, as documented in detail by Anderson & Anderson (1983). They may have belonged to a complex of hybridizing species. The Andersons have identified aberrant fossil leaves with narrow segments (*Dicroidium coriaceum* and *D. elongatum*) in some parts of the frond, and wide ones (*D. odontopteroides*) elsewhere on the same frond. These may represent hybrid leaves. Disregarding these as sports and considering variation in natural populations of these leaves (Anderson & Anderson, 1983, figs. 3, 4), *Umkomasia granulata* probably included leaves referred to *Dicroidium odontopteroides*, as well as those which have been referred to "*D. lancifolium*" and "*D. obtusifolium.*"

Stomates were distributed on both sides of the leaf but were much more abundant on the abaxial side, which had a thinner cuticle covered in papillae (Anderson & Anderson, 1983; Petriella, 1985). Fossil leaves have been found in radial groups and with asymmetric basal petioles (Anderson & Anderson, 1983).

The ovulate and pollen-bearing structures were pinnately organized and helically arranged on a larger stem (shown well in "*Umkomasia* sp. A" and "*Pteruchus* sp. B" illustrated by Anderson & Anderson, 1983, 1985). Only the ovule-bearing structure has been found in an apical position on slender shoots (Thomas, 1933; Holmes, 1987).

Reproduction. Individual laminar heads of the pollen organ bore hundreds of pendent, elongate pollen sacs (Townrow, 1962a). Pollen grains were bisaccate, nonstriate, and of moderate size (corpus averaging 46 by 32 μm in size: Townrow, 1962a). It is likely that the saccae were areas of porous exine (as indicated by Taylor et al., 1984, for a closely allied fossil species, really from the Ipswich Coal Measures near Dinmore, Queensland, according to these authors' erratum) rather than completely detached from the corpus. These are all indications that *Umkomasia granulata* probably was wind pollinated.

Only in specimens with small ovules does the elongate micropyle protruding from under the cupule appear to have been turgid and open. This was probably the stage of pollination, because in specimens with larger, more elongate ovules, the micropyle is withered and torn. The pollen chamber was narrow and tubular. It has been compared (by Thomas, 1933) to the salpinx of Paleozoic seed ferns such as *Lagenostoma lomaxii* reconstructed here. However, there is no sign of a central column, and it was not exposed like the salpinx. In these respects it was more like the pollen chamber of *Callospermarion pusillum.* Both were passive receptacles, not sealed from within by a plug of tissue, but sealed by the overarching sclerotesta of the integument. As the ovule enlarged and elongated, three broad ribs developed in the sclerotesta. This period of growth may have been when the megagametophyte and archegonia developed during the time between pollination and fertilization, as already described for *Callospermarion pusillum.*

Mature ovules and seeds were shed from the cupules by abscission from their stalk and by the cupule splitting into two lobes. Cupules at this open stage, revealing fully the degree of lobation of their margins, are the easiest of these remains to identify (Retallack, 1977). The branching fructifications found as fossils were presumably aborted or torn from the trees during storms. Much more common are isolated seeds, which were presumably the propagules. The seeds were neither exceptionally large nor small (3.5 to 7 mm long by 2.2 to 5 mm wide: Thomas, 1933), nor especially woody or fleshy, winged or spiny, even compared with the variety of associated fossilized propagules (Anderson & Anderson, 1983). They were probably dispersed by generalized methods, mainly by wind and water.

Habitat. This plant is best known from the Late Triassic locality in the Umkomaas Valley of South Africa (Fig. 2C), already described for *Peltaspermum thomasii.* Remains of these species drifted into a lake and were mixed with a variety of other plants. Fossil leaf litters preserved in paleosols at Konings Kroon, South Africa (locality Kon 111 of Anderson & Anderson, 1983) and at

Nymboida Open Cut, New South Wales, Australia (Retallack, 1977) are better evidence of its habitat and associated plants. As already discussed for *Peltaspermum thomasii*, the soils were periodically (probably seasonally) waterlogged in lowland floodplains. High soil acidity and deeply weathered parent material of this humid region depleted nutrients in these fossil soils. Stumps and root traces penetrate deeply into these carbonaceous paleosols (Hatch & Corstorphine, 1909). This is unlike roots of modern plants in permanently waterlogged soils (Jenik, 1978). Although waterlogged for some part of the year, thus retarding decay of carbonaceous material in the soil (Retallack, 1984), these soils were moderately well drained at other times.

Also relevant to the former habitat of this plant are the distinctive wide parenchymatous rays of the wood here included in our reconstruction. This wood structure has been compared to that of modern vines, in which wide parenchymatous rays bestow flexibility (Walton, 1923). These plants are unlikely to have been vines, considering their size, but some flexibility may have been advantageous during seasonal fluctuations in water availability (Carlquist, 1975).

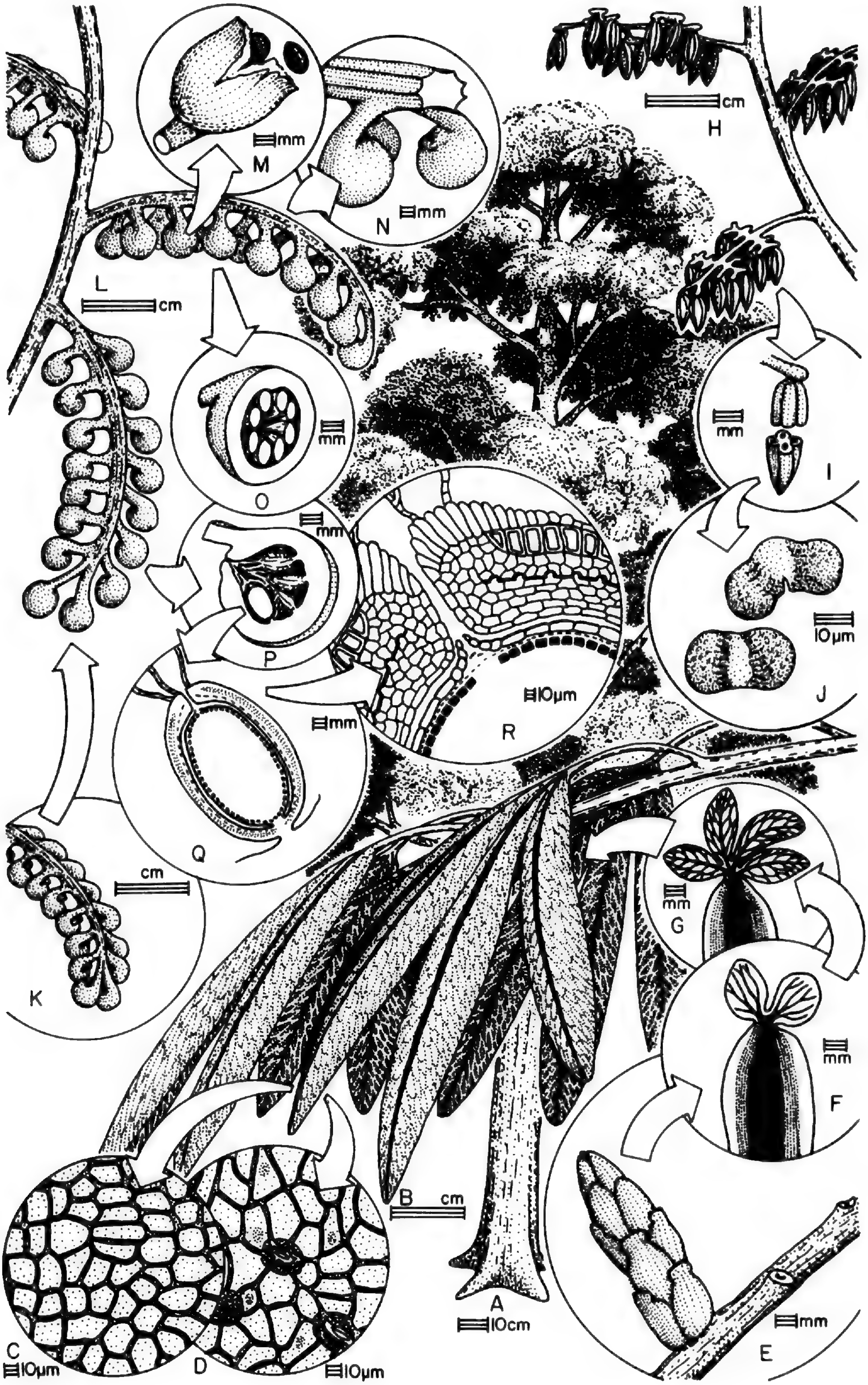
Judging from its abundance and likely stature, *Umkomasia granulata* was probably a dominant canopy tree of lowland mesophytic woodlands in humid, cool temperate regions of Gondwana (Retallack, 1977). Other trees included rare conifers (*Rissikia media*) and plants with ginkgolike leaves (*Sphenobaiera stormbergensis*). Among the understory plants were other seed ferns (*Peltaspermum thomasii*), cycadophytes (*Pseudoctenis* and *Taeniopteris*), ferns (*Cladophlebis*), and horsetails (*Neocalamites*). These last-mentioned pteridophytes also may have colonized disturbed parts of the forest, because they are found in other nearby localities (such as Konings Kroon localities Kon 211 and 221 of Anderson & Anderson, 1983) where they form distinctive early successional assemblages in very weakly developed paleosols (Entisols of Soil Survey Staff, 1975: G.J.R., pers. obs.).

Paleogeographic setting. *Umkomasia granulata* is best known from the same locality and region as *Peltaspermum thomasii*.

CAYTONIA NATHORSTII

Hypothesized reconstruction. We reconstruct this plant as a forest tree of an extensive Middle Jurassic (Bajocian or 175 to 183 million years old) coastal plain, in what is now northeastern England (Fig. 11). Climate in England at this time was subtropical, monsoonal, and seasonally dry, with an annual rainfall within the humid range. The compound leaves (*Sagenopteris phillipsii* (Brongniart) Presl in Sternberg, 1838) of this plant had four leaflets paripinnately arranged but so close together that they appear palmately compound. Leaves developed by elaboration of the apical region of an initial scale into the four leaflets and by modification of the body of the scale into a petiole. The adaxial cuticle of the leaflets was thick and lacked stomates. The abaxial side had a thin cuticle, stomates, and papillae. Both ovulate (*Caytonia nathorstii* (Thomas) Harris, 1940) and pollen-bearing structures (*Caytonanthus arberi* (Thomas) Harris, 1941) were organized imparipinnately and arranged in a helix on slender axes. The pollen (*Vitreisporites pallidus* (Reissinger) Nilsson, 1958) were moderately sized (22–28 μm wide), bisaccate, and produced in large quantities. These are typical features of wind-pollinated plants. Pollen grains in coprolites provide evidence that these were also eaten by small animals that may have been effective as pollinators. The ovules (*Amphorispermum pullum* Harris, 1943) were borne on the inside of fleshy, berrylike cupules. At the time of pollination, ovules were small and poorly developed, and the ovulate structure consisted of cuplike inrolled flaps. Pollen were probably entrapped by a pollination drop at the opening of the ovulate structures and drawn back into the micropyles of the ovules along a series of guiding filaments as the droplet dried out. In mature cupules the ovules were completely enclosed by the overarching pressure of the turgid fleshy "fruit" and by sealing the entrance with bands of cutin and perhaps also of other substances. The fleshy, berrylike cupules have been found burst and split. They may have spilled ovules as they fell on the ground. More effective in their dispersal may have been reptiles and small mammals attracted by these fleshy fructifications. The seeds were fortified against crushing and acidity during ingestion by their sclerotesta.

Evidence for reconstruction. *Caytonia nathorstii* is best known from a thin (1 m) shale bed (Fig. 2D) in the rock platform south of Cayton Bay, Yorkshire, England (Harris, 1964). This is the Gristhorpe Bed of the Cloughton Formation, Ravenscar Group (Kent, 1980), and is Middle Jurassic (Bajocian) in age, or some 175 to 183 million years old (in the time scale of Palmer, 1983). This plant has been reconstructed from compression remains of leaves, buds, pollen organs, and ovule-bearing organs with similar cuticles; from the similarity of pollen in pollen sacs and ovules; and from close association at several localities (Harris, 1964).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At the best-known locality, Cayton Bay, the fructifications of most of the other associated fossil plants are known to be different (Harris, 1961, 1964, 1969, 1979; Harris et al., 1974).

Habit. There is evidence from association with poorly preserved fossil stumps (Thomas, 1925; Black, 1929; Harris, 1971) in a forested paleosol (Spodosol or Inceptisol, Fig. 2D) that this plant was part of a mixed fern–cycadophyte–conifer forest. Its exact habit within this vegetation is less certain. Harris (1971) has argued that *Caytonia nathorstii* was a tree, as shown by finds such as leaves attached to stout woody shoots and of budlike short shoots of young leaves. As he argued, few shrubby plants have such stout leafy limbs, and those that do are often more succulent or more completely invested with leaf bases. Buds are typical of a perennial deciduous plant.

The four leaflets of the compound leaves appear palmately compound but are paripinnately arranged with very close points of contact (Harris, 1951). The diffuse, anastomosing venation of leaflets of *Caytonia nathorstii* is superficially like that in leaves of *Dictyopteridium sporiferum*, also reconstructed here. *Sagenopteris* differs from *Glossopteris* in having compound leaves, a true midrib to the leaflets, and secondary venation in which radiating and dichotomizing veins are undeviated by confluent strut veins. These differences from *Glossopteris* have been indicated also by Delevoryas & Person (1975) for *Mexiglossa* leaves, which we regard as closely related to, if not congeneric with, *Sagenopteris*.

Fossil buds (Harris, 1964) indicate that short shoots of leaves developed synchronously, presumably after a period of leaf fall, then dormancy during a harsh season. Leaves developed from the scalelike organs by the differentiation of two orbicular apical leaflets, followed by a second pair on either side behind them (Harris, 1940). Most of the scales became differentiated into the petiole of the compound leaf. The developing leaves were pilose, as are many young organs (Esau, 1977), but mature leaves were glabrous.

The ovules and pollen sacs were arranged paripinnately on leaflike structures on either side of an axis, which had a different adaxial and abaxial cuticular structure, more like a petiole than a stem. The ovulate structure was unipinnate (Harris, 1964), and the pollen-bearing structure was bipinnately arranged (Harris, 1951). These fructifications probably formed paniculate structures, like those of other Mesozoic seed ferns reconstructed here.

Pollen sacs of this plant are thought to have been attached to the abaxial side of the leaflike microsporophyll (Thomas, 1925; Harris, 1964), but the orientation of the ovules is more controversial. For the following reasons we believe that they were also morphologically abaxial, as were the openings to the cupules. The most important evidence is a single specimen of *Caytonia nathorstii* attached to another axis (Thomas, 1925, pl. 12, fig. 16). This specimen was thought lost (Harris, 1971) but was discovered during 1980 by us in the paleobotany teaching collection of Cambridge University. We confirm that the megasporophyll at right angles to the axis is attached, as are two berrylike cupules displayed with their occluded opening crushed on top of their stalks. From our interpretation of the creasing at the attachment points, clearly visible in Thomas's excellent photograph, the attachment does not appear twisted into an unusual orientation. The occluded opening of the fruit appears to be abaxial, and the ovules enclosed by the fruit wall are also morphologically abaxial. This is because, as Harris (1964) and Reymanowna (1974) argued, the cupule is homologous with an infolded leaf. By our interpretation, papillae and hair bases consistently characterize the abaxial surface of leaves, microsporophylls, and megasporophylls (Thomas, 1925; Harris, 1940, 1964). In addition, the outer cuticles of the cupules lack stomates and have a structure in thinner areas (probably lenticels) very similar to

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FIGURE 11. *A reconstruction of* Caytonia nathorstii *of Middle Jurassic (Bajocian) age from Cayton Bay, Yorkshire, England.—A. Habit as a tree of bottomland forest.—B. Leafy shoot.—C, D. Upper and lower (respectively) cuticles of leaf, with stomates on lower side.—E–G. Successive stages in the growth of young leaves.—H. Pollen organ.—I. Cutaway view of quadrilocular synangium.—J. Bisaccate pollen.—K. Ovulate organ at time of pollination.—L. Mature ovulate organ.—M. "Fruits" at time of dispersal.—N–P. Cutaway views of mature fruits and ovules.—Q, R. Longitudinal sections of ovule, showing sclerotesta (stipple and double wall cells), "spotted layer" (heavy dimpled line), "aleurone layer" (black rectangles), and hair bases around micropyle.*

the adaxial cuticles of the leaves (Harris, 1940). Interpretation of the ovules as abaxial brings these plants into line with closely allied plants and with seed ferns as a whole.

We have taken pains to justify our reconstruction on this point, because it runs contrary to the opinion of the leading authority on *Caytonia nathorstii* (Harris, 1940, 1964). Since the thickest cuticle on the rachis of this fructification is on the narrow side, Harris argued that the ovules of *Caytonia* were morphologically adaxial. He interpreted this as similar to the thicker adaxial cuticle of leaves and pollen organ of this plant. We, on the other hand, have pointed out other ways of viewing cuticular homologs between different organs of this plant and regard the thick narrow cuticle of the abaxial side of the rachis as a structural thickening that prevented drooping of the heavy cupules.

Reproduction. It is difficult to determine whether fertile shoots of this plant were bisexual or unisexual. Thomas (1925) argued that individual plants were unisexual, because the best-preserved fructifications of either sex were found in different parts of the same bed. We confirmed this during our own collecting. This is compatible with the view that this plant, like modern plants that have unisexual fructifications, was wind pollinated. The fossil plant produced copious amounts of weakly sculptured, moderately sized (22–28 μm wide: van Konijnenburg-van Cittert, 1971), bisaccate pollen. Shriveling of the saccae on release, as observed in modern pine pollen by Wodehouse (1935: 254), would have greatly reduced the size of the pollen grains. The central body of the grains is only 12–18 μm long by 6–12 μm wide (van Konijnenburg-van Cittert, 1971). They could not have shrunk this much because the sacci contained an internal mesh of sporopollenin, in some ways like that found in pollen from the corystosperm microsporophyll *Pteruchus* (Pedersen & Friis, 1986). Some possible evidence for animal pollination of this fossil comes from small (4 mm diameter) coprolites full of these pollen grains. These were produced by small animals that lacked the ability to digest sporopollenin (Harris, 1964), perhaps a small arboreal mammal or lizard. Australian honey possums (*Tarsipes spencerae*), and a variety of other small animals are known to be effective pollinators, even though they are unable to fly, as is usual among the most important modern pollinators (Rourke & Wiens, 1977). Apart from dinosaur footprints (Kent, 1980), no fossil vertebrates or insects have been found in association with these plants, but from what is known of Middle Jurassic life on land elsewhere in Britain (Clemens et al., 1979; Savage, 1984), there were varied small mammals and arboreal gliding and flying reptiles. Birds had not yet appeared, and despite the diversity of insects at this time, the fossil coprolites are too large for them.

As is common in modern conifers with bisaccate pollen (Doyle, 1945), pollination may have been aided by pollination droplets. In this case it probably emerged from the mouth of the cupules at an early stage of development, when they were little more than infolded flaps (Harris, 1943, 1964). As in *Dictyopteridium sporiferum* reconstructed here, there may have been a reticulum of filaments, which guided pollen toward the micropyles of ovules inside. Filaments were observed in preparations of ovules by Thomas (1925) and Krassilov (1977) but were not noticed by Harris (1933). Pollination must have occurred when ovules were young and the cupule was open, because later in development the opening was sealed by inflation of the fleshy fruit wall and the development of cutinous bands, and perhaps also waxy or other substances (Harris, 1933, 1943). This subsequent development may have disrupted internal filaments so that they were difficult to see in mature fruits. This closure also prevented penetration of clay in the fallen mature fruits. Early ideas (Thomas, 1925) about stigmatic, angiospermlike pollination of these plants were long ago disproved by the discovery of pollen grains within the ovules inside the cupules (Harris, 1933, 1940).

At maturity the berrylike cupules were swollen and completely enclosed the ovules. Each ovule had a well-developed sclerotesta. An enigmatic layer within the ovular coat, the "spotted layer," is quite unlike a true cuticle, but nevertheless somewhat maceration-resistant (Harris, 1958a). It could be the basal layer of a zone of osteosclereids or lagenosclereids, as found in the seed coat of modern soybean (*Glycine max*: Esau, 1977). Inside the nucellus of the ovule was a layer of poorly preserved brown cell contents. Harris (1958a) called it an "aleurone layer," which is a distinctive outer enzyme-producing layer of the endosperm well known in modern angiospermous cereals, such as barley (*Hordeum vulgare*: Esau, 1977).

Dispersal of seeds may have been by bursting on impact or by rotting of the cupule. Many comparably fleshy modern fruits with stony seeds are animal dispersed. The same kinds of small reptiles and mammals already discussed as possible pollinators of this plant may also have aided in its dispersal.

Habitat. The fossiliferous shale (Gristhorpe Bed) at Cayton Bay (Fig. 2D) is a sequence of flood deposits overlying a thick (1.3 m), moderately developed sandy paleosol with a white surface (E) and orange-red subsurface (Bs) horizon (Thomas, 1925; G.J.R., pers. obs.). It was probably a base-poor, forested soil (Gley Podzol of Stace et al., 1968, or Spodosol or spodosolic Inceptisol of Soil Survey Staff, 1975) of periodically waterlogged lowlands. Stumps and large roots have been found within this paleosol (Black, 1929). These are surrounded by a layer of carbonaceous shale, which when macerated yields many fruits and seeds of *Caytonia nathorstii* and other plant debris. We interpret this as an imperfectly decayed (mor) humus layer of leaf litter in a periodically (perhaps seasonally) wet soil. Plants preserved in the overlying shales represent other leaf litter entrapped as clay and floodwaters were slowed around the trees, as in cumulic horizons of modern floodplain soils (modern examples are discussed by Birkeland, 1984). The shale layer becomes more silty and sandy higher towards the next overlying paleosol. This reflects an increase in the power and frequency of flood disturbance, which would have introduced early successional species of plants not usually found in undisturbed lowland forest.

A great variety of plants have been found in the Gristhorpe Bed (Harris, 1961, 1964, 1969, 1979; Harris et al., 1974). The commonest tree species from near the base of the bed are the seed fern *Caytonia nathorstii* and the taxodiaceous conifer *Elatides williamsonii*. Other common remains likely to have been understory plants include the osmundalean fern *Todites williamsonii*, the cycad *Nilssonia compta*, and the cycadeoid *Nissoniopteris vittata*.

Caytonia nathorstii was not common in other habitats in the coastal plains of Yorkshire. Fluvial levees were colonized largely by ginkgoes (*Ginkgo huttonii*: van Konijnenburg-van Cittert, 1971; Nami, 1976) and other nearstream, early successional environments by horsetails (*Equisetum columnare*: Harris, 1961). Near-coastal peat swamps were vegetated by cycads (*Nilssonia kendallae*), cycadeoids (*Ptilophyllum pectinoides*), and czekanowskialeans (*Sphenobaiera gyron*); and the most marine-influenced vegetation of tidal creeks was dominated by another seed fern (*Pachydermophyllum papillosum*: Thomas & Bose, 1955; Spicer & Hill, 1979). Compared with these other plants, *Caytonia nathorstii*, although a lowland plant, lived in more inland and stable sites.

Paleogeographic setting. During Middle Jurassic time Yorkshire was a flat deltaic coastal plain between moderately elevated plateaus of older rocks to the north, south, and east. To the west was a shallow sea, which connected to the south past several low islands and a broad shelf of tropical reefs to the open Tethys Ocean (Sellwood, 1978).

Yorkshire at this time was at a paleolatitude of about 35° north (Briden et al., 1974). Climatic zonation was less marked than at present, and this region enjoyed a subtropical climate (Hallam, 1975). Overall rainfall was probably in the humid range, considering the lush vegetation of pteridophytes (Harris, 1961), noncalcareous and podzolic nature of paleosols (Fig. 2D), and corrosion of the umbos of fossil unionid bivalves (Wilson, 1948). Growth zones in fossil shoots (Harris, 1971, 1979) are evidence of seasonality. The harsh season was probably dry and a time of forest fires (Harris, 1958b). As in modern continents at about this latitude and orientation, climate was probably monsoonal and winter dry (Hallam, 1975).

DISCUSSION

The reconstructions given here range from vines to stately forest trees, from plants of intertidal swamps to those of well-drained soils in locations ranging from the tropics to the high latitudes. These extinct broadleaf plants appear to have occupied many niches. In the face of such diversity it is difficult to characterize seed ferns. Certainly, they were not merely small swampland shrubs. They were a prominent component of much late Paleozoic and Mesozoic vegetation.

The seed ferns reconstructed here, representing well-understood examples of these plants, have a few features in common. They are all characterized by fernlike leaves, ovule-bearing structures which are leaflike or adnate to leaves, and gymnospermous anatomy, more or less as originally envisaged by Potonié (1899) and Oliver & Scott (1904) in proposing the terms "cycadofilicales" and "pteridosperms." However, we think it unlikely that they form a natural group or clade, because the same features distinguish other groups of plants, such as cycads. The earliest gymnosperms were probably seed ferns (Rothwell, 1982, 1986). Cycads, cycadeoids, pentoxylans, ginkgoes, czekanowskians, cordaites, conifers, and other gymnosperms all probably were derived from seed ferns (Meyen, 1984). Seed ferns were thus central to the evolutionary radiation of seed plants, and in this sense represent a grade of evolution embracing the evolutionary roots of these various other gymnosperms.

The phylogenetic relationships of gymnosperms can be expected to become clearer as lineages of seed ferns are better understood. Phylogenetic inference is beyond the scope of this article, but we point out two quite different groups of seed ferns to underscore the artificiality of seed ferns as a taxon. The plants with fernlike prepollen (*Stamnostoma huttonense, Lyrasperma scotica, Calathospermum fimbriatum, Lagenostoma lomaxii,* and *Pachytesta illinoensis*) were different in many ways from those with true pollen (*Callospermarion pusillum, Dictyopteridium sporiferum, Peltaspermum thomasii, Umkomasia granulata,* and *Caytonia nathorstii*). The group with fernlike prepollen was similar in many ways to modern cycads, whereas the others were more like conifers. The second group includes both Paleozoic and Mesozoic plants, some of which show a number of important biological similarities (Reymanowna, 1974). The supposed morphological gap between Mesozoic and Paleozoic seed ferns, apparent in many general discussions of these plants, may be seen as a study bias. It arose from the varied experience of different investigators of these plants and from quite distinctive styles of preservation and geological settings for Paleozoic and Mesozoic plants, rather than from the plants themselves.

A variety of seed ferns have been considered as possible ancestors of angiosperms: especially forms allied to the plants here reconstructed as *Stamnostoma huttonense* (Long, 1966, 1977b), *Dictyopteridium sporiferum* (Retallack & Dilcher, 1981), and *Caytonia nathorstii* (Doyle, 1978). Another gymnospermous group thought to be ancestral to angiosperms, the cycadeoids (Arber & Parkin, 1907) were probably also derived from seed ferns. The origin of angiosperms is still a puzzle, for which more detailed understanding of seed ferns is needed.

In our role as arbitrators of conflicting views on the nature of the plants reconstructed here, we have become aware of the ease with which mistakes can be made. We do not imagine that our reconstructions will be the last word (or image) for these plants, and hope that they will serve as hypotheses that stimulate as well as instruct.

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FLORA OF THE VENEZUELAN GUAYANA—V[1]

Julian A. Steyermark[2]

ABSTRACT

In the preparation of various families for the Flora of the Venezuelan Guayana, *many new taxa have been detected. These include specimens collected from recently completed expeditions and earlier herbarium material. The following new taxa are described:* Portulaca insignis, P. pygmaea *(Portulacaceae);* Maytenus huberi, M. insculpta, M. longistipitata, M. neblinae, M. pustulata, Zinowiewia aymardii *(Celastraceae);* Matayba affinis, M. longipes *subsp.* yutajensis, M. oligandra *var.* occidentalis, M. yutajensis, Talisia amaruayana, T. caudata, T. glandulifera, T. heterodoxa, T. pentantha, T. sancarlosiana, Toulicia anomala *(Sapindaceae);* Gouania wurdackii, Rhamnus longipes, R. sipapoensis *(Rhamnaceae);* Pochota ewelii, P. fuscolepidota, P. gracilis *subsp.* bolivarensis, P. liesneri, P. mawarinumae, P. redmondii, P. tepuiensis *(Bombacaceae);* Schefflera simplex, S. yutajensis *(Araliaceae);* Symbolanthus huachamacariensis, S. yaviensis *(Gentianaceae);* Remijia sessilis, Simira ignicola *(Rubiaceae). In addition, comments are supplied, where pertinent, on the affinities of various taxa in the several families treated.*

PORTULACACEAE

PORTULACA

Portulaca insignis Steyermark, sp. nov. TYPE: Venezuela. Bolívar: laja granítica con bosque y matorral seco, cerca del afluente del Río Aro, carretera Ciudad Bolívar–Maripa, 100 km W of Ciudad Bolívar, 100–200 m, 26 Feb. 1980, *G. Morillo & G. Carnevali 8260* (holotype, VEN). Figure 1.

Planta herbacea annua diminutiva 4.5–10 cm alta, radice palari elongata; caulibus aliquot procumbentibus vel erecto-adscendentibus vel curvatis e basi exorientibus a pilis lanosis albis 8–15 mm longis omnino densissime obtectis absconditisque; foliis per longitudinem vel apicem versus dense confertis, alternis carnosis applanatis, laminis lanceolato-linearibus apice obtusis basi in petiolum angustatis 4.5–6 mm longis 0.5–1 mm latis; petiolis 0.8 mm longis 0.6 mm latis; foliis involucralibus 10–12 foliorum caulinorum similaribus; sepalis 4 mm longis; petalis 4–5 mm longis; staminibus 13–15; lobis stigmatosis quattuor; capsulis 2.5 mm longis 1.5 mm diam. prope medium circumscissilibus; seminibus numerosis lenticularibus 0.5–0.6 mm diam., a latere compressis conspicue tuberculatis, tuberculis apice subacutis anguste elevatis basi 4–5 radiatis angustis ornatis.

Herbaceous diminutive annual, 4.5–10 cm tall with an elongated slender tap root. Stems several, procumbent to erect-ascending or curving, simple or sparingly branched, densely foliose up to the apex, densely covered and nearly concealed by a dense, white, woolly mass of elongate hairs 8–15 mm long; internodes conspicuously abbreviated. Leaves alternate, densely imbricate to the apex of the stem, fleshy, flattened, lance-linear, obtuse at apex, 4.5–6 mm long, 0.5–1 mm wide, base attenuate. Petioles 0.8 mm long, 0.6 mm wide. Involucral leaves 10–12, similar to the cauline, 4–7 mm long, 1 mm wide. Sepals 4 mm long, subacute. Petals 4–5 mm long, slightly connate at base. Stamens 13–15; filaments ca. 2 mm long, attached 0.5–0.8 mm above base of petals. Stigmatic lobes 4; style filiform, 0.8 mm long. Capsules 2.5 mm long, 1.5 mm diam., circumscissile near the middle. Seeds numerous, lenticular, 0.5–0.6 mm diam., laterally compressed, conspicuously tuberculate, the tubercules with a subacute apical projection, at the base with 4–5 spreading narrow rays.

Paratype. VENEZUELA. BOLÍVAR: Dist. Paez, Laguna Larga, 8 km SE of Upata, sabanas con chaparrales, 350 m, July 1978, *Delascio & Liesner 6882* (MO, VEN).

In this species the entire plant is more or less concealed by a dense cover of white, woolly or cottony hairs up to 15 mm long. It differs from *Portulaca elatior* Mart. in its much smaller size, shorter stems, shorter cauline and involucral bracts, fewer stamens, 4-fid style, and much denser woolly covering over the entire plant.

Portulaca pygmaea Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: 1 km E of Hotel Amazonas, Puerto Ayacucho, gravel pockets

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ANN. MISSOURI BOT. GARD. 75: 1058–1086. 1988.

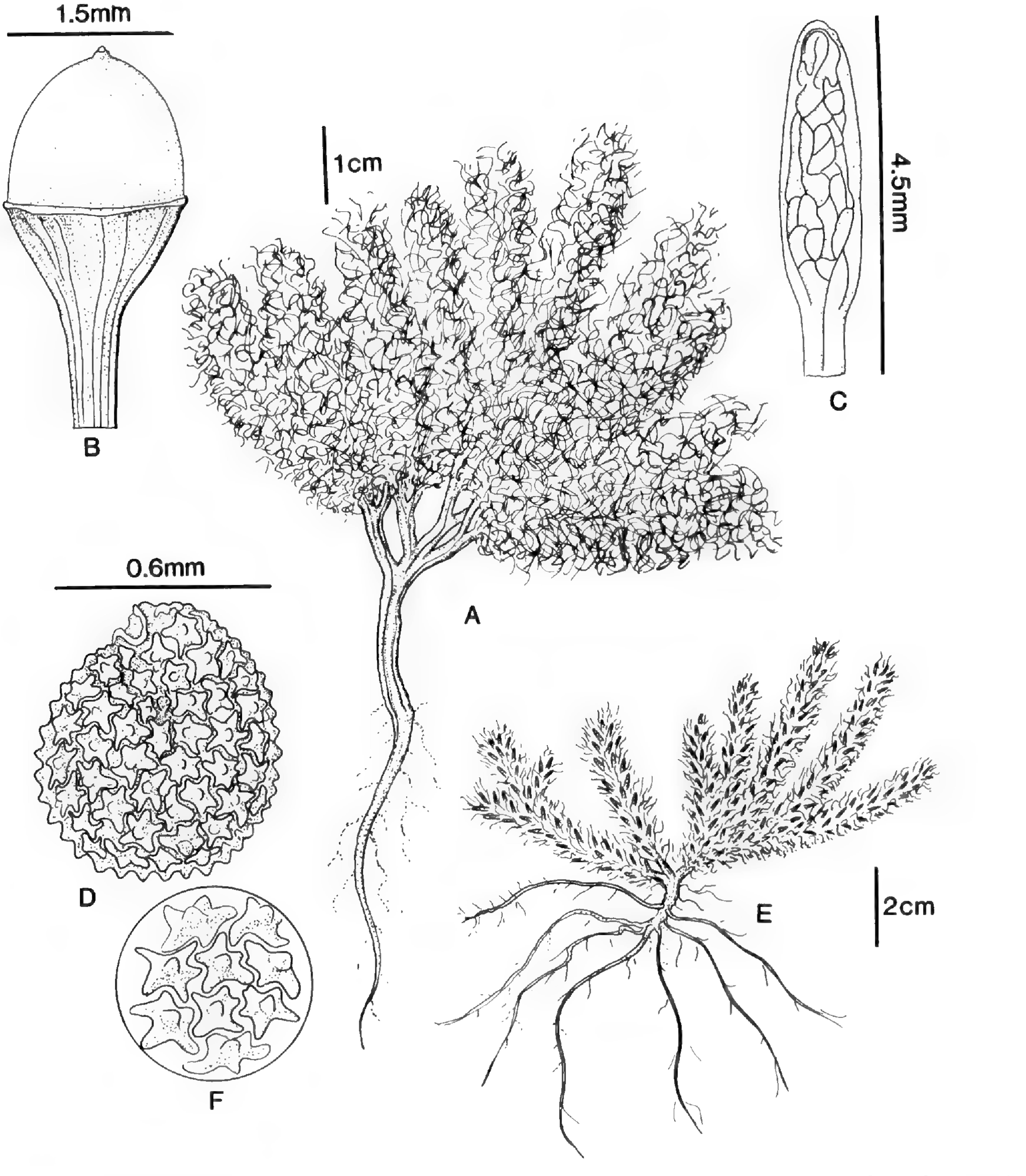

FIGURE 1. Portulaca insignis.—*A. Habit of fully mature plant with woolly aspect.—B. Capsule, exterior view.—C. Single leaf, detached, the venation as seen in transparent light.—D. Seed with small projecting tubercules.—E. Habit of younger plant.—F. Detail of surface of seed showing tubercule raised at apex above stellulate rays.*

on laja, along contact between laja and Orinoco gallery forest, 100 m, 12 Nov. 1953, *Bassett Maguire, John J. Wurdack & George S. Bunting 36188* (holotype, NY). Figure 2.

Planta herbacea diminuta 2–3 cm alta glabra vel fere; foliis sub capsulis oppositis aliter alternis, laminis suborbicularibus suborbiculari-obovatis ovalisque apice rotundatis basi acutis vel subacutis 1.5–4(–6) mm longis 1.5–3 mm latis glabris vel interdum pilis in axillis plerumque desunt vel interdum axillaribus inconspicuis 0.2–0.6 mm longis; petiolis 0.7–1 mm longis; sepalis suborbicularibus obtusis, 3 × 3 mm; petalis luteis 4.5–5 mm longis; capsulis depresso-hemisphaericis prope basem circumscissilibus 1.5–2.3 mm longis 1.7–2.3 mm latis; seminibus griseis 0.5 mm diam., superficie tuberculato, tuberculis tessellatis haud projectantibus marginibus arcte contiguis.

Diminutive herbaceous plant 2–3 cm tall, glabrous or nearly so; roots napiform, the short tuberous root 1–1.5 cm long, 4–8 mm thick. Leaves subtending the capsules opposite, otherwise alternate; leaf blades suborbicular, oval, or obovate, rounded at the apex, acute at base, 1.5–6 mm long, 1.5–3 mm wide, glabrous or sometimes with minute hairs present in the axils; petioles 0.7–1

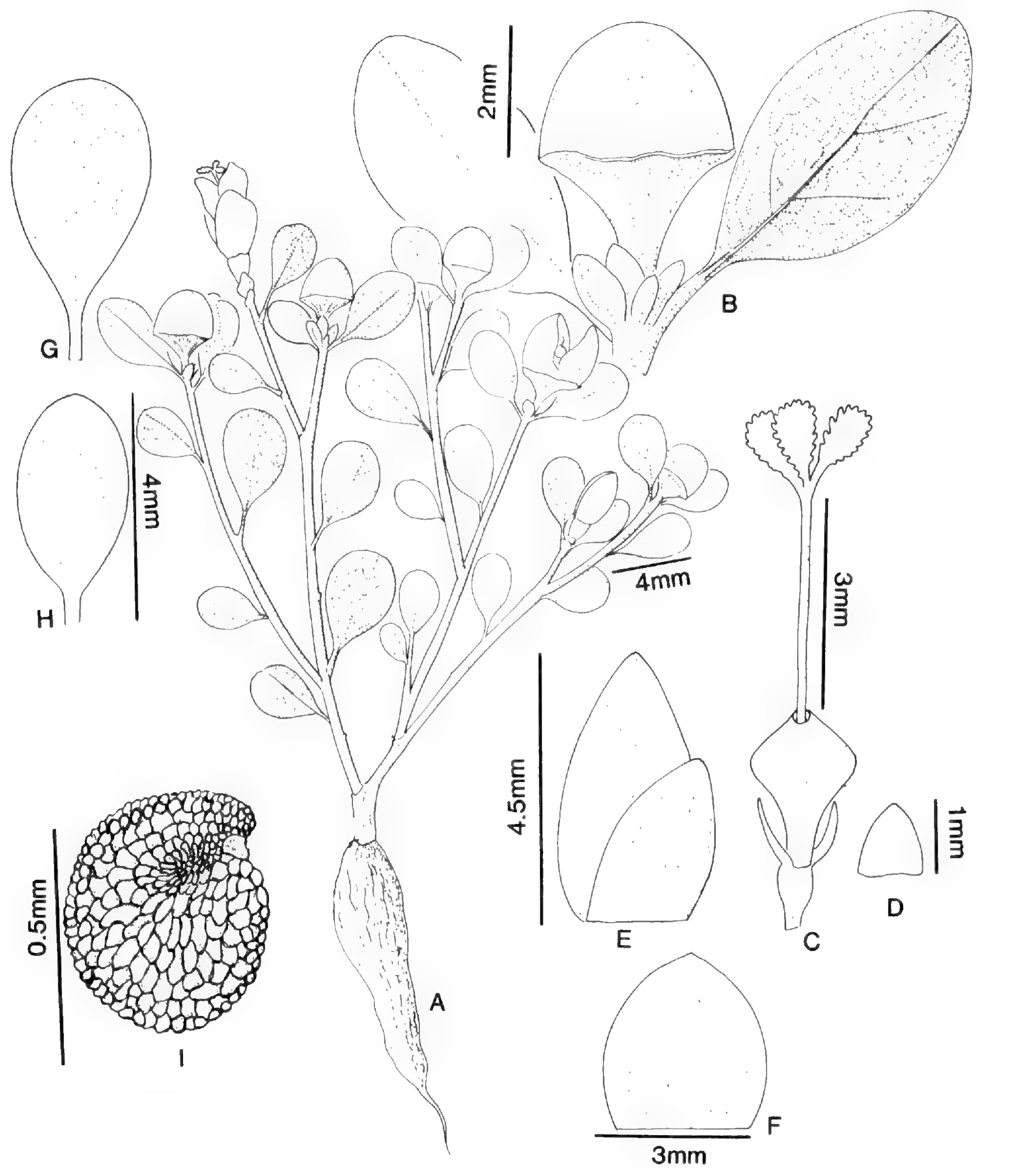

FIGURE 2. Portulaca pygmaea.—*A. Habit, showing tuberoid root.—B. Capsule subtended by uppermost opposite leaves.—C. Pistils subtended by bracts.—D. Ovate-triangular bracteole.—E. Petal subtended by sepal, lateral view.—F. Sepal, dorsal view.—G, H. Leaves, showing different shapes.—I. Seed, showing platelike, subflattened tubercules.*

mm long. Flowers bibracteate, slightly substipitate, the bracts 1 mm long. Sepals suborbicular, broadly obtuse, 3 × 3 mm. Petals yellow, ligulate-oblong, rounded at the apex, 4.5–5 mm long, 2 mm wide in the upper half, 0.7–1 mm wide at the base. Stamens 5; filaments 2.7 mm long; anthers suborbicular, 0.5 × 0.5 mm. Style 3 mm long; stigmas 3, spathulate, 1.2 mm long. Capsules hemispherical, subdepressed at the apex, 1.5–2.3 mm long, 1.7–2.3 mm wide, circumscissile near the base. Seeds gray, 0.5 mm diam., tessellate-tuberculate, the tubercules scarcely projecting, their margins strongly contiguous.

This is a rarely collected species, occurring on the lajas in the vicinity of Puerto Ayacucho with *Portulaca pusilla* H.B.K. and *P. sedifolia* N. E. Brown. It differs from the very similar dwarf *P. pusilla* in the yellow petals; napiform, short, thickened tuberous root; 5 stamens; longer and broader

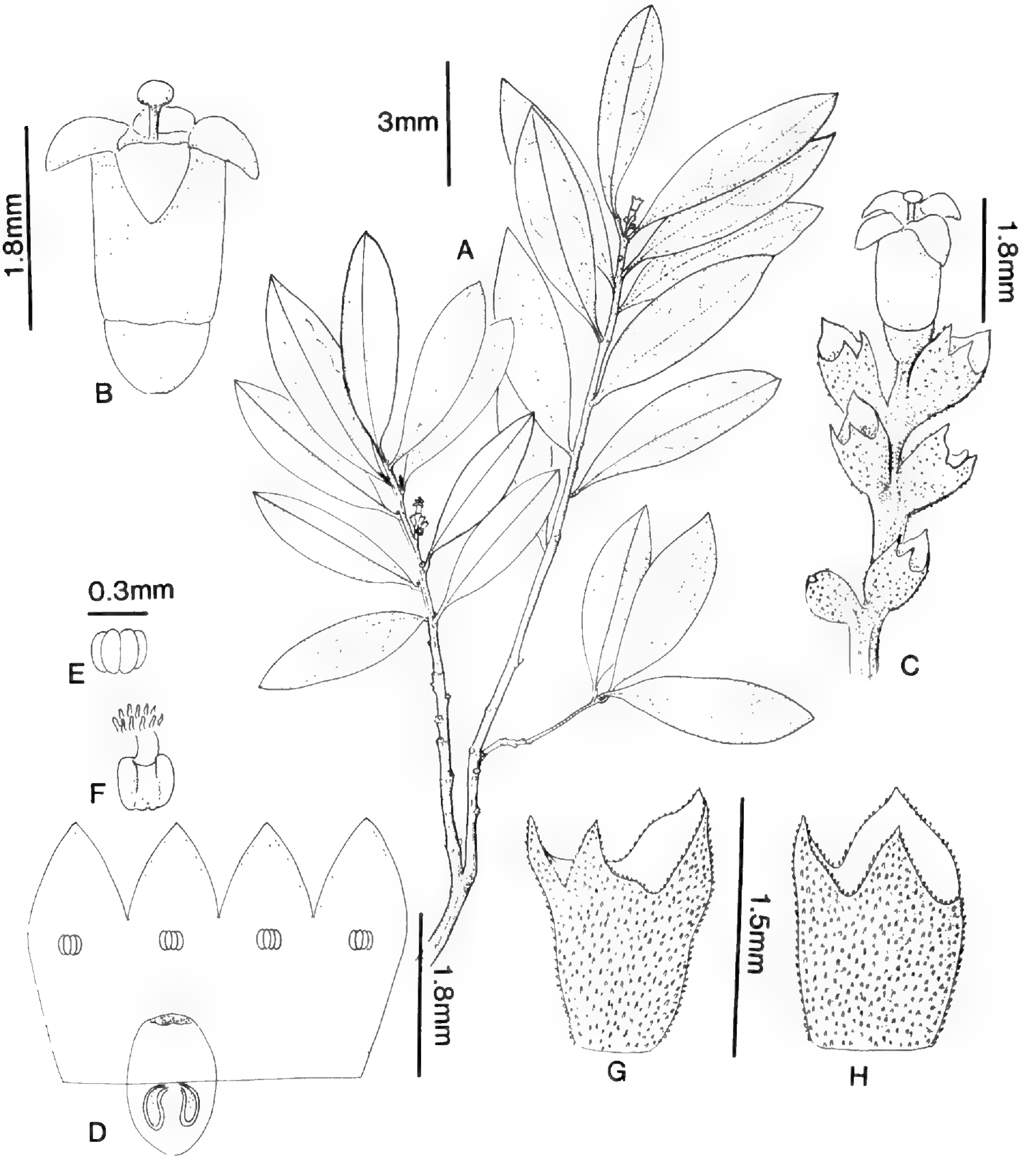

FIGURE 3. Schoepfia clarkii.—*A. Habit of flowering branch.—B. Flower.—C. Inflorescence.—D. Interior of corolla with disk and longitudinal section through ovary in position.—E. Anther, ventral view.—F. Stamen turned back to show minute puberulence on corolla tube.—G, H.—United bracteoles and bract (epicalyx), two views.*

leaf blades; depressed-hemispherical capsule opening very close to the base; and seeds with gray, flattened, contiguous tubercules that do not protrude above the general surface contour. It differs from *P. sedifolia* and *P. teretifolia* H.B.K. in its general glabrity and leaf shape.

OLACACEAE

SCHOEPFIA

Schoepfia clarkii Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Mari's bana (low Amazon caatinga), 10.8 km NE of San Carlos on Solano road, 1°56′N, 67°3′W, 119 m, 16 Aug. 1987, *H. L. Clark 8111* (holotype, MO). Figure 3.

Frutex 2 m; foliorum laminis anguste lanceolato-ellipticis apice acutis vel subacutis base cuneatim acutis, 4.5–5 cm longis 1.2–1.5 cm latis glabris integerrimis; nervis lateralibus obsoletis utroque latere 3–4; petiolis 4–5 mm longis; inflorescentia axillari spiciformi simplici usque ad 7-flora 6–7 mm longa; pedunculis ut videtur solitariis; floribus sessilibus; bracteolis bracteisque (epicalyce) supra medium connatis 1.5–1.8 mm longis apicem versus 1.5 mm latis extus dense papillato-puberulentibus; corolla late cylindrico, tubo 1.8–2 mm longo 1.6 mm lato glabro, lobis 1.2 × 1.2 mm; ovario infero 0.8 mm longo.

Shrub 2 m tall. Leaf blades narrowly lance-elliptic, acute or subacute at apex, cuneately acute at base, 4.5–5.5 cm long, 1.2–1.5 cm wide, glabrous, entire; lateral nerves obsolete, 3–4 each side; petioles 4–5 mm long. Inflorescence axillary, spiciform, simple, up to 7-flowered, 6–7 mm long; peduncle solitary, 2 mm long. Flowers sessile. Bracts and bracteoles (epicalyx) connate more than halfway, forming a 3-lobed involucre 1.5–1.8 mm long, 1.5 mm wide, narrowing to 0.9 mm wide at base, densely papillate-puberulent without; 1 larger lobe broadly triangular-ovate, abruptly acute at apex, 0.8 mm long, 0.9 mm wide at base; 2 smaller lobes narrower, broadly triangular, slenderly acuminate-attenuate, 0.5 mm long, 0.4 mm wide; tube of epicalyx shallowly campanulate, 1 mm long, 1 mm broad at summit, 0.6 mm broad at base. Corolla greenish yellow, thick-cylindric, the tube 1.8–2 mm long, 1.6 mm wide, glabrous without, glabrous within except for a minute tuft of papillate hairs behind the anthers; lobes 4, spreading-squarrose, broadly triangular-ovate, obtusely acute or subacute at apex, 1.2 × 1.2 mm. Stamens 4, subsessile, suborbicular, 0.2 mm long, 0.3 mm wide; filaments 0.2 mm long. Disk depressed-subglobose, fleshy, annular, 0.7 mm long, 1 mm wide. Ovary inferior, 0.8 mm long, 1.3 mm broad at the truncate summit, narrowed at base to 0.3 mm wide. Style 1.8 mm long; stigma capitate, 0.4 mm long, 0.7 mm wide.

This taxon is characterized by small corollas with a short tube 1.8–2 mm long, bracts and bracteoles of the epicalyx upwardly connate more than halfway, narrowly lance-elliptic leaf blades up to 1.5 cm wide, and spiciform solitary inflorescence with sessile flowers on a short rachis.

CELASTRACEAE

MAYTENUS

In preparing an account of the genus *Maytenus* for the *Flora of the Venezuelan Guayana*, the near uniformity of the floral structures and general inflorescence types has necessitated greater reliance on vegetative characters, especially those of leaf venation. In the majority of the taxa studied, the calyx lobes are uniformly suborbicular and rounded with erose-fimbrillate or ciliolate margins. Rarely, as in *M. apiculata* Steyerm. and *M. kanukensis* A. C. Smith, they are acute or apiculate. Likewise, the fruit does not vary sufficiently to separate taxa. In a few cases, such as in *M. apiculata*, the apex is noticeably prolonged to form a more prominent beak, while in *M. longistipitata* Steyerm. the base is greatly extended into a longer stipitate portion. In both *M. longistipitata* and *M. oblongata* Reiss., the fruit is larger than in the other species studied. In *M. neblinae* Steyerm. the leaves are smaller, while the leaf margins are more prominently dentate with more numerous teeth than in the other taxa examined. An insculpted type of venation characterizes the leaves of *M. insculpta* Steyerm., whereas a pustulate lower leaf surface is characteristic of *M. laevis* Reiss., *M. huberi* Steyerm., and *M. pustulata* Steyerm. In *M. sieberiana* Krug & Urban, the upper leaf surface has a finely lineolate-striolate character.

A partial treatment of the genus was published by Reissek (1861) for the Brazilian species. An account of the West Indian taxa by Urban (1904), together with descriptions of additional South American species by Briquet (1919) and A. C. Smith (1939a, b) contain the remainder of the known species from South America and the West Indies. The numerous collections from the Venezuelan Guayana have yielded the new taxa described here.

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Maytenus huberi Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Dept. Atures, cuenca del Río Manapiare, sabanas situadas en los cerros ubicados entre el Cerro Morrocoy al sur y Serranía Colmena al Norte, 5°21′N, 66°10′W, 200–300 m, 29 Jan. 1977, *Otto Huber 441* (holotype, VEN).

Frutex 2–6 metralis; foliorum laminis crasso-coriaceis saepe pruinosis vel subglaucis oblongis elliptico-lanceolatisque vel ovato-oblongis apice late obtusis vel obtuse acutis basi rotundatis subcordatis subobtusiusculis vel rariter acutis (4.5–)6–15.5 cm longis (2.5–)3–9 cm latis integerrimis, nervis lateralibus obsoletis vel inconspicuis utroque latere 8–10, venulis tertiariis obsoletis, in superficiebus amabus folii pustulatis; inflorescentia 1–8-flora fasciculata, pedicellis sub anthesi 1–5 mm longis sub fructu 3.5–5 mm longis; calycis lobis suborbicularibus rotundatis ciliolatis; capsulis majoribus obovoideis apice rotundatis 10–11 mm longis 7–8 mm latis.

Shrub 2–6 m tall. Leaf blades thick-coriaceous, often pruinose or subglaucous on one or both surfaces, oblong, elliptic-lanceolate, or ovate-oblong, broadly obtuse or obtusely acute at the apex, rounded, subcordate, subobtuse, or rarely acute at the base, (4.5–)6–15.5 cm long (2.5–)3–9 cm wide, entire; lateral nerves obsolete or inconspicuous, 8–10 each side; tertiary venation obsolete; both surfaces pustulate. Petioles 4–11 mm long, 1.5–2 mm wide. Inflorescence 1–8-flowered, fasciculate; pedicels 1.5 mm long in anthesis, 3.5–5 mm long in fruit. Calyx lobes suborbicular, rounded, ciliolate. Petals broadly ligulate-oblong, rounded apically, 1.1–1.5 mm long, 0.8–1 mm wide. Capsules obovoid, rounded at summit, mature ones 10–11 mm long, 7–8 mm wide.

Paratypes. VENEZUELA. ATURES: cuenca del Río Manapiare, sabanas al pie de los cerros al N de Cerro Morrocoy, alrededores del sitio Pozo de la Carolina, 12 km W de San Juan de Manapiare, 5°19′N, 66°6′W, 225 m, *Huber 1223* (MO, VEN); 4.5 km N de Puerto Venado, E de Sanariapo, 5°15′N, 67°47′W, 85 m, *Huber & Tillett 16764* (MO, VEN); vegetación de laja sobre afloramiento granítico en raudal Pereza en el Río Autana, 4°48′N, 67°18′W, 100–115 m, *Guánchez & Melqueiro 3403* (MO, TFAV).

This species is distinguished by the thick-coriaceous, pustulose or verruculose leaf blades; these are usually pruinose on one or both surfaces, often drying discolored, and have scarcely evident or obsolete venation adaxially. It differs from the newly described *M. pustulata* Steyerm. in the pruinose leaf blades, inconspicuous or obsolete nervation of the upper leaf surface, and the mainly rounded or subcordate leaf base.

Maytenus insculpta Steyermark, sp. nov. TYPE: Venezuela, T. F. Amazonas: Dept. Atures, cuenca del Río Manapiare, sabanas al pie de los cerros al N del Cerro Morrocoy, alrededores del sitio "Pozo de la Carolina," 12 km W of San Juan de Manapiare, 05°19′N, 66°6′W, 225 m, 16 Oct. 1977, *Otto Huber 1229* (holotype, VEN; isotype, MO).

Frutex 3-metralis, ramulis juvenilibus teretibus tenuiter corrugatis; foliorum laminis elliptico-oblongis apice obtuse acuminatis basi subobtusis vel subacutis 11–18 cm longis 5–7 latis, marginibus haud revolutis integerrimis, nervatione ubique omnino insculpta, nervis lateralibus utroque latere 7–10 obsoletis, nervatione tertiaria ubique tenuiter insculpta-reticulata, in superficiebus amabus folii pustulatis, inconspicue decurrentibus; petiolis 6–9 mm longis; inflorescentia pauciflora breviter pedunculata, pedunculis 1.5–2.5 mm longis; pedicellis 1 mm longis; calycis lobis suborbicularibus rotundatis 0.8 × 0.8 mm valde ciliato-erosis; petalis ligulato-oblongis 1.5 mm longis 0.8 mm latis.

Shrub 3 m tall, the young stems terete, finely corrugated. Leaf blades subcoriaceous, drying concolorous, elliptic-oblong, obtusely acuminate at apex, the acumen 3–7 mm long, 3–4 mm wide, subobtuse or subacute at base, 11–18 cm long, 5–7 cm wide, the margins not revolute, entire; both lateral and tertiary nervation completely finely insculpted on both sides; lateral nerves very faint, 7–10 each side; lower and upper surfaces pustulate. Petioles 6–9 mm long, the base of leaf blade inconspicuously decurrent. Inflorescence few-flowered, shortly pedunculate; peduncles 1.5–2.5 mm long; pedicels 1 mm long. Calyx lobes suborbicular, rounded, 0.8 × 0.8 mm, strongly erose-ciliolate. Petals ligulate-oblong, 1.5 mm long, 0.8 mm wide.

This species is distinct in having the venation of both sides of the leaf blade delicately insculpted with a prominent pustulate surface between the veins. It is related to *Maytenus nitida* of Brazil, from which it differs by having rounded, suborbicular, strongly ciliolate calyx lobes, and by having larger leaf blades that are more conspicuously pustulose on the lower surface.

Maytenus laevis Reissek, in Mart., Fl. Bras. 11(1): 27. 1861.

This taxon, as Reissek noted, has the upper portion of the young stems distinctively carinate-angled and leaves "sub lente marginatis repandisque" and "subtus opacis scrupulosis." The leaves, petioles, and the young branches often take on a grayish color upon drying. While many of the specimens can be satisfactorily delimited by the application of such vegetative differences, one encounters atypical specimens on the higher slopes and summits of the table mountains in the Territorio Federal Amazonas and Estado Bolívar that indicate possible introgression from another source, such as *Maytenus guianensis* Kl. Specimens from the summit of Cerro Guaiquinima, Estado Bolívar (*Steyermark et al. 113333, 113424, 113428, 117216*), from Cerro Sarisariñama, Estado Bolívar (*Steyermark et al. 109252*—type of *M. jauaensis* Steyerm.), and from Cerro Yutaje, Territorio Federal Amazonas (*Maguire & Maguire 35441, 35455; Holst & Liesner 3272, 3357; Liesner & Holst 21807*) generally preserve the grayish dried leaf blades, petioles, and young stems as well as the thickened repand leaf margins, but the carinate-angled young stem is either lacking or scarcely apparent. These specimens may represent a variation of this taxon at higher altitudes, or may indicate introgression from *M. guianensis*, which possesses terete young stems and occurs in the Paragua and the Caura river basins, where Cerro Guaiquinima and Cerro Jaua are located, respectively.

Maytenus longistipitata Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Cerro Uroi, summit, north portion, Río Uroi, Río Chicanán, 700 m, 12 Sep. 1962, *B. Maguire, J. Steyermark & C. K. Maguire 53731* (holotype, VEN; isotype, MO).

Arbor 10 metralis, foliorum laminis lanceolato-ellipticis apice basique acutis 15–18 cm longis 5.5–6 cm latis integerrimis; nervis lateralibus principalibus utroque latere 8–10 tenuibus supra impressis subtus paullo elevatis, venatione tertiaria tenui laxe irregulariter reticulatis; petiolis 8–9 mm longis; pedicellis fructiferis fasciculatis 9–10 mm longis; capsulis late obovoideis apice rotundatis 21–26 mm longis 12–14 mm latis conspicue longistipitatis, stipite 5–7 mm longo.

Tree 10 m tall. Leaf blades lance-elliptic, acute at apex and base, 15–18 cm long, 5.5–6 cm wide, entire; main lateral nerves 8–10 each side, with finer intermediate nerves, impressed above, slightly elevated below, arcuate-ascending at an angle of 35–45°, scarcely anastomosing; tertiary venation fine, laxly irregularly reticulate and subelevated below, inconspicuous above. Petiole 8–9 mm long. Fruiting pedicels fasciculate, 9–10 mm long. Capsules broadly obovoid, rounded at summit, 21–26 mm long, 12–14 mm wide at and above the middle, conspicuously long-stipitate, the stipitate portion 5–7 mm long.

The conspicuously stipitate fruit readily distinguishes this species from *Maytenus oblongata* Reiss.

Maytenus neblinae Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Cerro de la Neblina, ridge at divide between Brazil and Venezuela, 26 km ENE of Base Camp, wet cloud forest on steep SW-facing slopes, 0°53′N, 65°56′W, 2,000 m, 15 Apr. 1984, *Timothy Plowman & Wayt Thomas 13610* (holotype, MO; isotypes, F, MO, VEN).

Arbor 8-metralis; foliorum laminis ovatis vel elliptico-ovatis vel oblongo-ellipticis apice obtusis vel obtusiusculis basi acutis vel subacutis 4.5–9.5 cm longis 2.5–3.5 cm latis, utroque margine uniformiter 30–40 crenulato-dentatis praedito, dentibus 7–8 per cm conspicuis 1–1.5 mm latis; nervis lateralibus utroque latere 8–13 supra impressis vel subelevatis subtus vix manifestis; venatione tertiaria supra manifesta subtus paullo manifesta; pagina inferiore subpustulata; petiolis 6–9 mm longis.

Tree 8 m tall. Leaf blades coriaceous, ovate or elliptic-ovate or oblong-elliptic, obtuse at apex, acute or subacute at base, 4.5–9.5 cm long, 2.5–3.5 cm wide; margins uniformly 30–40-crenulate-dentate, the dentations 7–8 per cm, conspicuous, 1–1.5 mm wide. Lateral nerves 8–13 each side, impressed or subelevated and more conspicuous on the upper side, scarcely evident beneath, ascending at an angle of 45–50°, anastomosing 3–6 mm from the margin. Petioles 6–9 mm long.

This taxon differs from some of the variations of *Maytenus guianensis* Kl. and *M. ficiformis* Reiss. with crenulate margins, in the smaller, differently shaped leaf blades with more numerous teeth per centimeter.

Maytenus pustulata Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Cerro de la Neblina, north branch of river in canyon, Camp IV, 15 km NNE of Pico Phelps, 0°51′N, 65°57′W, 780 m, 5 Mar. 1984, *Ronald Liesner 16720* (holotype, MO; isotype, VEN).

Arbor 5-metralis; foliis elliptico-oblongis apice obtusis, acumine 3–4 mm lato, basi obtusis vel subacutis 14–17 cm longis 6–7.5 cm latis integerrimis; nervis lateralibus utroque latere 9–13 supra paullo elevatis subtus obsoletis; venatione tertiaria ubique obsoletis, in superficie inferiori folii pustulatis; petiolis 11–18 mm longis; pedicellis fructiferis 6–10 mm longis; fructu ellipsoideo-obovoideo 15–16 mm longo 8–9 mm lato, apice rotundato.

Tree 5 m tall. Leaf blades coriaceous, 14–17 × 6–7.5 cm, elliptic-oblong, narrowed to an obtuse apex with an acumen 3–4 mm wide, obtuse to subacute at base, decurrent on the petiole; lateral nerves 9–13 on each side, slightly elevated on upper surface, obsolete on lower surface; tertiary veins obsolete both sides, the lower surface pustulate. Petiole 11–18 mm long, strongly canaliculate, 2–2.5 mm wide. Fruiting calyx lobes 0.5 mm long, rounded, unequally long-ciliolate around apex. Fruiting pedicels 6–10 mm long, 1–1.5 mm wide. Fruit ellipsoid-obovoid, 15–16 mm long, 8–9 mm wide toward summit, narrowed to 2.5 mm wide basally, rounded at summit.

The pustulate lower leaf surface, obsolete tertiary venation, large leaf blades, and stout pedicels distinguish this species from *Maytenus huberi* Steyerm., in which the tertiary and lateral nerve venation is insculpted.

ZINOWIEWIA

Zinowiewia aymardii Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Dist. Sifontes: bosques húmedos intervenidos por actividades mineras del sector "La Hoya" (Peray-tepuy), 7 km NW of Caserio El Pilón, 58 km W of Sta. Elena de Uairén, 4°40′N, 61°33′W, 850 m, 21 Oct. 1986, *Gerardo Aymard 4631* (holotype, MO; isotype, PORT).

Arbor 10–45 metralis, foliorum laminis ovatis vel lanceolato-ellipticis apice obtuse acuminatis basi attenuato-acutis vel acuminatis decurrentibus 5.5–10 cm longis 2.5–3.5(–4.5) cm latis; nervis lateralibus utroque latere (5–)8–12 supra subelevatis, venatione tertiaria ubique manifestis grosse reticulatis; petiolis 4–10 mm longis; inflorescentia cymosa axillari terminalique 5–6-plo ramosa 2.5 cm longa 4–6 cm lata, axibus primariis 3–9 mm longis; floribus 5-meris; pedicellis 1–1.5 mm longis; calycis lobis suborbicularibus rotundatis 0.5 mm longis 0.7 mm latis; fructu oblique obovato 14–20 mm longo apicem versus 7–9 mm lato arcte venoso; seminibus anguste ellipsoideis 6.5–7 mm longis 2–3 mm latis.

Tree 10–45 m tall. Leaf blades ovate or lance-elliptic, obtusely acuminate at apex, narrowly acute to acuminate at the shortly decurrent base, 5.5–10 cm long, 2.5–3.5(–4.5) cm wide; lateral nerves (5–)8–12 each side, ascending at an angle of 45–60°, anastomosing 3–5 mm from margin, conspicuous and impressed or subelevated above, less conspicuous below; tertiary venation manifest both sides, grossly reticulate, more conspicuous below; midrib impressed above with a slender narrow ribbonlike border on each side. Inflorescence cymose, axillary and terminal, 5–6 times branched, 2.5 cm long, 4–6 cm wide, the primary axes 3–9 mm long. Flowers 5-merous, the pedicels 1–1.5 mm long. Bracts subtending opposite pairs of the dichotomous axes. Calyx papillose-pustulose without, the lobes suborbicular, rounded, 0.5 mm long 0.7 mm wide, margins slightly uneven but eciliate, the apex ending slightly higher than the lateral margins and crowned by 3 darker minute appendages. Petals broadly ovate-oblong, rounded at apex, 1.1 mm long, 0.5–0.8 mm wide. Anthers orbicular, 0.2–0.3 mm × 0.2–0.3 mm; filaments 0.3–0.4 mm long, slightly wider basally. Disk annular-cupuliform, lance-deltoid, acute, 0.5–1 mm long, the margins with dark squamellate appendages. Fruit obliquely obovate, broadly rounded at apex, 14–20 mm long, 7–9 mm wide toward the distal end, about 3 times longer than broad, strongly venose, the main nerves at first parallel. Seeds narrowly ellipsoid, 6.5–7 mm long, 2–3 mm wide.

Paratype. VENEZUELA. BOLÍVAR: lower portion of Quebrada Oparumá, tributary to Río Pacairao, below Santa Teresita de Kavanayén, 915–1,065 m, 25 Nov. 1944, *Steyermark 60580* (F, VEN). T. F. DELTA AMACURO: bosque pluvial, E of Río Grande, ENE of El Palmar, near limits of Bolívar, 13 Jan. 1965, *Marcano Berti 562* (MER, MO, NY, VEN).

Common names. Ata-caramá-yek (Arekuna); guatacare montanero.

This taxon differs from *Zinowiewia australis* Lundell of the northern Coastal Range of Venezuela in the more numerously flowered, larger inflorescence with longer primary and secondary axes, and especially in the shorter seed body and shorter fruit with the wing narrower in proportion to the width. Also the leaf blades are more shortly and less abruptly decurrent.

RHAMNACEAE

GOUANIA

Gouania wurdackii Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Dist. Cedeño: Cerro San Borja, middle Orinoco River, 100–300 m, 12 Dec. 1955, *J. J. Wurdack & J. V. Monachino 39810* (holotype, MO; isotypes, NY, VEN).

Frutex scandens; foliorum laminis discoloribus anguste ovatis vel oblongo-ovatis apice acutis vel subacutis basi cordatis vel subcordatis 4–7 cm longis 2.5–4 cm latis supra tenuiter rugulosis sulcinerviis sulcis adpresso-pubescentibus subtus densissime arcte cinereo-vel stramineo-tomentellis, marginibus arcte serratis, dentibus utroque margine 15–20 late deltoideis subacutis apice in glandulis callosis obtusis parvis paullo incrassatis terminantibus; costa media supra nervis lateralibus tertiariisque sulcatis subtus manifeste elevatis, nervis lateralibus utroque latere 6–8; petiolis 5–10 mm longis; floribus extus dense cinereo-tomentosis; calycis lobis ovatis subacutis 1.2 mm longis extus albido-pilosis intus glabris; disco dense minuteque pubescenti, circa stylum elevato pilis setosis munito, lobis triangulari-lanceolatis ad apicem attenuatis subemarginatis subobtusis 0.5 mm longis; capsulis suborbicularibus alatis 9–10 × 9–10 mm, omnino dense pilosulis alis sublunatis longioribus quam latioribus 9–10 mm longis 2.5–4 mm latis.

Woody vine or climbing shrub with striate, densely fulvous-tomentellose branches. Leaf blades discolored (dry), olive green above, cinereous or stramineous below, narrowly ovate or oblong-ovate, acute to subacute at apex, cordate or subcordate at base, 4–7 cm long, 2.5–4 cm wide, finely rugulose and sulcate-nerved above, minutely appressed-pubescent in the sulcations, below densely tomentellose with cinereous or stramineous hairs completely covering the surface and nerves, the hairs on the lower surface densely intertwining and matted, the margins closely and rather uniformly serrate with 15–20 broadly deltoid, subacute teeth 2–4 mm wide and averaging 4 per cm, terminating in a small, brown or maroon-brick-colored, thickened callosity, glabrous on the lower side and with axillary hairs on the upper leaf surface; lateral nerves 6–8 each side, sulcate above; midrib and lateral and tertiary nerves conspicuously elevated, the tertiary ones conspicuously transverse between the finer elevated veinlets. Petioles 5–10 mm long, densely pubescent with stramineous or pale yellow-brown hairs. Inflorescence interruptedly spiciform, the lower inflorescences simple and axillary, the upper becoming paniculately branched; rachis deeply stramineous or pale brown pubescent. Flowers sessile or nearly so. Calyx lobes ± densely pilose without, with pale hairs, ovate, subacute, 1.2 mm long, 1.2–1.3 mm wide at the base, glabrous within; hypanthium obconic, 1.2 mm long, densely pubescent. Petals cucullate, about length of calyx lobes. Disk completely and densely short pubescent, elevated into an annulus near the style, where densely setose; disk lobes triangular-lanceolate, attenuate to a subobtuse subemarginate apex ca.0.5 mm long, about ⅓ the width of the calyx lobe. Capsules fulvous brown or gray-brown, sessile or up to 2 mm pedicellate, suborbicular, about as broad as long, 9–10 × 9–10 mm, ± densely pilosulous throughout; axis of fruit 7–9 mm long, the wings sublunate, longer than broad, 9–10 mm long, 2.5–4 mm wide, about as wide as the central body.

Paratypes. VENEZUELA. BOLÍVAR: Dist. Cedeño: east slopes of Cerro Pijiguao, N end of Serranía Suapure, above Pijiguao, ca. 70 km from mouth of Río Suapure, 110–520 m, 19 Jan. 1956, *Wurdack & Monachino 41310* (MO, NY, VEN). T. F. AMAZONAS: Dpto. Atures, 18 km al SE de Puerto Ayacucho, laja cerca de la Piedra con Petroglifos, ± 2 km al N del pueblo de Pintado, 5°32′N, 67°32′W, 1,000 m, 8 Dec. 1977, *Huber 1370* (NY, VEN).

This taxon is distinguished vegetatively from the common and widely distributed *Gouania mollis* H.B.K. by the narrowly lance-ovate, acute leaves with conspicuous discolored nerves on the stramineous lower surface and by the finely rugulose sulcate nerves of the upper surface. Also, the tertiary venation abaxially is conspicuously elevated and prominent transversely and the marginal teeth are closer together, shorter, narrower, and terminate more abruptly in smaller callosities. The taxon is restricted to the granitic sector of the Distrito Cedeño of northwestern Estado Bolívar and adjacent northwestern Territorio Federal Amazonas, a region of high endemism.

RHAMNUS

Rhamnus longipes Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Serranía Parú, cumbre, SSE to edge of descent, to tributary of Caño Asisa, mostly rocky sabanita open areas, 2,000 m, 10 Feb. 1951, *R. S. Cowan & John J. Wurdack 31388* (holotype, NY).

Frutex 2-metralis, ramulis juvenilibus sparsim pilosulis; foliorum laminis ovatis vel oblongo-ovatis apice acutis vel subacuminatis basi obtusis majoribus 5–6.5 cm longis 2.5–3.2 cm latis obscure repando-crenulatis, costa media subtus sparsim pilosula, aliter ubique glabris; nervis lateralibus utroque latere 5–8; petiolis 4–8 mm longis paullo pilosulis; calyce fructifero sparsim pilosulo pilis adpressis munito; infructescentia 1–2-fructifera; pedunculo fructifero maturo 10–15 mm longo sparsim pilosulo; pedicellis fructiferis maturis 10–15 mm longis sparsim pilosulis; fructibus subglobosis 5–7 mm longis 6–7 mm latis.

Shrub 2 m tall. Young stems sparsely pilosulous with pale hairs. Leaf blades ovate or oblong-ovate, acute to subacuminate at apex, obtuse at base, the larger ones 5–6.5 cm long, 2.5–3.2 cm wide, the margins subrevolute, obscurely repand-crenulate with ca. 3 depressed crenulations per cm, the leaf surface glabrous both sides; midrib above sulcate, glabrous, below sparsely pilosulous with pale hairs. Principal lateral nerves 5–8 each side, inconspicuous above, slightly elevated below; tertiary venation slightly sulcate above, more conspicuously so below. Petiole 4–8 mm long, slightly pilosulous with pale hairs. Fruiting calyx sparsely pilosulous, the lobes triangular-lanceolate, subacute, 1.3 mm long. Infructescence with 1–2 fruits; mature fruiting peduncle and pedicels 10–15 mm long, pilosulous with pale hairs. Fruit subglobose, 5–7 mm long, 6–7 mm broad, glabrous.

This species is characterized by the relatively elongated, sparsely pilosulous fruiting peduncle with 1–2 elongate, sparsely pilosulous pedicels 10–15 mm long; subrevolute, shallowly repand-crenulate leaf margins with an average 3 crenulations per cm; and the slightly elevated tertiary venation of the lower leaf surface.

Rhamnus sipapoensis Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Cerro Sipapo (Paraque), rim head of South Basin, occasional in woodland, rugged terrain, 1,970 m, 26–28 Jan. 1949, *Bassett Maguire & Louis Politi 28656* (holotype, NY; isotype, MO).

Arbor 3-metralis, ramulis junioribus dense brunneo-tomentosis; stipulis haud persistentibus; foliorum laminis oblongis elliptico-oblongis vel ovato-oblongis apice obtuse acutis vel abrupte breviter acutis mucronatis basi rotundatis vel obtusis 2.5–7.5 cm longis 1.5–3.8 cm latis, supra glabris subtus pallido-stramineis dense velutinis, marginibus revolutis integerrimis vel fere integerrimis; costa media nervisque supra sulcatis subtus dense tomentellis; nervis lateralibus utroque latere 7–11; petiolis 4–10 mm longis dense tomentellis; inflorescentia epedunculata vel pedunculo usque ad 6 mm longo; pedicellis sub anthesi 6–9 mm longis post anthesim usque ad 11 mm longis dense brunneo-pubescentibus; calyce 3.5–4 mm longo extus dense brunneo-tomentelloso; ovario dense pubescenti.

Tree 3 m tall, the young branches densely dull brown tomentellous. Stipules not persistent. Leaf blades oblong, elliptic-oblong, or ovate-oblong, mucronate at the obtusely acute to abruptly short acute apex, obtuse to rounded at base, 2.5–7.5 cm long, 1.5–3.8 cm wide, glabrous above, densely pale buff velutinous below with the tomentum concealing the leaf surface; margins revolute, entire or nearly so; midrib and lateral nerves sulcate above, below densely brown tomentellous. Lateral nerves 7–11 each side, spreading-ascending at an angle of 25–45°, ending at margins. Petioles 4–10 mm long, densely tomentellous. Inflorescence epedunculate or with a peduncle up to 6 mm long. Pedicels 6–9 mm in anthesis, up to 11 mm long after anthesis, densely brown pubescent. Calyx campanulate, 3.5–4 mm long, 3.2–3.5 mm broad, densely brown tomentellous; lobes 5, lanceolate-ovate, acute, 1.5–2.1 mm long, 1–1.5 mm wide. Petals unguiculate, bilobate, 1.5 mm long, the lamina suborbicular-obovate, 0.8 mm long, 1.3 mm wide. Anthers oblong-subquadrangular, 0.5 mm long; filaments 1 mm long, glabrous. Ovary subglobose, 1.5 mm long, densely pubescent; style 0.4 mm long, glabrous.

This species has a close affinity with *Rhamnus marahuacensis* Steyerm. & Mag., from which it differs in the mainly epedunculate inflorescence, or the peduncle may be developed to 6 mm in length. It differs further in the densely tomentose calyx, pedicels, and stems; the mainly entire leaf margins; the obtusely acute to abruptly short-acute, mucronate leaf blades; and the more densely tomentose lower leaf surface.

SAPINDACEAE

MATAYBA

Matayba affinis Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Dept. Atabapo. Cucurital de Caname, southern bank of the middle part of Caño Caname, 3°40′N, 67°22′W, 100 m, 30 Apr.–1 May 1979, *Gerrit Davidse, Otto Huber & Stephen Tillett 17011* (holotype, MO; isotype, VEN). Figure 4.

Arbor 4-metralis; foliis 3 dm longis, foliolis 3–5 oblongo-obovatis vel elliptico-oblongis apice rotundatis vel obtuse acutis basi acutis majoribus 14–15 cm longis 6–7 cm latis, praesertim secus costam mediam nervos lateralesque glandulis microscopicis rufis obsitis aliter glabris integerrimis; calycis lobis late suborbicularibus apice rotundatis vel subacutis 1–1.2 mm longis 1.2–1.5 mm latis; antheris pilosis; disco sparsim piloso; stylo elongato 1.2 mm longo; ovario 3-loculari.

Tree 4 m, the branches strongly lenticellate. Leaves, including the petiole, 3 dm long. Petioles 3–4 cm long, microscopically puberulent. Leaflets 3–5, alternate, oblong-obovate to elliptic-oblong, rounded to obtusely acute at apex, acutely narrowed at the base, the upper larger ones 14–15 cm long, 6–7 cm wide, the lower smaller ones 7–11 cm long, 3–5 cm wide, glabrous except for the microscopic rufous glands especially abundant along the midrib and lateral nerves, entire; lateral nerves 6–8 on each side, inconspicuous, ascending at an angle of 45–50°; tertiary venation finely and obscurely reticulate both sides; petiolule 5–6 mm long, glabrous. Panicle terminal, 15–18 cm long; rachis moderately puberulent with 2–4 unbranched axes 2.5–7 cm long, bearing numerous sessile clusters of pedicellate flowers. Pedicels 1.5–3 mm long, densely puberulous. Calyx moderately appressed-puberulous without, the margins cut ⅔ the length; calyx lobes broadly suborbicular-deltoid, rounded or subacute at apex, 1–1.2 mm long, 1.2–1.5 mm wide at the base. Petals narrowly oblong-ovate, obtuse, 1.2 mm long, 0.4 mm wide; petaliferous scales rhomboid-oblong, rounded, slightly exceeding the petal, 1.3–1.5 mm long, 0.5 mm wide, densely villous as is the petal. Anthers suborbicular, 0.5 × 0.5 mm, densely pilose; filaments 2 mm long, pilose except in uppermost portion. Disk sparsely pilose. Style 1.2 mm long, elongated, sparsely strigillose. Ovary ovoid-subglobose, trigonous, 2 mm long, 1.5 mm wide, 3-celled, moderately strigillose.

This species is allied to *Matayba macrostylis* Radlk., but the anthers are pilose, the disk is sparsely pilose, the calyx lobes are rounded or subacute, the ovary is 3- instead of 2-celled, the petals are shorter, and the leaflets are rounded or obtusely acute, and only 3–5.

Matayba longipes Radlk., Sitzungsber. Bayer. Akad. IX. 536. n. 479. p. 626. n. 7. 1879; in Engler, Das Plfanzenreich, Heft 98e (IV. 165). Sapindaceae. 1085. 1933. *Matayba tovarensis* Radlk., Sitzungsber. Bayer. Akad. IX. 536. n. 494. p. 626. n. 8. 1879.

Radlkofer (1933) distinguished *Matayba tovarensis* Radlk. from *M. longipes* Radlk., both described from the area of Colonia Tovar, Venezuela, on vegetative characters only, such as supposed differences in texture (membranous in *M. longipes* contrasted with coriaceous in *M. tovarensis*), leaf shape (oblong- or subacute-lanceolate in *M. longipes* vs. lanceolate in *M. tovarensis*), and degree of narrowing of the base of the leaflet blade into the petiole (abruptly attenuate in *M. longipes*, but gradually narrowed in *M. tovarensis*). Study of type material and of additional col-

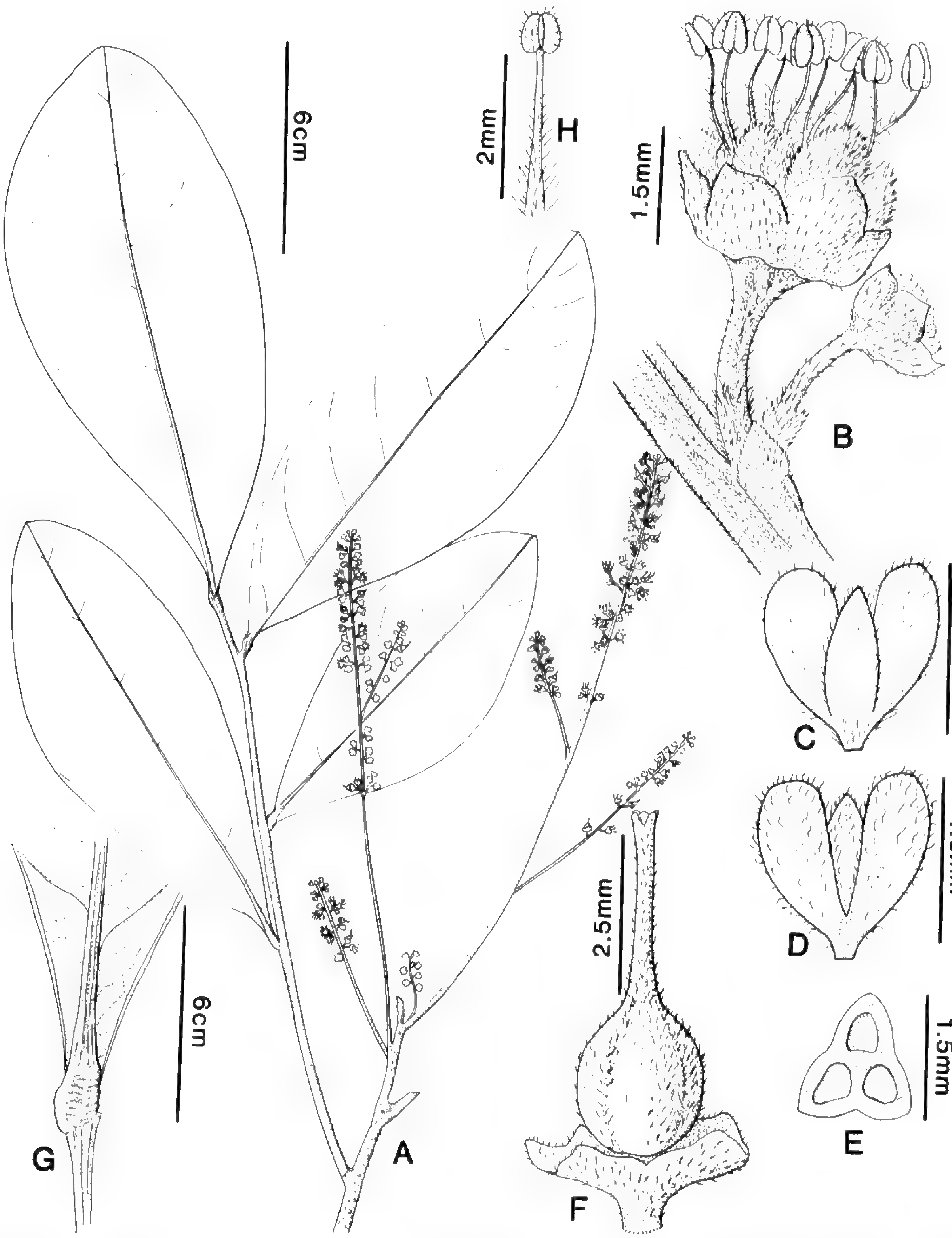

FIGURE 4. Matayba affinis.—*A. Habit of flowering branch.—B. Detail of small portion of flowering rachis.—C. Petal, dorsal view.—D. Petal, ventral view.—E. Diagrammatic transverse section through ovary.—F. Pistil and calyx.—G. Basal portion of leaf blade, abaxial view, with portion of petiole.—H. Stamen.*

lections from near the type locality and elsewhere in the coastal mountains of northern Venezuela indicates that these differences break down and that the two taxa must be united. Even on the type specimen of *M. longipes* (*Fendler 1748*), a few leaflets show their bases gradually tapering into the petiole as in *M. tovarensis*. The leaflet shape varies within a given population, and there appears to be no difference in the texture of the two taxa. I am uniting them under *M. longipes*.

The fruit of *Matayba longipes* has a stipe described as being 1.8–2 cm long (Radlkofer, 1933). However, an isotype specimen at MO has stipes mostly only 1.5 cm long.

Fruiting specimens collected in the Venezuelan Guayana from Cerro Yutaje, Serraní Parú, and the Brazilian side of the Cerro de La Neblina in Territorio Federal Amazonas agree in all essential respects with *Matayba longipes* of the Venezuelan coastal mountains, except for the constantly shorter fruiting stipe, only 5–9 mm long, whereas in typical *M. longipes* the length varies from 9–18 (−20) mm. Other minor differences are in the sometimes smaller number of leaflets, relatively larger length and width of the leaflets, and in their slightly longer, more slender leaf apex. This difference in foliage is somewhat more marked in the specimens from Serranía Yutaje and Neblina than those from the vicinity of Cerro Yutaje.

In view of the differences in stipe length and the geographically isolated distribution on the sandstone mountains of the Venezuelan Guayana, together with some tendency in foliar divergence, I consider that the Guayana population shows a sufficient degree of separation as to warrant a subspecific status.

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Matayba longipes Radlk. subsp. **tepuiensis** Steyerm., subsp. nov. TYPE: Venezuela. T. F. Amazonas: Serranía Parú, Caño Asisi, Top Camp to Caño Camp, talus slopes, 1,400 m, 13 Feb 1951, *R. S. Cowan & J. J. Wurdack 31450* (holotype, MO, as 2997923; isotype, NY).

A *M. longipes* praesertim fructus stipite 5–9 mm longo recedit; foliolis quattuor quinque vel sex 9–21 cm longis 3–8 cm latis; infructescentiis 2–12 cm longis.

Tree 8–20 m tall. Leaves 4–6-foliolate; leaflets elliptic-ovate to oblong-lanceolate, obtusely to slenderly acutely acuminate, 9–17(−21) cm long, 3–6.5(−8) cm wide, the acumen 1.5–2.5 cm long, abruptly to gradually acutely narrowed to the base; main lateral nerves 8–10(−12) each side, elevated below; tertiary venation prominently reticulate. Petiole 4–8 cm long; petiolule 2–10 mm long. Disk tomentose. Infructescence 2–12 cm long, the peduncle and rachis mostly densely strigose-pubescent. Fruiting pedicel 4–7 mm long, sparsely strigillose. Stipe of fruit 5–9 mm long, sparsely strigillose. Fruiting capsule lobed, horizontally divaricate, 7–12 mm high, 1.5–2.2 cm broad, glabrous or very sparsely puberulent without, the valves densely tomentose within. Style persistent in fruit, 2–3 mm long.

Paratypes. VENEZUELA. T. F. AMAZONAS: Depto. Atures, valley of Río Coro-Coro, west of Serranía de Yutaje, east base of forested mountain 5 km W of river, 5°41′N, 66°9′30″W, 1,100 m, 10 Mar. 1987, *Holst & Liesner 3405*. BRAZIL: DEPARTAMENTO AMAZONAS: Serra da Neblina, between Palmito and Tatú Camp, 400–600 m, 19 Dec. 1965, *Silva & Brazão 6069* (MO, NY).

Matayba oligandra Sandwith var. **oligandra**

Matayba oligandra Sandw., Kew Bull. 1935: 123. 1935.
Trichilia ptariana Steyerm., Fieldiana, Bot. 28(2): 278. 1952.
Matayba oligandra var. *ptariana* (Steyerm.), Bol. Soc. Venez. Ci. Nat. 26: 426. 1966.
Matayba jauaensis Steyerm., Bol. Soc Venez. Ci. Nat. 33 (132/133): 347, fig. 15. 1976.

Matayba oligandra Sandw. var. **occidentalis** Steyermark, var. nov. TYPE: Venezuela. T. F. Amazonas: West Mountain Caño Grande, Río Cuao, Río Orinoco, 125 m, 17 Jan. 1949, *Bassett Maguire & Louis Politi 28399* (holotype, MO; isotype, NY).

A *M. oligandra* foliolis ovatis elliptico-ovatisve 2.5–4.5 cm latis (2.8–)3–3.6-plo longioribus quam latioribus, acumine longitudine ¼–⅙ laminae partes aequanti recedit.

Leaves 10–12-foliolate. Leaflets ovate or elliptic-ovate, abruptly slenderly and obtusely acuminate at apex, acute at base, 5.5–10.5 cm long, 2.5–4.5 cm wide, (2.8–)3–3.6 times longer than broad, the acumen 10–20 mm long, ¼–⅙ the length of the leaf blade; petiolules 5–10 mm long. Petioles (3–)5.5–8 cm long. Infructescence 9–17 cm long. Fruit 1.5–1.8 cm long, 1.5–2 cm diam., the valves glabrous without and within.

Paratypes. VENEZUELA. T. F. AMAZONAS: Cerro Sipapo, Campo Grande, 1,500 m, 8 Dec. 1948, *Maguire & Politi 27558* (MO, NY); Cerro Arauicaua, Río Yatua, 1°35′N, 66°10′W, 125–150 m, 12 Apr. 1970, *Steyermark & Bunting 102560* (VEN).

Matayba oligandra Sandw. var. *oligandra*, described from Guyana (Sandwith, 1935: 123), has the leaflets principally oblong or oblong-lanceolate, 2–3.8 cm wide, chiefly 2.2–3 times longer than broad, and with an acumen ⅙–⅐ the length of the leaf blade. It is confined to Estado Bolívar in the eastern half of the Venezuelan Guayana. Var. *occidentalis*, on the other hand, is restricted to the western part of the Venezuelan Guayana in Territorio Federal Amazonas. *Matayba jauaensis* Steyerm. and *M. oligandra* var. *ptariana* Steyerm. appear to represent merely minor variations of leaflet size and cannot be maintained apart from var. *oligandra*.

The type collection of *Matayba oligandra* and *M. chimantensis* Steyerm., the latter possibly synonymous with *M. oligandra*, have only 4–6 stamens, whereas *M. jauaensis* Steyerm. and *M. oligandra* var. *ptariana* have 8 stamens. However, no additional characters have been found to separate those collections having 8 stamens from typical *M. oligandra*.

LITERATURE CITED

SANDWITH, N. Y. 1935. Contributions to the Flora of Tropical America: XXIII. Bull. Misc. Inform. 1935: 117-132.

Matayba yutajensis Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Serranía Yutaje, Northwest Ridge, 1,400 m, 11 Feb. 1953, *Bassett & C. K. Maguire 35143* (holotype, MO; isotypes, NY, VEN). Figure 5.

Arbor 3-5-metralis; foliis 2-4-foliolatis; foliolis alternis, oblongis vel oblanceolato-oblongis apice rotundatis retusisque 10-18 cm longis 2.5-8 cm latis; nervis lateralibus principalibus utrinque latere 8-15; venulis tertiariis utrinque conspicue elevatis reticulatisque; petiolis 1-1.7 cm longis; calyce 3.5-4 mm lato extus glabro; filamentis ubique dense pilosis; fructu 2 cm longo 2.3 cm lato extus glabro; endocarpio intus glabro.

Tree 3-5 m. Leaves 2-4-foliolate. Leaflets alternate, oblong to oblanceolate-oblong, rounded and retuse at apex, subacute to acute at base, 10-18 cm long, 2.5-8 cm wide, glabrous throughout; principal lateral nerves rather inconspicuous, 8-15 each side, spreading at an angle of 10-20°; tertiary venation prominently elevated and reticulate on both sides. Petioles 1-1.7 cm long, glabrous; petiolules 3-8 mm long, glabrous. Inflorescence terminal or subterminal, including the peduncle, 15-18 cm high, 5 cm wide, sparsely branched, the individual axes ascending, 2-5 cm long, sparsely strigillose. Rachis sparsely strigillose to glabrescent. Flowers pedicellate. Pedicels 1-1.5 mm long, sparsely strigillose. Bract subtending pedicels and axes lanceolate, acute, 0.7-1 mm long, sparsely strigillose. Calyx 3.5 mm long, 3.5-4 mm wide, glabrous without or sparsely strigillose near base; lobes suborbicular, rounded with narrowed to subacute apex, 1 mm high, 2 mm wide. Petal suborbicular-flabelliform, 1.5 mm long, 1.6-1.7 mm wide, glabrous without, pilose within; petaliferous scales obovate-oblong, rounded-truncate at summit, 1 mm long, 0.5 mm wide, with long brownish hairs, the margins (especially around the apex) laciniate-pectinate, pubescent both sides. Anthers suborbicular, basally bilobed, 0.7 × 0.7 mm; filaments 3 mm long, 0.3 mm wide at base, densely pilose throughout. Fruit 3-lobed, shortly stipitate, the stipe 3 mm long, 4 mm wide; fruit body 2 cm long, 2.3 cm wide, glabrous without; endocarp glabrous within.

Paratypes. VENEZUELA. T. F. AMAZONAS: Serranía Yutaje, Cerro Yutaje, left hand fork of Caño Yutaje, 1,300-1,400 m, 15 Feb. 1953, *B. & C. K. Maguire 35242* (MO, NY); 1-2 km E of Río Coro-Coro, W of Serranía Yutaje, 9 km N of Yutaje settlement, 5°42'N, 66°07'30"W, 500-730 m, 28 Feb. 1987, *Liesner & Holst 21484* (MO, NY, VEN); valley of Río Coro-Coro, W of Serranía Yutaje, W of valley, 5°42'30"N, 66°10'W, 1,300 m, *Holst & Liesner 3368* (MO, NY, VEN); Dept. Atabapo, Cerro Marahuaca, above branch of Caño Negro, S-central part of meseta, downstream from "Sima" camp, 3°43'N, 65°31'W, 1,220-1,350 m, 23-24 Feb. 1985, *Steyermark & Holst 130642, 130671* (MO, VEN); Cerro Marahuaca, Río Yameduaka, 3°38'N, 65°28'W, 1,225 m, 17-18 Feb. 1985, *Liesner 17614* (MO, VEN).

This species is related to *Matayba atropurpurea* Radlk., from which it differs in the retuse, rounded apex of the leaflets; fewer leaflets; shorter petioles; filaments densely pilose throughout their length; and the much larger fruit. Further, *Matayba yutajensis* occupies higher altitudes of montane forest of the sandstone table mountains, whereas *M. atropurpurea* is a lowland tree.

TALISIA

Talisia amaruayana Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Amaruay-tepui, 5°54'N, 62°15'W, 550-810 m, 26 Apr. 1986, *Ronald Liesner & Bruce Holst 20394* (holotype, MO; isotype, VEN).

Arbor 3-metralis; foliis 12-foliolatis; foliolis lanceolatis apice acuminatus basi acutis vel subacutis 26-38 cm longis 4-8 cm latis praeter costam mediam subtus sparsim puberulentam glabris; nervis lateralibus utroque latere 16-25; panicula usque 8.5 dm longa; calycis lobis intus glabris extus puberulis longiciliatis; petalis 6 mm longis 2.5-2.8 mm latis longiciliatis; squamis petaliferis parte dorsali praeter margines inferiores dense sericeos glabra; staminibus 5; filamentis praeter partem superiorem pilosis; disco hirsutulo.

Tree 3 m, with simple unbranched stem. Leaves 12-foliolate. Leaflets chartaceous, lanceolate, acuminate at apex, acute to subacute at base, 26-38 cm long, 4-8 cm wide, glabrous except sparsely puberulent on the midrib below; lateral nerves 16-25 each side, conspicuously elevated beneath, impressed above, anastomosing 4-7 mm from margin; tertiary venation minutely reticulate above, grossly reticulate below with elevated veins. Petiolules 7-9 mm long, hirtellous. Panicle terminal, up to 8.5 dm long, the rachis and axes hirtellous. Axes simple or branched, 12-20 cm long. Flowers crowded in several-flowered fascicles, sessile. Calyx

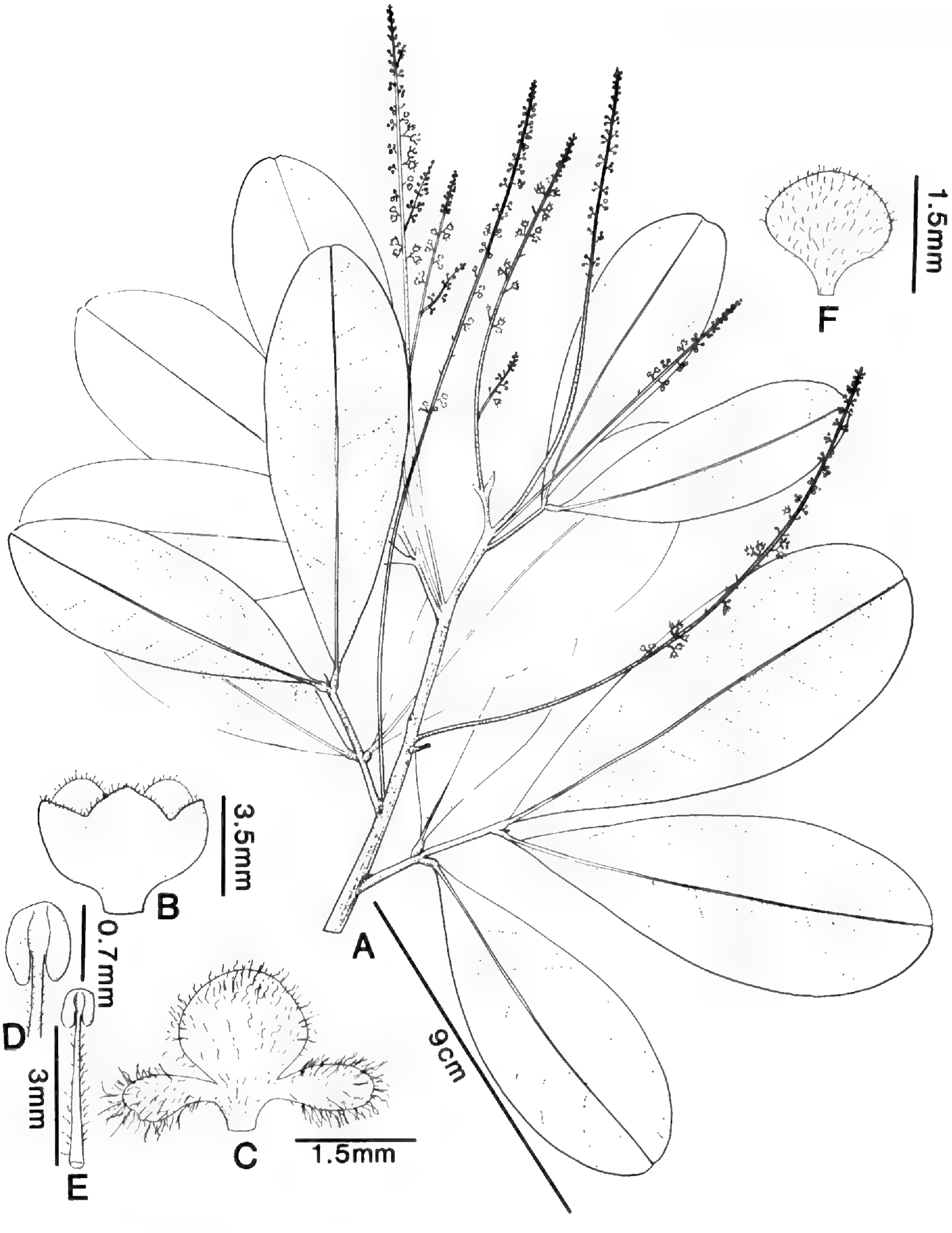

FIGURE 5. Matayba yutajensis.—*A. Habit of flowering branch.—B. Calyx.—C. Petal with 2 scales spread out, ventral view.—D. Upper portion of stamen.—E. Stamen.—F. Petal, dorsal view.*

3.5 mm long, cut ⅔ way down; lobes ovate-oblong, rounded at summit, 2 × 2 mm, puberulous without, glabrous within, long-ciliate. Petals lance-oblong, obtuse at summit, 6 mm long, 2.5–2.8 mm wide below the middle, glabrous both sides, long-ciliate. Petaliferous scales lanceolate, obtuse-subtruncate, slightly shorter than the petal, 3–3.5 mm long, 2 mm wide at base, the ventral portion densely sericeous above the glabrous basal sector, the dorsal portion densely sericeous along the lower margins, glabrous elsewhere. Stamens 5; filaments 1.3 mm long, pilose except in the uppermost part; anthers linear-oblong, 1.5–1.8 mm long, 0.2 mm wide, the appendage broadly lanceolate, acute, 0.3 mm long, the base bilobed. Disk shallowly undulate-lobulate, 2.8 mm diam., hirsutulous except on the outer concavities. Style 3 mm long, strigose. Fruiting pedicels 2 mm long, densely pubescent. Fruit ovoid-subglobose, 2 cm long, 1.7–1.8 cm wide, minutely appressed-puberulent.

Paratype. VENEZUELA. BOLÍVAR: Amaruay-tepui, 5°55′N, 62°15′W, 550–800 m, 20 May 1986, *Liesner & Holst 20935* (MO, VEN).

From the closely related *Talisia tiricensis* Steyerm., *T. amaruayana* differs by having ciliate petals and puberulous lower midrib.

Talisia caudata Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Cerro Sipapo, trail from Base Camp, 125 m, 25 Jan. 1949, *Bassett Maguire & Louis Politi 28615* (holotype, MO; isotype, NY). Figure 6.

Arbor 2-metralis; foliis 6 dm longis, 25-foliolatis; foliolis alternis lanceolatis apice longicaudatis basi acutis 9.5–14 cm longis 2.5–3 cm latis, acumine 17–25 mm longo, subtus praeter costam mediam dense hirtellam glabris eglandulosis; nervis lateralibus utroque latere 14–17; rachidi dense puberula pilis divaricatis munita haud glandulosa; petiolulis 7–10 mm longis minute denseque puberulentibus pilis divaricatis praeditis; infructescentia paniculata 14 cm longa 7 cm lata, axibus 8–9 simplicibus 0.5–3 cm longis adpresso pubescentibus; fructibus obovoideo-oblongis apice rotundato-subtruncatis basi rotundatis 2.2–2.4 cm longis 1–1.2 cm latis obtuse trigonis adpresso puberulis; stylo sub fructu deciduo vel persistenti 2 mm longo dense strigoso.

Tree 2 m. Leaves 6 dm long, petiolate. Petiole 17 cm long, minutely and densely puberulent with divaricate hairs. Leaflets mainly alternate, 25, lanceolate, long-caudate at apex, asymmetrically acute at base, 9.5–14 cm long, 2.5–3 cm wide, the caudate portion 17–25 mm long, 3 mm wide at base, the upper surface glabrous with impressed or slightly raised, minutely puberulent midrib, the lower surface glabrous except for the densely minutely hirtellous, eglandular midrib. Lateral nerves 14–17 each side, slightly sulcate above, elevated below, slightly ascending at an angle of 25–30°, strongly anastomosing below 3–5 mm from margin; tertiary venation reticulate below, slightly elevated, inconspicuous and scarcely manifest on upper side. Leaf rachis densely puberulous with divaricate nonglandular hairs. Petiolules 7–10 mm long, minutely and densely puberulent with divaricate hairs. Infructescence paniculate, 14 cm long, 7 cm wide, the rachis densely appressed-pubescent; axes 8–9, unbranched, the lower and middle ones 2–3 cm long, the upper ones 0.5–1 cm long, densely appressed-pubescent. Fruit obovoid-oblong, rounded-subtruncate at summit, rounded at base, 2.2–2.4 cm long, 1–1.2 cm wide, obtusely trigonous, appressed-puberulous. Style in fruit deciduous or persistent, 2 mm long, densely strigose. Calyx lobes in fruit persistent, strigose without, ciliate.

This taxon differs from the related *Talisia erecta* Radlk. in the much longer caudate, lanceolate leaflets with longer petiolules, more numerous lateral nerves, and eglandular pubescence without stipitate glands. The leaflets are longer than broad, but less so than in *T. erecta*, which has more closely spaced leaflets.

Talisia glandulifera Steyermark, sp. nov. TYPE: French Guiana. Saul: Monte La Fumée, 3°37′N, 53°12′W, 200–400 m, 1 Oct. 1982, *Scott Mori et al. 15027* (holotype, MO; isotype, NY). Figure 7.

Arbor usque 15 m altis; foliis 25–40 cm longis; foliolis 4–7-jugis plerumque oppositis elliptico-lanceolatis apice longiacuminatis basi acutis majoribus 10–18 cm longis 3.5–5 cm latis, costa media supra impressa subtus elevata minute puberulenti pilis divaricatis praedita; petiolulis 2–5 mm longis; calyce 3.5 mm longo extus dense glanduloso-piloso, lobis ovato-oblongis apice rotundatis; petalis subovato-oblongis apice rotundatis extus glabris intus sparsim prope basim secus mediumque sparsim adpresso-glanduloso-puberulentibus; filamentis glabris; disco dense hispido.

Tree 15 m tall. Leaves 25–40 cm long, the petiole 6.5–10 cm long. Leaflets 4–7 pairs, mainly opposite, elliptic-lanceolate, long-acuminate at apex, asymmetrically acute at base, the larger ones 10–18 cm long, 3.5–5 cm wide, the midrib impressed above, elevated below, minutely puberulent with short, divaricate hairs, otherwise glabrous; lateral nerves 13–18 each side, conspicuous and elevated below, slightly ascending at an angle of 15–25°; tertiary venation finely reticulate above, more grossly reticulate below; rachis terete, minutely puberulent with a few glandular hairs; petiolule 2–5 mm long. Inflorescence subterminal, paniculate, densely flowered, 13–23 cm long, 8–20 cm wide, with 6–12 ascending axes, the lower ones 4–15 cm long, densely hirtellous intermixed with glandular hairs. Peduncle 1 cm long or none. Flowers pedicellate or subsessile; pedicels 1.5 mm long, densely hispidulous. Bracts ovate-lanceolate, acute, 0.75–1.5 mm long, densely hirtellous with some glandular hairs. Calyx 3.5 mm long, cut ⅔ distance, densely glandular-pilose; calyx lobes ovate-oblong, rounded at summit, 2.5 mm long, 1.5–1.8 mm in upper half, ciliate. Petals subovate-oblong, rounded at summit, 5.5 mm long, 2.2 mm wide in upper half, glabrous without, ciliate in lower half, within sparsely appressed-glandular-puberulent near base and along median line; petaliferous scale about equaling or slightly shorter than petal, 3.5 mm long, 1.5 mm wide, densely barbate-villous for most of length on inner face, the outer face glabrous basally, pubescent in upper half, densely appressed-ciliate. Stamens 8; anthers oblong, obtusely apiculate, 1.3–1.4 mm long; filaments 3.8 mm long,

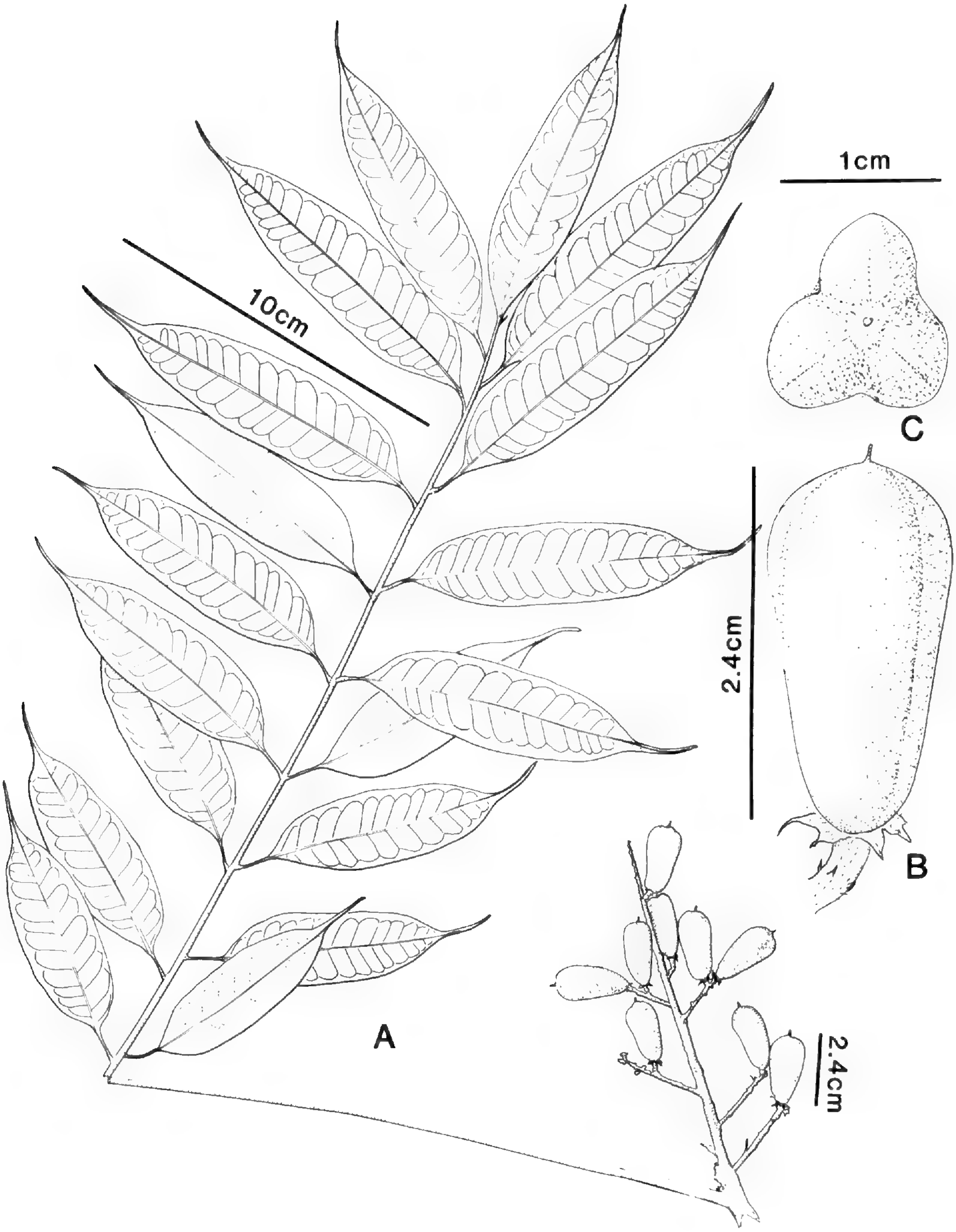

FIGURE 6. Talisia caudata.—*A. Habit of fruiting branch.—B. Fruit, lateral view.—C. Fruit, apical view.*

glabrous. Disk lobulate, 2 mm diam., densely hispid. Fruit not seen.

Paratypes. VENEZUELA. BOLÍVAR: El Paraiso Camp, 53 km NE of caserío Los Rosos, San Félix, 1–10 June 1965, *Luis Marcano-Berti 677* (MER). FRENCH GUIANA. SAUL: Monte La Fumée, 3°37′N, 53°12′W, 200–400 m, 24 Sep. 1982, *Mori et al. 14988* (MO, NY).

This species is apparently most closely related to *Talisia cupularis* Radlk. within the group of species 32–36 of Radlkofer's sect. III "*Eutalisia*" (sect. *Talisia*). It is characterized by calyx lobes densely glandular externally, minutely puberulent rachis with a few gland-tipped hairs, glabrous outer surface of the petals, glabrous filaments, densely hirsutulous disk, and petals glandular on the inner surface. From *T. cupularis* Radlk. it may be differentiated by the glandular-puberulent inner surface of the petals and the strongly glandular pubescent outer surface of the calyx lobes.

Talisia heterodoxa Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Represa Guri, islands 6–

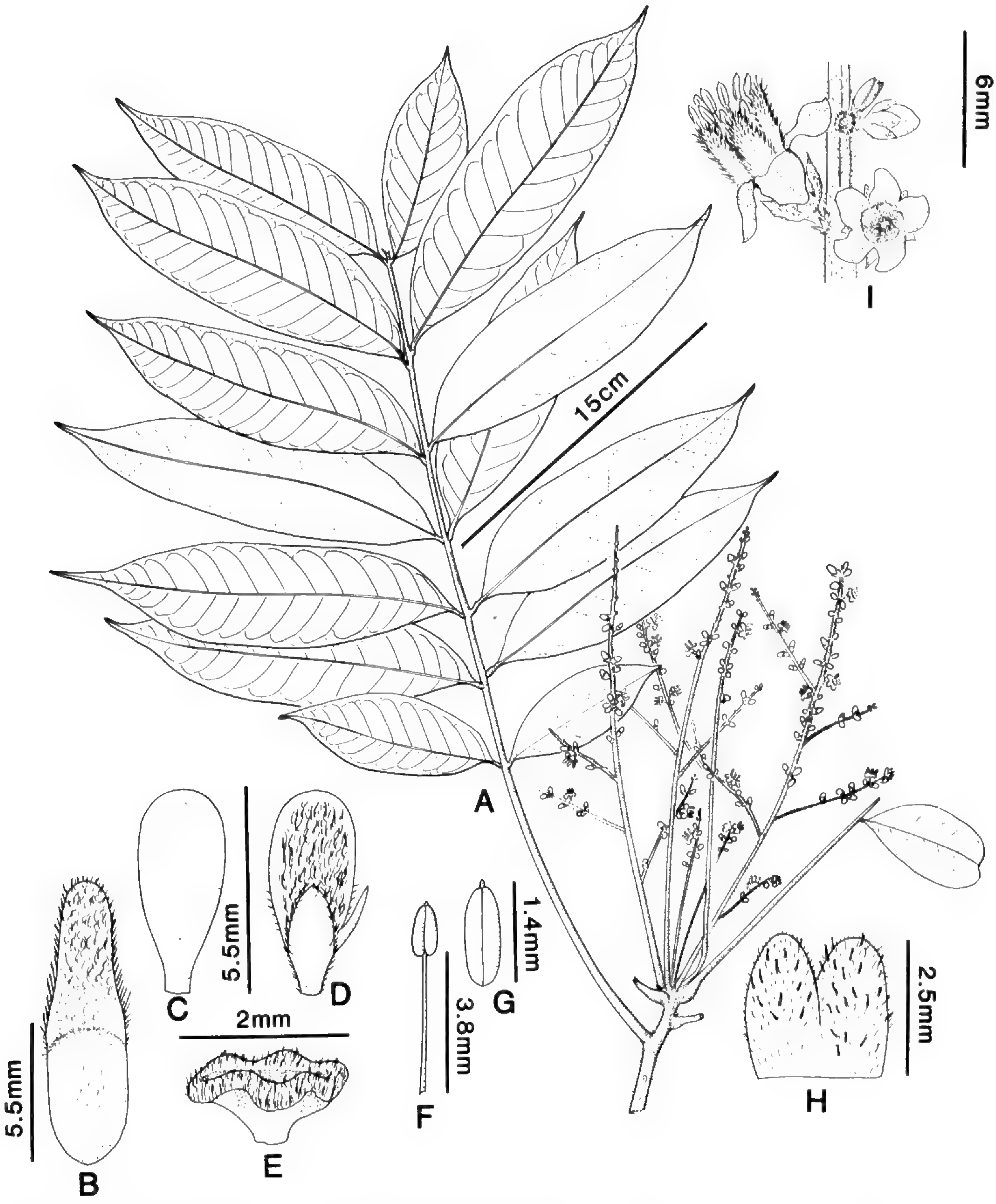

FIGURE 7. Talisia glandulifera.—*A. Habit of flowering branch.—B. Pubescent scale with interior surface of petal reflexed.—C. Exterior view of petal.—D. Interior view of petal.—E. Disk.—F. Stamen.—G. Anther with apiculate connective.—H. Two of the calyx lobes showing glandular hairs, exterior view.—I. Portion of flowering branch.*

18 km S of dam, 7°38'N, 62°58'W, 220–240 m, *Ronald Liesner & Angel González 11151* (holotype, MO; isotype, VEN).

Arbor 10-metralis; foliolis 6–8 oppositis vel suboppositis elliptico-oblongis vel oblanceolato-oblongis apice rotundatis saepe retusis 9–16 cm longis 3.5–6.7 cm latis glabris; petiolulis 5–6 mm longis glabris; calycis lobulis suborbiculari-ovatis dense ciliatis extus puberulis intus adpresso-puberulis; squamis petaliferis extus in quarta parte superiore pubescentibus prope basim glandulosis; staminibus 8, filamentis glabris; disco glabro.

Tree 10 m tall. Leaves 6–8-foliolate. Leaflets opposite, subopposite, or slightly alternate, elliptic-oblong or oblanceolate-oblong, rounded and often retuse at apex, cuneate at base, 9–16 cm long, 3.6–6.7 cm wide, glabrous; lateral nerves slender, slightly ascending at an angle of 25–45°, 12–13 each side, finely prominulous both sides; intermediate nerves finer; tertiary venation finely reticulate both sides, the reticulations more elevated and larger below; rachis of leaf 7–15 cm long, minutely puberulous to glabrous. Petiolule 5–6 mm long, glabrous. Petiole 4–9.5 cm long. Inflorescence terminal, 38 cm long with 7–8 widely spreading, sparingly branched axes, the lower ones 10–16 cm long, 2 mm wide, minutely puberulous with short spreading hairs; peduncle 3–4 cm long. Calyx cut ¾ distance, the lobes suborbicular-ovate, rounded at summit, 2.2 mm long; 1.5–2 mm wide, densely ciliate, puberulous without, within appressed-puberulous ⅔ distance upwards. Petals ovate-oblong, broadly rounded at summit, 4.5 mm long, 2.5 mm wide, glabrous both sides, the margins slightly papillate. Petaliferous scale ligulate, obtuse, 3.5 mm long, 1 mm wide, densely hirsutulous ventrally, pubescent within dorsally in the upper ¼ and pubescent basally, elsewhere glabrous. Stamens 8; anthers 1.5 mm long with a short, triangular, obtuse apical appendage, rounded at base; filaments 3 mm long, glabrous. Disk lobulate, glabrous. Fruit 3–3.5 cm long, 3 cm wide, subglabrous.

Paratype. VENEZUELA. BOLÍVAR: Represa Guri, islands 6–18 km S of dam, 7°38′N, 62°58′W, 220–240 m, *Liesner & Gonzalez 11116* (MO, VEN).

This species is closely related to *Talisia retusa* Cowan but differs in having the interior of the calyx lobe pubescent only in the middle portion rather than densely sericeous throughout and in having the petals glabrous instead of partly or wholly retrorsely ciliate. Moreover, in *T. retusa* the petiolules are mainly shorter, and the leaflets smaller and narrower.

Talisia pentantha Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Canaima, W of Avensa Camp, gallery forest, 500 m, 4 Oct. 1974, *F. Ehrendorfer 74104-23* (holotype, VEN).

Arbor; foliis 10-foliolate; foliolis oppositis, lanceolato-ellipticis apice acutis basi acutis majoribus 13.5–16 cm longis 3.7–4.5 cm latis, infimis 8.5–10.5 cm longis 3.5 cm latis utrinque glabris; nervis lateralibus principalibus utrinque 8–11; inflorescentia 37 cm longa, pedunculo 8 cm longo; floribus pedicellatis; calyce extus sparsim puberula, lobis intus glabris; petalis minute ciliatis aliter glabris; squamis dorsaliter glabris; staminibus 5; antheris linearibus appendiculatis, apice subacuto 1.8 mm longis; disco profunde lobato glabro.

Tree. Leaves 10-foliolate. Leaflets opposite, lanceolate-elliptic, acute at apex, acute at the slightly asymmetric base, mostly 13.5–16 cm long, 3.7–4.5 cm wide, the lowest smaller, 8.5–10.5 cm long, 3.5 cm wide, glabrous both sides, ascending at an angle of 20–25°; tertiary venation inconspicuous. Inflorescence 37 cm long, bearing interrupted short groups of flowers borne on short axes 5–15 mm long; peduncle 8 cm long; rachis ridged, with vertical lines of spreading pilosity on the angles, 2.5 mm diam. Flowers pedicellate, pedicels 1 mm long, densely pilosulous with spreading hairs. Bracts of inflorescence lanceolate, subacute, 0.75 mm long, puberulous. Calyx 3 mm long, cut ⅔ distance; lobes oblong-lanceolate, subacute or subobtuse, 2 mm long, 1 mm wide, sparsely puberulous without, glabrous within, imbricate, densely ciliate. Petals ligulate, obtuse, 4.5 mm long, 1.3 mm wide in late bud, minutely ciliate on the margins, otherwise glabrous; petaliferous scale 3 mm long, dorsally glabrous, densely sericeous ventrally. Stamens 5; anthers linear, appendiculate with a subacute lanceolate apex 0.2 mm long, 1.8 mm long. Disk deeply 5-lobed, glabrous.

The glabrous disk relates this species to *Talisia guianensis* Aubl., which, however, has eight stamens.

Talisia sancarlosiana Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: between San Carlos and Solano, 11–17 Mar. 1970, *Luis Marcano-Berti & P. Alcedo 119-979* (holotype, MER).

Frutex; foliis 17-foliolatis foliolis suboppositis vel alternis, oblongo-lanceolatis apice acuminatis basi subacutis superioribus 30–35 cm longis 8.5–9 cm latis utrinque glabris; nervis lateralibus utrinque 7–9; petiolulis 3–8 mm longis; inflorescentia 13 cm longa 15 cm lata; calycis lobis ovato-oblongis late obtusis extus sparsim pubescentibus intus glabris manifeste ciliatis; petalis lanceolatis late obtusis 5–6 mm longis 1.5–1.8 mm latis extus glabris intus pilis glandulosis praeditis exterioribus ciliatis; squamis petaliferis ligulatis dorsaliter glabris; staminibus 5; filamentis glabris; antheris linearibus 2 mm longis apice obtuse appendiculatis; disco glabro.

Shrub. Leaves 17-foliolate. Leaflets subopposite or alternate, oblong-lanceolate, acuminate at apex, subacute at the base, the upper leaflets larger, 30–35 cm long, 8.5–9 cm wide, the smaller alternate lower ones 19 cm long, 6 cm wide, glabrous both sides; lateral nerves 7–9 each side, elevated below; rachis glabrous; petiolules 3–8 mm long, glabrous; petiole 13–15 cm long, glabrous. Inflorescence paniculate, widely branching, 13 cm long, 15 cm broad, the rachis minutely pubescent in lines. Calyx lobes ovate-oblong, broadly obtuse, 2.3 mm long, 1.5 mm wide, sparsely pubescent without, glabrous within, conspicuously ciliate. Petals lanceolate, broadly obtuse at apex, 5–6 mm long, 1.5–1.8 mm wide below middle, glabrous without, glandular within, the outer ones ciliate. Petaliferous scale ligulate, 2.5 mm long above the glabrous basal 2-mm portion, densely sericeous ventrally, glabrous dorsally. Stamens 5; filaments 2.5 mm long, glabrous; anthers linear, 2 mm long, the obtusely oblong appendage 0.1 mm long, bilobed at base. Disk glabrous. Ovary obovoid, 3 mm long, glabrous; style 3.5 mm long, mainly glabrous, stigmatic in the apical 1.5 mm.

From *Talisia guianensis* Aubl. this species differs in having five stamens, short inflorescence, fewer lateral nerves, and pubescent inflorescence rachis.

TOULICIA

Toulicia anomala Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Río Suapure, Middle Orinoco, along river between Raudal Budare and Raudal Punta Brava (70–80 km from mouth), 110–120 m, 17 Jan. 1956, *J. J. Wurdack & J. V. Monachino 41253* (holotype, MO; isotype, NY).

Frutex vel arbor 2–3-metralis, ramulis glabris; foliis abrupte pinnatis, 6–10-foliolatis, foliolis oppositis vel alternis subsessilibus vel 1–2 mm petiolulatis lanceolatis apice acutis vel acuminatis basi asymmetricis acutis vel obtusis 4–8.5 cm longis 1.5–2.5 cm latis obscure repando-undulatis glabris; petiolis 1.5–4 cm longis 1 mm latis; inflorescentia 5–7 cm longa 2–3.5 cm lata, axibus 8–12 adpresso-pubescentibus 2–17 mm longis 3–8 floris; pedicellis 0.5 mm longis adpresso-pubescentibus; sepalis 4 inaequalibus, exterioribus minoribus suborbicularibus rotundatis 1–1.2 mm longis 1.2–1.5 mm latis extus glabris intus prope basin pubescentibus marginibus ciliatis; petalis 4 esquamatis obovatis 0.8–1 mm longis 0.7–1 mm latis 0.5 mm unguiculatis integris vel 2–3-lobatis, marginibus conspicue longifimbriatis pilis 0.5 mm longis ornatis; staminibus plerumque 6–7, filamentis 2.5 mm longis parte basali 1 mm pilosa; disco regulari leviter lobulato glabro; pistillodio 1 mm longo; pistillo 3.5 mm long 1.5 mm lato, stylis duobus, ovario 2-loculari, ovulo uno in quoque loculo.

Shrub or tree 2–3 m tall, the branches glabrous. Leaves abruptly pinnate, 6–10-foliolate, the leaflets opposite or alternate, subsessile or 1–2 mm petiolulate, chartaceous, lanceolate, acute to acuminate at apex, acute to obtuse at the asymmetrical base, 4–8.5 cm long, 1.5–2.5 cm wide, obscurely repand-undulate, glabrous; lateral nerves 10–12 each side, ascending at an angle of 15–25°, terminating near the margin, there anastomosing; tertiary venation finely reticulate and prominulous on both sides; midrib elevated below, impressed or sulcate above, bordered by a slender, ribbonlike lateral extension 0.25 mm wide on each side; lower leaf surface often with foveolate depressions at the junction of the midrib and lateral nerves accompanied by thickened portions of the lower epidermis. Rachis glabrous, 1 mm wide. Petioles 1.5–4 mm long, 1 mm wide. Inflorescence paniculate, 5–7 cm long, 2–3.5 cm wide, with 8–12 short axes 2–17 mm long, the rachis and axes appressed-pubescent; axes 3–8-flowered, sparsely branched. Peduncle 0.7–3 cm long. Sepals 4, unequal, the outer ones smaller, suborbicular, rounded, 1–1.2 mm long, 1.2–1.5 mm wide, glabrous without, within pilose near the base, long-ciliate on margins. Petals 4, esquamate, unguiculate, obovate, 0.8–1 mm long, 0.7–1 mm wide, the unguiculate portion 0.5 mm long, entire, 2-cleft or 2–3-lobate, densely long-fimbrillate with elongate hairs 0.5 mm long. Stamens usually 6–7; filaments hypogynous, 2.5 mm long, pilose in the basal 1 mm; anthers dorsifixed, suborbicular, 0.5 × 0.5 mm. Disk contiguous but not adnate to the ovary, regular, shallowly lobulate, glabrous, 2 mm across, 0.1–0.2 mm high. Pistillode ovate-elliptic, 1 mm long, 0.8 mm wide. Pistil 3.5 mm long, 1.5 mm wide; styles 2; ovary 2-locular, with 1 ovule in each cell.

This species is anomalous in having 4 sepals, and usually 6–7 stamens. The esquamate petals align it in the genus to section *Aphanolepis* Radlk. I thank Dr. Aaron Goldberg of the Smithsonian Institution for valuable help in critical observations and for comments.

BOMBACACEAE

POCHOTA

In Steyermark & Stevens (1988), the generic name *Pochota* was shown to have priority over *Bombacopsis*, and *Rhodognaphalopsis* A. Robyns was synonymized with *Bombacopsis*. Thus the following taxa are assigned to *Pochota*.

Pochota amazonica (A. Robyns) Steyerm. & W. D. Stevens, Ann. Missouri Bot. Gard. 75: 396–398. 1988.

Bombacopsis amazonica A. Robyns, Bull. Jard. Bot. Etat 33: 186. 1963.
Bombacopsis wurdackii A. Robyns, Mem. N.Y. Bot. Gard. 17(1): 194. 1967.

Bombacopsis amazonica and *B. wurdackii* intergrade and cannot be maintained as two distinct taxa. In his original description of *B. amazonica*, Robyns (1963: 186) stated that the pedicels vary from 3.5 to 9.5 cm long. This description was based on the US holotype. The isotype (*Foldats 3794*) at VEN, however, has pedicels only 2.5–3 cm long. Moreover, the calyx was described from the US holotype as 1–1.2 cm long and 1.6–1.8 cm wide, whereas the VEN isotype has the calyx only 1.1–1.2 cm wide. This disparity in the measurements of the holotype and isotype is manifested again in the measurements of the calyx of *B. wurdackii*, which are described from the MO holotype as 0.6 cm long, whereas the VEN isotype measures 0.8–1 cm.

Additionally, dimensions of leaflet blades (and their apex shapes), petioles, and petiolules overlap and real differences are not discernable. In both taxa the leaflet blades are thick-coriaceous with a prominent midnerve beneath. Both possess a fine reticulate tertiary venation on the lower surface of the leaflets. One of the principal characters employed by Robyns in separating *Bombacopsis wurdackii* from *B. amazonica* was the presence of glands on the receptacle in the former. Removal of the mass of stamens that had previously hidden the receptacle area on the VEN isotype of *B. amazonica* revealed glandular depressions, thus eliminating one of the key separating characters between the two taxa. Robyns differentiated *B. wurdackii* further from *B. amazonica* by the relatively smaller staminal tube of the former, which is described as "circa 5–7 mm long." Examination of the VEN isotype reveals a length closer to 8 mm.

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ROBYNS, A. 1963. Essai de monographie du genre *Bombax* s.l. (Bombacaceae). Bull. Jard. Bot. État 33: 186.

STEYERMARK, J. A. & W. D. STEVENS. 1988. Notes on *Rhodognaphalopsis* and *Bombacopsis* (Bombacaceae) in the Guayanas. Ann. Missouri Bot. Gard. 75: 396–398.

Pochota ewelii Steyermark, sp. nov. TYPE: Brazil. Dept. Amazonas: near Venezuela frontier, camino al Cerro Neblina desde Rio Tucano (afluente del Rio Cauaburi), 1,250 m, 23 Apr. 1964, *J. Ewel 135* (holotype, MY).

Arbor foliis 5-foliolatis, foliolis coriaceis late elliptico-ovatis apice acutis vel obtuse acutis basi obtusis vel rotundatis majoribus 9.5–12.5 cm longis 4.5–7 cm latis supra sparsim lepidotis basi conspicue petiolatis; petiolulis 9–12 cm longis; pedicellis 3 cm longis lepidotis; receptaculo conspicue glanduloso; calyce 10 mm longo 20 mm lato extus lepidoto intus sericeo-tomentoso; petalis linearibus acutis 12–12.5 cm longis 1.8–1.9 cm latis; staminibus ca. 150, 8 cm longis; staminali tubo 13 mm longo basi glabro deinde superne stellato-piloso; stylo 10 cm longo glabro; ovario lepidoto.

Tree with glabrous branches. Leaves 5-foliolate, the leaflets thick coriaceous, broadly elliptic-ovate, acute to obtusely acute at apex, obtuse to rounded at base, the larger 9.5–12.5 cm long, 4.5–7 cm wide, the upper surface sparsely lepidote except the more densely lepidote midrib, the lower surface and midrib strongly lepidote; primary lateral nerves on each side 12–14, impressed below, inconspicuously above, anastomosing 5–8 mm from margin; tertiary venation reticulate and manifestly impressed or subelevated below, inconspicuous above; midrib prominently elevated below, slightly elevated above. Petiole 3.6 cm long, 3 mm thick; petiolules 9–12 mm long. Flowers solitary, axillary. Pedicels 3 cm long, 3 mm wide, moderately lepidote. Receptacle conspicuously glandular. Calyx 10 mm long, 20 mm wide at subtruncate summit, moderately lepidote without, densely sericeous within. Petals linear, acute, 12–12.5 cm long, 1.8–1.9 cm wide, minutely stellate-squamose without, more densely stellate-puberulent within with slightly longer trichomes. Stamens numerous, ca. 150, 8 cm long, with 10 phalanges 1 cm long; staminal tube 13 mm long, glabrous below, moderately stellate-pilose above. Ovary lepidote; style 10 cm long, glabrous.

This taxon differs from *Pochota gracilis* (Robyns) Steyerm. & W. D. Stevens in the pubescent upper part of the staminal tube, broader and shorter calyx, and the thick-coriaceous, longer and broader, conspicuously lepidote leaves. The leaflets resemble in their size and thickness those of *P. amazonica* (Robyns) Steyerm. & W. D. Stevens, which, however, has narrower leaflets less rounded at the base, and shorter petals. The new species is dedicated to Dr. John Ewel, one of the early explorers of Cerro de La Neblina, who reached the summit from the Brazilian side.

Pochota fuscolepidota Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Dept. Atabapo, Cerro Marahuaca, forested slopes 1–2 km N of Sima Camp, 3°40'N, 65°31'W, 1,100 m, 8–9 Mar. 1985, *Ronald Liesner 18452* (holotype, MO; isotype, VEN).

Arbor 5–8-metralis; foliolis 3–5 oblongo-ovatis vel elliptico-oblongis apice acutis basi obtusis vel subacutis 16–22 cm longis 7–10 cm latis supra glabris subtus densissime fusco-ferrugineo-lepidotis, marginibus subrevolutis; nervis lateralibus principalibus utroque latere 12–15 subtus manifeste elevatis; petiolis 5.5–9.5 cm longis; petiolulis 1–

2.5 cm longis; fructu pedicello fructigero 5 cm longo 5 mm lato densissime fusco-lepidoto; calyce fusco-lepidoto; fructu obovoideo apice rotundato densissime fusco-ferrugineo lepidoto 6 cm longo apice 3 cm lato basi 0.7 cm lato.

Tree 5–8 m tall, the young stems densely ferrugineous-fuscous lepidote. Leaflets 3–5, oblong-ovate or elliptic-oblong, acute at apex, obtuse or subacute at base, 16–22 cm long, 7–10 cm wide, glabrous above, densely dark brown–ferruginous below, glabrous above with impressed nerves, densely and thickly covered below by dark brown, ferruginous lepidote scales, the principal lateral nerves 12–15 each side, prominently elevated, anastomosing 7–15 mm from the margin; margins subrevolute; midrib subsulcate above, prominently elevated below. Petioles 5.5–9.5 cm long; petiolules 1–2.5 cm long, densely fuscous lepidote. Flowers not seen. Fruiting pedicels 5 cm long, 5 mm thick, densely fuscous lepidote. Calyx tube in fruit 10 mm long, 17 mm wide, subtruncate at apex, dark lepidote without, densely buff sericeous within. Fruit obovoid, rounded above, 6 cm long, 3 cm wide at summit, 0.7 cm wide at base.

Paratypes. VENEZUELA. T. F. AMAZONAS: Dept. Atabapo, Cerro Marahuaca, Sima Camp, S-central portion of forested slopes along E branch of Caño Negro, 3°43′N, 65°31′W, 1,140 m, 21–24 Feb. 1985, *Steyermark & Holst 130515* (MO, VEN); 9.2 km NE of San Carlos on Solano road, 1°56′N, 67°3′W, 119 m, *Clark 6920* (MO, NY, VEN).

This species is well characterized by the large leaflets that are densely dark brown-ferruginous lepidote beneath, the prominently elevated lateral nerves on the lower leaf surface, and the densely dark brown lepidote fruits.

Pochota gracilis (Robyns) Steyerm. & W. D. Stevens

This species was originally described (Robyns, 1967) from specimens collected on the Río Pacimoni of the Territorio Federal Amazonas of Venezuela at an altitude of 100–140 meters. Subsequent collections manifest variations in the apex and shape of the leaflets, and in the abundance and distribution of scales on the lower leaflet surface. Specimens collected from the eastern portion of the range in Estado Bolívar, Venezuela, have leaflets narrowly obovate or elliptic-obovate with the apex emarginate and rounded-truncate. Additionally, the scales on the lower surface of the leaflets are dark and close together. Specimens having these characteristics all come from localities associated with the sandstone table mountains at altitudes of 400–1,000 meters. In contrast, the collections originating from the Territorio Federal Amazonas all are found at low elevations of 95–140 meters in usually white sand savannas bordering streams of the lowland areas. The leaflets of these lowland populations are narrowly elliptic-oblong or narrowly oblong with broadly obtuse to rounded, rarely emarginate apex, and the scales on the lower surface are more scattered and less conspicuous than those of the Estado Bolívar populations. Since these differences can be segregated in eastern and western geographically separated populations, they may be considered to represent two subspecies as follows.

Pochota gracilis subsp. **gracilis**

Rhodognaphalopsis maguirei A. Robyns, Mem. N.Y. Bot. Gard. 17: 200. 1967.

Leaflets narrowly elliptic-oblong to narrowly oblong, broadly obtuse to rounded at apex, this rarely emarginate; scales on the lower surface of the leaflets small, scattered, rather noticeably separated.

Distribution. T. F. Amazonas, Venezuela, in usually white sand savannas bordering streams at altitudes of 95–140 meters.

Specimens examined. VENEZUELA. T. F. AMAZONAS: Río Pacimoni, 12 km below mouth of Río Yatua, 100–140 m, *Maguire, Wurdack & C. K. Maguire 41653* (holotype, MO; isotype, NY); Caño Caname del medio Río Atabapo, sabanita, 3°40′N, 67°27′W, 100 m, *Huber, Tillett & Davidse 3747* (VEN); bajo Río Ventuari, 10 km al NE de la desembocadura del Caño Marueta, 4°18′N, 66°16′W, 110 m, *Huber 6116* (MO); sabana, 1 km al E del caserío de Guarinuma, 3°37′N, 67°26′W, 95 m, *Huber 3350* (VEN); sabanita, 10 km al NE del Cerro Moriche, middle Río Ventuari, 4°48′N, 66°17′W, 120 m, *Huber 3437* (VEN); white sand savannas, Caño Caname, opposite Cucurital de Caname, 3°40′N, 67°22′W, 95 m, *Davidse, Huber & Tillett 17035* (MO, VEN); along lower Río Sipapo, *Maguire & Politi 27849* (NY).

Pochota gracilis subsp. **bolivarensis** Steyermark, subsp. nov. TYPE: Venezuela. Bolívar: wooded knoll in savanna, Río Kanarakuni, southern base of Cerro Sarisariñama, Meseta de Jaua, 400 m, 17–29 Mar. 1967, *Julian Steyermark 98206* (holotype, VEN; isotype, NY).

Local name. Wanabana (Maquiritare).

A ssp. *gracilis* foliolis anguste obovatis vel elliptico-obovatis apice subtruncato-rotundatis emarginatis, subtus squamis lepidotis conspicuis fuscatis confertis recedit.

Leaflets narrowly obovate to elliptic-obovate, subtruncate-rounded at the emarginate apex; scales on the lower surface conspicuous, darker, and closer together.

Paratypes. VENEZUELA. BOLÍVAR: Cerro Guaiquinima, summit, riverine forest, Salto de Río Szczerbanari (Río Carapo), 5°44'N, 63°41'8"W, central portion, 750 m, *Steyermark, G. & E. Dunsterville 113236* (VEN); Auyan-tepui, 1,100 m, *Tate 1155* (NY, VEN); upper Caura River, Cerro Marajanu, 550 m, *Cardona 2951* (VEN).

Rhodognaphalopsis maguirei A. Robyns was originally described as having a calyx 15 mm long and 7 mm wide, while *R. gracilis* was described with a calyx 12 mm long and 5 mm wide. Yet on the NY isotype of *R. gracilis* the older calyces attain a width of 6–6.5 mm; those in bud are 4–5 mm wide. In the holotypes of both *R. maguirei* and *R. gracilis* the staminal tubes are glabrous. Although the style in *R. maguirei* is described as glabrous and that of *R. gracilis* as sparsely stellate-puberulous at the base, it is doubtful if this last character can be used to separate the two taxa, since in all other respects they are alike. The type collection of *R. maguirei* from the lower Río Sipapo occurs within the general range of *Pochota gracilis* subsp. *gracilis*.

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ROBYNS, A. 1967. *Pochota gracilis. In:* B. Maguire & collaborators, The Botany of the Guayana Highland—Part VII. Mem. N.Y. Bot. Gard. 17: 198.

Pochota liesneri Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Dept. Atabapo, Salto Yureba, Cerro Yureba, lower Ventuari, 4°3'N, 66°1'W, 350 m, 14 Mar. 1985, *Ronald Liesner 18637* (holotype, MO; isotype, VEN). Figure 8.

Arbor 15-metralis; foliis 5–6, foliolis rugulosis elliptico-obovatis apice abrupte acutis basi acutis majoribus 12–26 cm longis 8–11 cm latis supra praecipue per nervos laterales atque costam mediam glandulis fuscis praeditis, subtus molliter pilosis pilis stellatis fuscis 0.5–1 mm longis obtectis; nervis lateralibus principalibus utroque latere 14–20 subtus prominente elevatis supra sulcatis, venulis tertiariis manifeste grosseque reticulatis; petiolis 13–20 cm longis glabris, petiolulis 7–13 mm longis glabris; pedicello 3 cm longo 5–7 mm crasso; calyce 3.5–3.7 cm longo apice 2–2.5 cm lato extus densissime fulvo stellato-tomentoso; petalis 25–31 cm longis 1 cm latis ubique densissime stellato-tomentoso; staminibus numerosis 18–25 cm longis; tubo stamineo 6–7 cm longo parte superiori glabra dimidia parte inferiori 3.5–4.5 cm dense stellulato-tomentoso in 10 phalangibus soluto; stylo 25–30 cm longo inferne dense stellato-villoso superne stellato-tomentoso; ovario conico 17 mm longo conspicue costato, costis dense ferrugineo-squamosis sulcis minute puberulis.

Tree 15 m tall. Leaves 5–6-foliolate, leaflets rugulose, elliptic-obovate, abruptly acute at apex, acute and long decurrent at base, the larger ones 12–26 cm long, 8–11 cm wide, upper surface with dark glandular dots dispersed more commonly along the lateral nerves and midrib, softly pilose below with brown stellate hairs 0.5–1 mm long on both the surface and nerves; principal lateral nerves 14–20 each side; tertiary veinlets prominently grossly reticulate below, subsulcate above. Petioles 13–20 cm long, glabrous; petiolules 7–13 mm long, glabrous. Flowers large, axillary, solitary, opposite on the stem. Pedicels 3 cm long, 5–7 mm thick, densely dark brown stellate-tomentose. Calyx tubular-campanulate, 3.5–3.7 cm long, 2–2.5 cm wide at the subtruncate, scarcely repand apex, densely fulvous stellate-tomentose without, the stellate tomentum with numerous small hairs and a few larger ones, densely buff-sericeous within. Petals tan (fide Liesner), linear, 25–31 cm long, ca. 1 cm wide, on both sides densely stellate-tomentose. Stamens about 50, 18–25 cm long; staminal tube 6–7 cm long, the upper portion glabrous, the lower portion 3.5–4.5 cm long with pale, minute, stellate tomentum, separating above into 10 phalanges 3–4 cm long. Style 25–30 cm long, densely stellate-pilosulous, especially in the lower half. Ovary conic, 17 mm long, 10 mm wide at base, conspicuously 5-costate, the ridges densely ferruginous squamose with minute pale appressed hairs in the sulcations.

This unusual species is at once distinguished by the softly brown long-pilose lower surface of the rugulose leaflets, relatively large flowers with markedly elongated petals and staminal tube, and minutely dense brown-stellate tomentose, elongated calyx tube. The collections of Ronald Liesner have contributed greatly to our knowledge of the rich flora of the Venezuelan Guayana.

Pochota mawarinumae Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Dept. Río Negro, near Cerro de La Neblina Base Camp, Río Mawarinuma, 0°50'N, 66°10'W, 140 m, 2 Mar. 1984, *Ronald Liesner 16355* (holotype, MO; isotype, VEN).

Arbor 15-metralis; foliis 5–7-foliolatis; foliolis coriaceis subtus glaucis argenteis late obovatis apice rotundatis minute mucronatis basi longiattenuatis 20–32 cm longis 8.5–10.5 cm latis subtus minute lepidotis, nervis lateralibus principalibus utroque latere (6–)8–10; petiolis 2.3–3.4 cm longis, petiolulis 1–4 cm longis; pedicellis 1.5–3.5 cm longis dense minuteque fulvo-stellato-puberulo; receptaculo manifeste glanduloso fulvo-stellato-puberulo; calyce breviter campanulato apice truncato 10–13 mm longo 15–20 mm lato extus dense minuteque fulvo-stel-

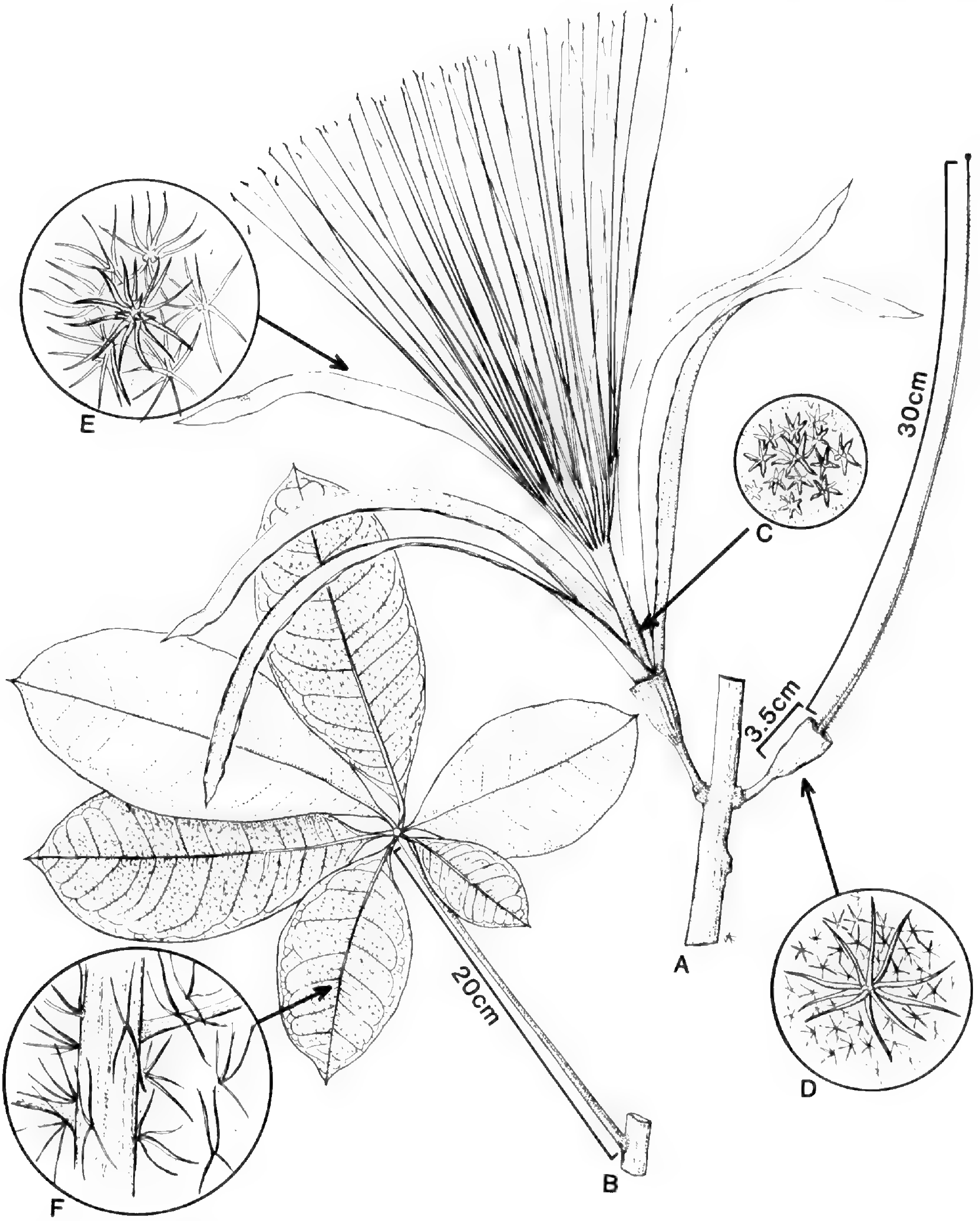

FIGURE 8. Pochota liesneri.—*A. Portion of flowering stem.—B. Single leaf attached to stem.—C. Showing larger and smaller stellulate hairs on staminal tube.—D. Showing one large and numerous smaller stellulate hairs on calyx tube and receptacle.—E. Stellulate pubescence on petal.*

lato-puberulo intus dense sericeo-tomentoso; petalis linearibus 13–16.5 cm longis 1.3–2 cm latis; staminibus 8–13 cm longis, tubo stamineo 20 mm longo dense minuteque cinereo-stellato-puberulo; stylo parte basali 2.5 cm minute stellato-tomentoso aliter glabro; ovario superne dense sericeo tomentoso aliter minute puberulenti; capsula nondum visa.

Tree 15 m tall. Branches robust. Leaves 5–7-foliolate. Leaflets coriaceous, pale or glaucous below, broadly obovate, rounded at the mucronate apex, attenuate to the acute base, the larger ones 20–32 cm long, 8.5–10.5 cm wide, minutely lepidote below. Petioles 2.3–3.4 cm long; petiolules unequal, 1–4 cm long. Principal lateral nerves (6–) 8–10 each side, arcuately ascending, conspicuously elevated on lower surface, subelevated on upper surface, branched, and anastomosing 1–2 cm from margin. Tertiary venation finely reticulate between larger areoles, impressed below. Midribs strongly elevated below. Flowers solitary, axillary. Pedicels in anthesis 1.5–3.5 cm long, densely brown stellate-tomentose. Receptacle conspicuously glandular, brown tomentose, 1 cm long, 1.5 cm wide. Calyx shortly campanulate, 10–13 mm long, 15–20 mm wide, densely brown tomentose without, sericeous within. Petals linear, 13–16.5 cm long, 1.3–2 cm wide, minutely densely tan stellulate-tomentose without, densely and paler stellulate-tomentose within. Stamens 8–13 cm long, numerous, ca. 80 in 10 phalanges 10 mm long; staminal tube 20 mm long, stellate-puberulent most of the length; anthers hippocrepiform-linear, 2.5–3.5 mm long. Style 10.5(immature)–14 cm long, glabrous most of the length, densely pale stellate-tomentose in the basal 2.5 cm. Ovary conic, 5-carinate, densely sericeous-tomentose in the upper ⅓, minutely appressed-puberulent in the lower ⅔ on the ridges and in the sulcations.

Paratype. VENEZUELA. T. F. AMAZONAS: Cerro de La Neblina, same data as type, 6 Mar. 1984, *Liesner 16460* (MO, VEN).

This species is most closely related to *Pochota obovata* (Robyns) Steyerm. & W. D. Stevens but differs in the longer petals, completely stellate-pubescent staminal tube, manifestly glandular receptacle, predominantly larger glabrous portion of the style, and more rounded, merely mucronulate apex of the somewhat narrower leaflets. The Base Camp along the Río Mawarinuma of Cerro de La Neblina served as a working base for the numerous scientists who participated in the recent expedition to that sandstone table mountain, and is the locale of many noteworthy species new to Venezuela or new to science.

Pochota redmondii Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Dept. Atures: stream 0.5–2 km E of Río Coro-Coro, W of Serranía de Yutaje, 3 km N of Yutaje settlement, 5°38′N, 66°30′W, 200 m, 19 Feb. 1987, *Ronald Liesner & Bruce Holst 21248* (holotype, MO; isotype, NY, VEN).

Arbor 6 m; foliolorum laminis late obovatis apice rotundatis 10.5–48 cm longis 5.5–15 cm latis haud manifeste lepidotis subtus haud glaucis; floribus solitariis, pedicellis 1.5–3 cm longis glabris; calyce late campanulato 8–10 mm longo 8–13 mm lato subtruncato; petalis ligulato-spathulatis 8 cm longis superne 9–10 mm latis basi 4.5–5 mm latis; tubo stamineo 13 mm longo 2.5 mm lato lineatis, lineis 5 minute stellato-puberulentibus cum zonis latioribus glabris 0.9–1 mm latis alternantibus munito; ovario dense tomentoso.

Tree 6 m tall, the branches glabrous, the terminal portion 1–1.2 cm diam. Leaves 5-foliolate; leaflets articulate, subcoriaceous, broadly obovate, rounded at apex, sometimes emarginate to abruptly cuspidate, cuneately acute and slightly decurrent at the base, 10.5–48 cm long, 5.5–15 cm wide, glabrous, not manifestly lepidote; lateral nerves 10–16 each side, impressed to subelevated above, subelevated below, anastomosing 5–8 mm from margin; tertiary venation conspicuously reticulate below, the larger areoles enclosing a minute network of elevated veins, less conspicuously reticulate above; petiole 18–22.5 cm long, 4 mm diam., glabrous, terete, not lepidote; petiolules unequal, 1–5 cm long, glabrous, articulate. Flowers solitary; pedicels 1.5–3 cm long, glabrous. Receptacle 5-glandular, glands oval, 1–1.5 mm long. Calyx broadly campanulate, 8–10 mm long, 8–13 mm wide at summit, truncate, densely buff stellate-tomentose without, densely pale sericeous within. Petals cream-tan, subcoriaceous, ligulate-spathulate, subobtuse at apex, 8 cm long, 9–10 mm wide in upper half, 4.5–5 mm wide at base, densely stellate-tomentose within, more densely stellate-tomentellose without. Staminal column 13 mm long, 2.5 mm wide, glabrous above and at base, with 5 vertical minutely stellate-puberulent lines in between alternating with broader glabrous zones 0.9–1 mm wide, branched into 10 phalanges, the main basal branches 10–13 mm long, each main basal branch again branched into several divisions with ultimate 18–24 filaments on each phalange, a total of ca. 240 filaments 4–4.5 cm long. Anthers linear-oblong, 2.5–3 mm long. Stigma 5-lobed, the lobes ovate-lanceolate, 1 mm long, 0.7 mm wide. Ovary suborbicular, densely tomentose.

Paratype. VENEZUELA: T. F. AMAZONAS: Dept. Atures, Río Coro-Coro, river and adjacent forested slopes, W of Serranía de Yutaje, 6–8 km N of Yutaje settlement, 5°41′N, 66°7′30″W, 23 Feb. 1987, 320 m, *Liesner & Holst 21337* (MO, VEN).

This species is related to *Pochota obovata* Robyns but differs in the shorter pedicels, narrower calyx and petals, alternately glabrous and stellate-pubescent vertical zones of the staminal tube, and nonlepidote, nonglaucous lower leaf surface. It is a pleasure to name this species for Parker Redmond, who kindly took care of the logistics for the expedition to the Serranía de Yutaje.

Pochota tepuiensis Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Meseta de Jaua, Cerro Sarisariñama, summit, 4°41′40″N, 64°13′20″W, parte NE, afloramiento arenisco con zanjones en formación de bosque achaparrado y árboles enanos, 1,380 m, 11–12 Feb. 1974, *Julian Steyermark, V. Carreño Espinoza & C. Brewer-Carias 108938* (holotype, VEN).

Arbor 2.5-metralis; foliolis 5 obovatis apice rotundatis emarginatisque basi cuneatim acutis 3–6 cm longis 1.5–2 cm latis subtus cinereis haud lepidotis valde revolutis; nervis lateralibus subhorizontalibus utroque latere 6–10; petiolis 1.3–2 cm longis glabris, petiolulis 2–3 mm longis glabris; pedicellis immaturis 4 mm longis; calycis tubo immaturo 5 mm longo apice 6 mm lato extus dense fusco-tomentoso intus sericeo; receptaculo conspicue glandulari; petalis immaturis dense fusco-sericeis.

Tree 2.5 m tall. Leaves 5-foliolate; leaflets obovate, rounded and emarginate at apex, cuneately acute at base, 3–6 cm long, 1.5–2 cm wide, grayish below, not lepidote below, 1.6–2.7 times longer than broad; lateral nerves subhorizontal, anastomosing near the margin, 6–10 each side, prominently impressed below, slightly sulcate above; tertiary venation prominent and impressed below. Petiole 1.3–2 cm long, 1.5–2.5 mm wide, glabrous, not lepidote; petiolules 2–3 mm long, glabrous, not lepidote. Pedicels (immature) 4 mm long, brown tomentose. Calyx (immature) 5 mm long, 6 mm wide at summit, densely brown stellate-tomentose without, tawny sericeous within. Receptacle (immature) prominently glandular. Petals in early bud densely brown sericeous.

This species is distinguished by the small size of the strongly revolute, apically rounded leaflets; cinereous nonlepidote lower leaf surface; and short petioles, petiolules, pedicels, and calyx. It is known only from the summit of the isolated Cerro Sarisariñama.

ARALIACEAE

SCHEFFLERA

Schefflera simplex Steyermark & Holst, sp. nov. TYPE: Venezuela. T. F. Amazonas: Cerro de La Neblina, ridge line on Venezuela–Brazil border, 1,900–2,100 m, 17 Apr. 1984, *Al Gentry & Bruce Stein 46694* (holotype, MO; isotype, VEN).

Arbor 6-metralis; foliis 4–5-foliolatis, foliolis oblongo-lanceolatis vel anguste elliptico-oblongis apice obtusis vel acutis, basi obtusis vel subobtusis 6.5–12 cm longis 2–5.5 cm latis supra praeter costam mediam minute pubescentem glabris subtus densissime velutinis; nervis lateralibus principalibus utroque latere 15 23; petiolulis inaequalibus 1–3 cm longis minute adpresso-pubescentibus; petiolis 9–14 cm longis minute adpresso-pubescentibus; inflorescentiis 2–4, brevipedunculatis, pedunculis sub anthesi 2.2–5 cm longis densissime tomentosis; inflorescentiis simplicibus solitariis capitatis, capitulis densifloris ca. 20-floris 9–12 mm longis 10–12 mm latis dense tomentosis; floribus sub alabastro sessilibus 2.5 mm longis dense pubescentibus; stylo 3-lobulato.

Tree 6 m tall. Leaves 4–5-foliolate; leaflets coriaceous, oblong-lanceolate to narrowly elliptic-oblong, obtuse to acute at apex, obtuse or subobtuse at base, 6.5–12 cm long, 2–5.5 cm wide, glabrous above except for the minutely pubescent midnerve becoming glabrous except at base, densely velutinous beneath; midrib elevated on both sides; principal lateral nerves 15–23 each side, 4–6 mm apart, extending to margin, subhorizontally spreading to slightly ascending at an angle of 10–20°, subsulcate above; tertiary venation subsulcate, subreticulate above. Petioles 9–14 cm long, 2.5–3 mm wide, minutely appressed-tomentellose. Petiolules unequal, 1–3 cm long, 2–2.5 mm wide, bicarinate above, minutely tomentellose. Peduncles 2–4, in anthesis 2.2–5 cm long, 3–4 mm wide, densely buff-tomentose; inflorescence simple, solitary, capitate, each one terminating a peduncle; heads densely ca. 20-flowered, 9–12 mm long, 10–12 mm wide, densely tomentose. Bracts subtending inflorescence deltoid-ovate, acute, 3–4 mm long, 2.5 mm wide at base, densely gray-buff tomentose without, glabrous within. Flowers in bud 2.5 mm long; calyx teeth acute, unequal, tomentose without, glabrous within; petals 2.5 mm long, 1.7–2 mm wide, ventrally carinate; style 1, shortly 3-lobulate.

This species is unusual among the Venezuelan Guayana taxa of *Schefflera* in having the inflorescence consisting of solitary heads terminating unbranched, short peduncles. *Schefflera globulifera*, a related taxon with capitate flowers, has a long-pedunculate inflorescence with the heads arranged in one or more verticils.

Schefflera yutajensis Steyermark & Holst, sp. nov. TYPE: Venezuela. T. F. Amazonas: Dept. Atures, valley of Río Coro-Coro, west of Serranía de Yutaje, E base of forested mountain 5 km W of river, 5°41′N, 66°9′30″W, 1,100 m, 11 Mar. 1987, *Bruce K. Holst & Ronald L. Liesner 3426* (holotype, MO; isotype, MO).

Arbor 28-metralis; foliis 6–7-foliolatis, foliolis oblongo-lanceolatis vel late elliptico-oblongis apice abrupte breviter caudato-acuminatis, basi obtusis vel subobtusis 15–25 cm longis 7–12 cm latis supra glabris subtus minute densissimeque breviter sericeis; petiolulis inaequalibus 3–9 cm longis minute denseque breviter sericeis; petiolis maturis 49–50 cm longis 6 mm latis dense breviter sericeis; inflorescentiis late racemoso-paniculatis, pedunculis inclusis sub anthesi 15 cm longis 10–12 cm latis sub fructu 22–25 cm longis 14–25 cm latis, axibus lateralibus primariis late divaricatis sub anthesi 5–11 cm longis sub fructu 6–15 cm longis racemose dispositis 15–30 umbellas simplices 10–20-flores gerentibus, omnino ferrugineo-sericeo-tomentellis; axibus umbelliferis sub alabastro 6–9 mm longis 1 mm latis sub fructu 3–6 cm longis; floribus sub alabastro subsessilibus 0.5 mm longis sub fructu 4–6 mm pedicellatis; inflorescentiarum pedunculis rachidibus axibus pedicellisque minute denseque ferrugineo-sericeo-tomentellis; bracteis sub axibus primariis late lanceolato-ovatis acuminatis 3–5 mm longis extus dense ferrugineo-sericeo-tomentellis; stylis sub fructu 5; fructibus globosis in sicco conspicue 5-carinatis maturis 1.5 × 1.5 cm praeter apicem minute pubescentem glabris.

Tree 28 m tall, the bark slightly rough with longitudinal rows of elevated brown lenticels and widely separated petiolar scars. Leaves 6–7-foliolate; leaflets coriaceous, dark green and shining above, bright copper-colored below when young, turning gray in age, oblong-lanceolate to broadly elliptic-oblong, abruptly short caudate-acuminate at apex, obtuse to subobtuse at base, 15–25 cm long, 7–12 cm wide, glabrous above, minutely and densely ferruginous-sericeous beneath. Lateral nerves 8–11 each side, forking 5–16 mm before reaching the margin. Petiolules unequal, 3–9 cm long, minutely and densely ferruginous-sericeous. Petioles of mature leaves 49–50 cm long, 6 mm wide, densely and minutely ferruginous-sericeous. Inflorescence paniculately branched with 10–13 widely spreading primary axes bearing 15–30 racemosely arranged, simple umbels, each of these 10–20-flowered; inflorescence pedunculate, including the peduncle, 15 cm long, 10–12 cm wide in anthesis, 22–25 cm long, 14–25 cm wide in fruit, the peduncular portion 7.5 cm long in anthesis, 14–15 cm long in fruit, all parts of the inflorescence and infructescence densely ferruginous-sericeous. Primary lateral axes alternate to subverticillate, widely spreading, 5–11 cm in bud, 6–15 cm long in fruit; bracts subtending primary axes broadly lance-ovate, acuminate, 3–5 mm long, ferruginous-sericeous, umbelliferous secondary axes 6–9 mm long, 1 mm wide in bud stage, 3–6 cm long, 1–2 mm wide in fruit; umbels simple, 10–20-flowered. Flowers (staminate) subsessile in bud, 4–6 mm-long pedicellate in fruit; calyx in bud shallowly 5-denticulate, the teeth deltoid, acute, densely ferruginous-sericeous. Styles 5, in fruit spreading over the summit and appressed, 1 mm long. Fruit pale green when mature, globose, sharply 5-carinate when dried, 1.5 × 1.5 cm, the apex minutely pubescent, elsewhere glabrous, 5-celled.

Schefflera yutajensis of Territorio Federal Amazonas is allopatric with *S. quinquecarinata* Steyerm. of eastern Venezuelan Guayana, having similar 5-carinately angled fruits with 5 styles and a paniculately branched inflorescence. The former differs by having the primary axes bearing numerous racemosely arranged many-flowered umbels, fruiting pedicels 4–6 (vs. 18–25) mm long, mostly glabrous (vs. tomentose) fruits, obtuse or subobtuse leaflet bases, and oblong-lanceolate or elliptic-oblong leaflets. The species inhabits seasonally dry, evergreen forested slopes of the Serranía Yutaje.

GENTIANACEAE

SYMBOLANTHUS

Symbolanthus huachamacariensis Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Cerro Huachamacari, diagonal ledge, cumbre, 1,700 m, 4 Dec. 1950, *B. Maguire, R. S. Cowan & John J. Wurdack 29859* (holotype, VEN; isotype, NY).

Planta herbacea 1-metralis, caulibus quadrangularibus; foliorum laminis lanceolato-ellipticis apice tenuiter acuminatis basi longiattenuatis cuneatis, majoribus 8.5–14.5 cm longis 3–5 cm latis; nervis lateralibus principalibus utroque latere duobus; petiolis 10–17 mm longis; bracteis sub pedicellis subulatis 9–13 mm longis 1–1.5 mm latis; calyce 30–32 mm longo, lobis lanceolatis acuminatis vel breviter caudatis sub anthesi 25–27 mm longis sub fructu usque ad 35 mm longis basi 10 mm latis; corolla hypocrateriformi 5.2–5.5 cm longa, tubo 3–4 cm longo 8–10 mm lato; lobis late ovato-suborbicularibus acutis 15–17 mm longis prope basin 15 mm latis.

Perennial herb 1 m tall. Stems quadrangular. Leaf blades lance-elliptic, slenderly acuminate at apex, long-attenuate cuneate at base, long-petiolate, the larger 8.5–14.5 cm long, 3–5 cm wide; main lateral nerves 2 on each side, the uppermost pair arising about ⅜ of the length of the leaf blade above its base; midrib and lateral nerves inconspicuous, at most impressed. Petiole 10–17 mm long. Flowers 2, terminal; pedicels slender, 15–35 mm long. Bracts at base of pedicels subulate, caudate at the apex, 9–13 mm long, 1–1.5 mm wide. Calyx 30–32 mm long, the lobes lanceolate, acuminate, or shortly caudate, 25–27 mm long in anthesis, elongating in fruit to 35 mm with caudate tips, 10 mm wide near the base. Corolla magenta-rose red with purple lines in the white throat, salverform, 5.2–5.5 cm long, the tube 3–4 cm long, 8–10 mm wide; lobes broadly ovate-suborbicular, acute, 15–17 mm long, 15 mm wide near the base. Anthers, including the subulate appendage, 7–8 mm long. Ovary lance-ovate, 11 mm long, 5 mm wide, with 5 squamellate truncate scales 1.5 mm long, 1.2 mm wide at base of ovary; style 3 cm long; stigmas ovate, obtuse, 3 mm long.

Paratype. VENEZUELA. T. F. AMAZONAS: Cerro Huachamacari, upper escarpment, 3 Dec. 1950, *Maguire, Cowan & Wurdack 29801* (NY, VEN); above diagonal ledge, Cerro Huachamacari, Camp II to escarpment and return, 1,200–1,500 m, 5 Dec. 1950, *Maguire, Cowan & Wurdack 29879* (NY, VEN).

This species is distinguished in having attenuate-acuminate calyx lobes that attain ⅔–¾ the length of the corolla tube, and in having a relatively small, tubular corolla.

Symbolanthus yaviensis Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Dept. Atures, summit of Cerro Yaví, headwaters of Río Parucito, eastern affluent of Río Manapiare, 5°43′N, 65°52′W, 100 m, 24 Oct. 1986, *Otto Huber 11849* (holotype, MO; isotype, VEN).

Suffrutex 1–1.5-metralis, caule quadrangulari 4–4.5 mm diam. glabro; foliorum laminis elliptico-ovatis apice subacutis basi cuneatim acutis 3–3.8 cm longis 1.2–1.6 cm latis ubique glabris; nervis lateralibus utroque latere duobus subtus elevatis in parte inferiori ¼ laminae exorientibus; petiolis 6–7 mm longis; floribus terminalibus solitariis, pedicello 6 mm longo; calyce 18 mm longo, tubo 4 mm longo 10 mm lato, sepalis late ovatis apiculatis appendice 0.2 mm longa praeditis, 15 mm longis 14 mm latis, marginibus scariosis integerrimis; corolla parte inferiori ⅔ pallido verde, tubo intus roseato, lobis cremosis, late infundibuliformi 6.4 cm long (tubo 4.7 cm longo, parte basali angusta 12 mm longa 5 mm lata; lobis suborbicularibus minute cuspidatis 17 mm longis in medio 21 mm latis); tubo staminali 17 mm longo supra basin corollae 10–11 mm longo inserto, libero 5–6 mm; filamentis paullo inaequalibus 3–3.5 cm longis glabris, squamis late ligulatis apice truncatis late 2-denticulatis 4 × 4 mm; antheris 7 mm longis, appendicibus 0.5 mm longis; stylo 3.8 cm longo; ovario lanceolato-ovoideo 9 mm longo 4.5 mm lato.

Suffruticose plant with subherbaceous stems, 1–1.5 m tall; stems quadrangular, 4–4.5 mm diam., glabrous. Leaves short-petiolate; leaf blades firmly membranous, elliptic-ovate, subacute at apex, cuneately acute at base, 3–3.8 cm long, 1.2–1.6 cm wide, glabrous both sides, decurrent; midrib sulcate above, elevated below; lateral nerves 2 on each side, arising within the lower ⅓, elevated below, obsolescent above; tertiary venation obscure or obsolescent. Petioles 6–7 mm long. Flowers terminal, solitary; pedicel 6 mm long, 3 mm wide. Calyx 18 mm long; tube 4 mm long, 10 mm wide; sepals broadly ovate, apiculate with a minute appendage 0.2 mm long, 15 mm long, 14 mm wide, scarious-margined, entire. Corolla pale green in lower ⅔, roseate within, creamy white on lobes, broadly infundibuliform, 6.4 cm long (tube and limb 4.7 cm long, the constricted basal portion 12 mm long, 5 mm wide; lobes depressed-suborbicular, minutely cuspidate, 17 mm long, 21 mm wide at middle). Staminal tube 17 mm long, attached 10–11 mm above the base of the corolla tube, free 5–6 mm above the attachment; filaments somewhat unequal, the longer ones 3.5 cm long, the shorter 3 cm long, glabrous. Squamellate scales at base of filaments broadly ligulate, 2-denticulate at the truncate summit, 4 mm long, 4 mm wide. Anthers curved, 7 mm long, 1.7–1.8 mm wide, dorsifixed in the lower ⅓, terminating in an attenuate appendage 0.5 mm long. Ovary lance-ovoid, 9 mm long, 4.5 mm wide; squamellate scales at base of ovary truncate, 1.5 mm long; style 3.8 cm long; stigmas ovate, 3 mm long.

From *Symbolanthus sessilis* Steyerm. & Mag. of the Meseta de Jaua (Cerro Sarisariñama) of Estado Bolívar, Venezuela, this species differs in the smaller corolla, calyx, and leaves; shorter pedicels; entire calyx margins; corolla color; and leaf shape. It is distinguished from *S. calygonus* (R. & P.) Griseb. by the smaller corolla, calyx, and leaves; shorter pedicels and petioles; and minutely mucronate corolla lobes.

RUBIACEAE

REMIJIA

Remijia sessilis Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: southwest side of Cerro de La Neblina, hills 2.5 km SW of Base Camp, 00°49′N, 66°10′W, 400–500 m, 20 Feb. 1985, *M. Nee 30967* (holotype, MO; isotypes, NY, VEN). Figure 9.

Frutex 2-metralis, ramulis petiolis foliorum laminisque longihirsutis pilis brunneis praeditis; petiolis alatis inflatis bulliformibus 2.5–3 cm longis; laminis supra rugosis late obovatis apice breviter acuminatis basi conspicue attenuatis 36 cm longis 16 cm latis utrinque longihirsutis pilis 2.5–4.5 mm longis; nervis lateralibus utroque latere 13–14; inflorescentia sessili dense multiflora 2 cm longa 1.5–2 cm lata; floribus sessilibus; calycis tubo tubuloso-campanulato 3.5–5 mm longo 3.5–5 mm lato extus hirsuto, lobis lato triangularibus attenuatis 1–1.2 mm longis hirsuto-ciliatis; hypanthio obconico 5 mm longo 2–2.5 mm lato dense brunneo-hirsuto; capsulis loculicide dehiscentibus, valvis lineari-oblongis 3.2–3.8 cm longis 5–11 mm latis extus hirsutis intus glabris.

Hollow-stemmed shrub 2 m tall, the branches brown-hirsute. Petioles winged, inflated-bladdery, 2.5–3 cm long with long, brown hairs. Leaf blades rugose, especially above, firmly membranous, broadly obovate, shortly acuminate at apex, conspicuously attenuate to the base, 36 cm long, 16 cm wide, brown hirsute with spreading hairs 2.5–4.5 mm long; lateral nerves 13–14 each side. Inflorescence sessile, densely many-flowered, 2 cm

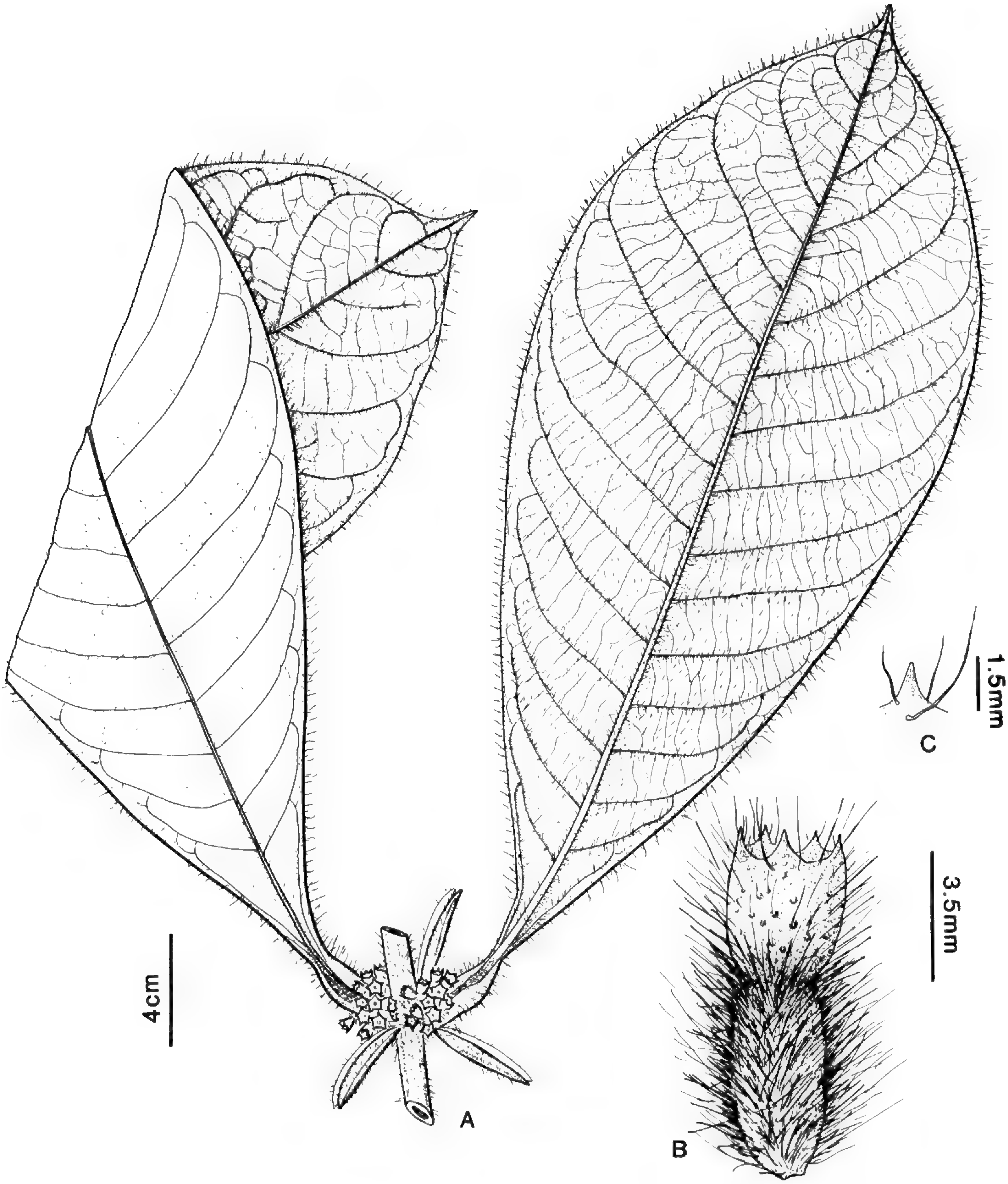

FIGURE 9. Remijia sessilis.—*A. Portion of stem with infructescence.—B. Calyx and hypanthium in post-anthesis.—C. Calyx lobe.*

long, 1.5–2 cm broad; flowers sessile, 12–15 in each cluster between the stem and base of petiole. Calyx tube campanulate, 3.5–5 mm long, 3.5–5 mm wide, brown hirsute with spreading hairs; lobes 5, broadly triangular, attenuate, 1–1.2 mm long, hirsute-ciliate. Hypanthium obconic, 5 mm long, 2–2.5 mm wide, densely brown hirsute. Capsules loculicidally dehiscent, the valves linear-oblong, 3.2–3.8 cm long, 5–11 mm wide, short-hirsute without, glabrous within.

This species is unique in the genus in having a congested, sessile inflorescence. It strongly simulates *Remija physophora* Benth. ex Schum. of the Río Vaupes, Colombia, in the conspicuous, long, brown-hirsute pubescence of the stem, petiolar leaf blades, and calyx, as well as shape of leaves and bladderiform, inflated petioles, but that taxon has conspicuously long-pedunculate, shortly cymosely branched inflorescences with scattered flowers. The calyx lobes of *R. sessilis* are also relatively shorter and more broadly deltoid. Except for the differences in the inflorescence, the two taxa are strikingly similar.

SIMIRA

Simira ignicola Steyermark, sp. nov. TYPE: Venezuela. Bolívar: Dist. Cedeño: shaded canyon on igneous cerro, 1 km S of Quebrada La Flore, affluent of Río Ore, affluent of Río Parguaza, 6°17'N, 67°5'W, 85 m, 9 Sep. 1985, *Steyermark, Holst & Manara 131659* (holotype, MO; isotype, VEN).

Arbor 15-metralis, foliis ovato-ellipticis apice acuminatis base cordatis 17–19 cm longis 11 cm latis subtus dense tomentosis, nervis lateralibus utroque latere 15–16; petiolis 12–16 mm longis dense tomentosis; inflorescentia trichotome cymosa, pedunculo 2–2.3 mm longo sparsim pubescenti; calyce hypanthioque in alabastro 2.5–3 mm longo; lobis calycinis 4 suborbicularibus; corolla in alabastro 3–3.2 mm longa 4-lobata extus minute hirtella.

Tree 15 m tall, the wood dull rose when cut. Leaves subcoriaceous, rugose above, dull green below with elevated nerves. ovate-elliptic, acuminate at apex, cordate at base, 17–19 cm long, 11 cm wide, glabrous above, soft tomentose below, densely so on midrib and lateral nerves; lateral nerves 15–16 each side, slightly ascending at an angle of 25–45°, terminating near the margins without forming any common anastomosing nerve; tertiary veins subsulcate above. Inflorescence terminal, cymosely trichotomous with 3 main axes, 5–5.5 cm long, 5–6.5 cm broad; peduncle 2–2.3 cm long, 3–3.5 mm wide, sparsely pubescent; lower main axes 2.5–3 cm long, densely brown tomentose, the upper main axes 1.5 cm long, densely brown tomentose; ultimate axes 3–6-flowered. Calyx and hypanthium 2.5–3 mm long in bud; calyx 4-lobed, the lobes suborbicular, rounded, ciliate. Hypanthium 2 mm long, 1–1.2 mm wide, subclavate, minutely hirtellous without. Corolla urceolate, 3–3.2 mm long in bud, 4-lobed, minutely hirtellous without. Stamens 4; anthers oblong. Style 2 mm long in bud, glabrous.

The small flowers and the leaf shape resemble *Simira cordifolia*, but the leaf blades and petioles are densely pubescent. From *S. rubescens* the new taxon differs in the pubescence of leaves and floral parts.

REVISED SYNOPSIS OF PANAMANIAN EUPHORBIACEAE[1]

Grady L. Webster[2] *and Michael J. Huft*[3]

ABSTRACT

Collections made in the last two decades have added 9 genera and 42 species to the 35 genera and 100 species included in the Flora of Panama *treatment of the Euphorbiaceae published in 1968. The new taxa and combinations proposed in this paper are* Richeria dressleri *Webster,* Phyllanthus gentryi *Webster,* Tragia correae *Huft,* Dalechampia canescens *Kunth subsp.* friedrichsthalii *(Muell. Arg.) Webster & Huft,* Tetrorchidium costaricense *Huft,* Tetrorchidium microphyllum *Huft,* Croton pachypodus *Webster,* Croton speciosus *Muell. Arg. subsp.* tacarcunensis *Webster,* Croton draco *Cham. & Schldl. subsp.* panamensis *(Klotzsch) Webster,* Croton billbergianus *Muell. Arg. subsp.* pyramidalis *(J. D. Smith) Webster,* Croton santaritensis *Huft,* Sebastiania panamensis *Webster,* Gymnanthes dressleri *Webster, and* Gymnanthes farinosa *(Griseb.) Webster. In addition, new or updated keys are provided where appropriate, as well as descriptions and specimen citations.*

When the treatment of the Euphorbiaceae for the *Flora of Panama* was originally published (Webster & Burch, 1968), it was anticipated that it would prove to be incomplete, but collections made during the past 20 years show that it was even more provisional than we had thought. Not only has *Pausandra* been found as predicted, but no fewer than nine other genera new to Panama: *Adenophaedra, Astrocasia, Croizatia, Drypetes, Gymnanthes, Maprounea, Richeria,* and *Senefeldera,* and an unpublished genus from Cerro Tacarcuna in Darién; this brings the number of native genera to 45. In addition, species new to Panama have been found in a number of genera, including *Acalypha, Alchornea, Cleidion, Croton, Dalechampia, Euphorbia, Hyeronima, Mabea, Manihot, Sapium, Sebastiania, Tetrorchidium,* and *Tragia.* The arrangement of genera within the family has become obsolete since the publication of a new classification (Webster, 1975); there are now five subfamilies recognized, of which four occur in Panama. This new treatment, with the order of the genera now following the revised classification, includes the taxa new to Panama as well as references to recent publications on these taxa.

In order to incorporate all of these additions and changes, the generic key has been revised, and new keys to species have been made for several genera. Citations of specimens are not given for species already included in the original treatment unless they represent new records for provinces or considerable range extensions. Descriptions are provided for most species new to Panama, but in a few cases, if the Panamanian material is not adequate for description or if the species has been recently described elsewhere, a literature reference is given in lieu of a description.

The preparation of this paper has involved us in the study of much extra-Panamanian material and has led to the resolution of a number of ancillary taxonomic and distributional problems. We have not hesitated to discuss these additional items where appropriate. The central position of Panama in the Neotropics certainly renders this account of Panamanian Euphorbiaceae of value to an understanding of the family throughout Central America and northern South America. It seems appropriate, therefore, to include peripheral items that, while not concerning Panamanian species directly, are definitely of relevance.

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[2] *Department of Biology, University of California, Davis, California 95616, U.S.A.; primarily responsible for key to genera and new treatments of genera 1, 3, 4, 5, 6, 8, 9, 23, 27, 32, 34, 36, and 37. The treatment of genus 28,* Cnidoscolus, *is furnished by Dr. Gary Breckon, University of Puerto Rico, Mayagüez.*

[3] *Missouri Botanical Garden. Mailing address: Department of Botany, Field Museum of Natural History, Chicago, Illinois 60605, U.S.A.; primarily responsible for new treatments of genera 2, 12, 13, 14, 17, 19, 20, 26, 30, 33, 39, and 42; the treatments of genera 16, 22, and 35 are the joint responsibility of both authors.*

ANN. MISSOURI BOT. GARD. 75: 1087–1144. 1988.

KEY TO THE GENERA OF EUPHORBIACEAE IN PANAMA

1a. Ovules paired in each cell of the ovary; seeds ecarunculate; milky latex absent; leaves unlobed, entire or obscurely toothed, usually without embedded laminar glands; indumentum simple or lepidote. [Subfamily Phyllanthoideae.]

2a. Petals present.

3a. Petals equalling or longer than the sepals; filaments connate; seeds with copious endosperm ... 1. *Astrocasia*

3b. Petals much shorter than sepals; filaments free or connate; seeds with endosperm scanty or absent.

4a. Monoecious; stipules intrapetiolar; petals glabrous; styles dilated, bifid; columella tapering from base, not apically winged ... 2. *Amanoa*

4b. Dioecious; stipules not projecting between petiole and stem; petals pubescent; styles twice bifid; columella distally expanded into 3 papery wings ... 3. *Croizatia*

2b. Petals absent.

5a. Dioecious; staminate flowers in spikes or racemes, with prominent pistillode.

6a. Indumentum simple; calyx deeply lobed, nearly chorisepalous; anther sacs not pendulous; carpels 2 or 3; fruits capsular; seeds fleshy ... 4. *Richeria*

6b. Indumentum mainly lepidote; calyx distinctly gamosepalous; anther sacs pendulous; carpels 2; fruits drupaceous ... 5. *Hyeronima*

5b. Monoecious or dioecious; staminate flowers in axillary clusters (or if racemose, then branchlets deciduous), lacking a prominent pistillode.

7a. Staminate flowers with a central (intrastaminal) disk; carpels 1 or 2; styles obsolete, the stigmas dilated; fruits drupaceous; seeds solitary in each locule ... 6. *Drypetes*

7b. Staminate flowers without a central disk; carpels 3–5 or more; styles distinctly bifid, the stigmas slender to dilated; fruits mostly dehiscent; seeds 2 per locule.

8a. Carpels 4 or 5 (rarely 3 or 6), irregularly dehiscent; seeds with fleshy bluish outer coat and bony inner coat; staminate flower with annular disk and 4 free stamens; dioecious tree ... 7. *Margaritaria*

8b. Carpels 3 (rarely 2), dehiscent into valves (except in *P. elsiae*); seeds neither fleshy nor bony; stamens 2 or 3 (or if 4, then disk absent); monoecious or dioecious, the habit various ... 8. *Phyllanthus*

1b. Ovules solitary in each cell of the ovary; seeds carunculate or ecarunculate; sap often colored or milky; leaves often dentate and/or palmately veined or lobed, often with laminar or petiolar glands; indumentum various.

9a. Floral bracts not glandular at base (except in *Tetrorchidium*); sepals imbricate to valvate, usually completely covering the anthers in bud; petals present or absent; disk often present; indumentum various; leaves simple to palmately lobed or compound.

10a. Petals absent, or if present then leaves pinnately veined; stalked petiolar glands absent (embedded laminar glands often present); pollen grains mostly 3-colporate; seeds mostly ecarunculate (carunculate only in *Ricinus* and *Pera*); indumentum simple or malpighiaceous (lepidote in *Pera*); flowers in axillary clusters, racemes, or spikes (these sometimes aggregated into panicles). [Subfamily Acalyphoideae.]

11a. Petals present; flowers in racemes; stamens 10; seeds more or less foveolate.

12a. Leaves finely serrate, the lateral veins distinctly parallel; hairs simple or glandular; staminate flowers with pistillode ... 9. *Caperonia*

12b. Leaves entire, the lateral veins not distinctly parallel; hairs malpighiaceous (at least in part); staminate flowers without pistillode ... 10. *Argythamnia*

11b. Petals absent.

13a. Flowers neither sessile nor enclosed in a stalked involucre; seeds not carunculate, black, or shiny.

14a. Flowers not enclosed in a bilabiate involucre formed by 2 palmately veined bracts.

15a. Stamens fasciculate-ramified, anthers numerous; leaves peltate, palmately lobed; inflorescences terminal, paniculate, the pistillate flowers distal; seeds carunculate ... 18. *Ricinus*

15b. Stamens not branched; leaves neither peltate nor palmately lobed; inflorescences otherwise; seeds ecarunculate or the caruncle very small.

16a. Staminate sepals valvate; stamens mostly 3 or more (if 2, connectives not enlarged); latex not distinctly reddish or purplish; fruit less than 8 cm across.

17a. Stinging hairs absent.

18a. Styles free or basally connate; inflorescences unisexual; carpels 2 or 3, not prominently carinate; trees or shrubs, not climbing.

19a. Anthers not vermiform; pistillate bracts not strikingly larger or differently shaped from staminate bracts; styles various, often bifid or unlobed (but not slender and lacerate except in *Adelia*).

20a. Carpels 3; styles bifid (or if unlobed, then seeds fleshy).

21a. Stamens fewer than 10; stipules absent or caducous; dioecious.

22a. Pistillode present in staminate flowers; inflorescences axillary; seed coat fleshy; leaves triplinerved .... 11. *Alchorneopsis*

22b. Pistillode absent; inflorescences terminal (at least in part); seed coat not fleshy; leaves pinnately veined.

23a. Leaves with laminar glands; staminate disk massive, pulviniform; stamens 4–7; styles elongate; seeds over 1 cm long .... 12. *Caryodendron*

23b. Leaves eglandular; staminate disk absent; stamens 3; styles broadly dilated, stigmatiform; seeds less than 1 cm long .... 13. *Adenophaedra*

21b. Stamens more than 10; stipules sometimes persistent.

24a. Stamens less than 30; anther connective not enlarged; pistillate disk present; stipules thin.

25a. Styles 1 or 2 times bifid; pistillate flowers sessile or with short pedicels (less than 5 mm long); leaves with conspicuous foliar glands near base .... 14. *Bernardia*

25b. Styles laciniate; pistillate flowers with long pedicels (at least 20 mm); leaves eglandular .... 15. *Adelia*

24b. Stamens more than 50; anther connective enlarged; pistillate disk absent; stipules indurate .... 17. *Cleidion*

20b. Carpels 2; styles elongate, free, entire; stamens usually 8; seeds tuberculate, ecarunculate, dry; indumentum minutely stellate (at least in part) .... 16. *Alchornea*

19b. Anthers vermiform; styles laciniate; inflorescences spicate; pistillate bracts much larger than the staminate bracts, or else the ovary densely verrucose .... 19. *Acalypha*

18b. Styles connate into a long column; inflorescences bisexual, axillary; carpels 4, prominently carinate; leaves biglandular at base; lianas .... 20. *Plukenetia*

17b. Stinging hairs present; styles unlobed, connate below; disk absent; seeds smooth, ecarunculate.

26a. Anthers with apical tuft of stinging hairs; dioecious shrubs or trees; leaves cuneate at base, glabrescent .... 21. *Acidoton*

26b. Anthers not apically tufted; monoecious twining vines; leaves cordate at base, copiously pubescent with stinging hairs .... 22. *Tragia*

16b. Staminate sepals 4, imbricate (in 2 whorls); stamens 2, the anther connectives greatly enlarged and fleshy; latex purplish or reddish; fruit pomiform, 8–12 cm across .... 24. *Omphalea*

14b. Inflorescences pseudanthial, bisexual; flowers subtended by a bilabiate involucre of 2 palmately veined (or lobed) bracts; styles connate to the stigmas; ovary and fruit armed with irritating hairs; twining or clambering vines with palmately veined, lobed, or dissected leaves .... 23. *Dalechampia*

13b. Flowers sessile in a stalked globose 2-valved involucre; seeds smooth, black, and shiny, carunculate; dioecious trees, indumentum lepidote .... 25. *Pera*

10b. Petals present, at least in staminate flowers, or else calyx petaloid (except in *Tetrorchidium*, with raised foliar glands, and in *Croton punctatus*); leaves often palmately veined or lobed; petioles or leaf bases often with raised or stalked glands; pollen grains with clavate exine, porate or inapurturate (3-colporate in *Tetrorchidium*); seeds carunculate or fleshy (except in *Garcia*); indumentum simple, malpighiaceous, stellate, or lepidote; latex clear, colored, or milky. [Subfamily Crotonoideae.]

27a. Petals absent; stamens 3, the anthers peltate and appearing 4-locellate; pollen grains 3-colporate; seeds fleshy; dioecious shrubs or trees; leaves with stalked petiolar glands and malpighiaceous hairs .... 26. *Tetrorchidium*

27b. Petals present (or else calyx petaloid or indumentum lepidote); stamens 8 or more, the anthers not appearing 4-locellate; pollen grains porate or inaperturate; seeds carunculate (except in *Garcia*), not fleshy.

28a. Petals absent; calyx petaloid; leaves palmately lobed; indumentum simple; latex milky; pollen grains porate; monoecious, the inflorescences terminal, dichasial or paniculate.

29a. Stinging hairs absent; calyx yellowish or greenish to purplish; stamens free; disk central and intrastaminal .... 27. *Manihot*

29b. Stinging hairs present (sometimes very sparse); calyx whitish; stamens connate; disk extrastaminal .... 28. *Cnidoscolus*

28b. Petals present (or else indumentum lepidote); latex not distinctly milky; pollen grains inaperturate.

30a. Anthers more or less erect in bud; indumentum neither stellate nor lepidote.

31a. Calyx of imbricate sepals; stamens not more than 12; staminate petals normally 5; seeds carunculate.

32a. Leaves palmately veined or lobed; stamens mostly 8–12, the filaments connate; monoecious, the inflorescences terminal, dichasial; indumentum simple or of more or less branched glandular setae .... 29. *Jatropha*

32b. Leaves pinnately veined; stamens 3–7, the filaments free; dioecious, the inflorescences axillary, spiciform; indumentum malpighiaceous .... 30. *Pausandra*

31b. Calyx rupturing into valvate segments; stamens 30–100 or more; staminate petals 6–13; seeds ecarunculate; monoecious shrubs or trees; indumentum simple .... 31. *Garcia*

30b. Anthers inflexed in the bud, the stamens 8–50 or more, free; indumentum (at least in part) stellate or lepidote; monoecious (in Panamanian taxa), the inflorescences mostly bisexual, racemose or spicate; seeds carunculate .... 32. *Croton*

9b. Floral bracts biglandular at base; sepals imbricate or reduced; anthers mostly not covered in the bud; petals absent; calyx not petaloid; disk reduced or absent; leaves unlobed; indumentum simple or absent (dendritic in *Mabea*); pollen grains tricolporate, tectate; styles unlobed (or else inflorescence a pseudanthium). [Subfamily Euphorbioideae.]

33a. Inflorescences spicate, racemose, or paniculate, not pseudanthial with a gamophyllous involucre; styles unlobed.

34a. Inflorescences thyrsoid or paniculate; stamens subsessile on an elevated receptacle.

35a. Indumentum dendritic; stylar column elongated; staminate flowers long-pedicellate, 2 or more per node; stamens (in ours) 10 or more .... 33. *Mabea*

35b. Indumentum absent; styles nearly free; staminate flowers subsessile, solitary at each node; stamens (in ours) 5 .... 34. *Senefeldera*

34b. Inflorescences spicate or racemose; stamens with filaments mostly well developed.

36a. Stylar column less than 2.5 cm long, diverging into slender tips; staminate flowers in glomerules, not rupturing bracts at anthesis.

37a. Ovary (2–)3-locular; fruits capsular.

38a. Seeds carunculate, the seed coat dry; petioles eglandular; pistillate sepals free.

39a. Columella without persistent 3-pronged gynobase; milky latex scanty (or perhaps sometimes absent); leaves without raised or stalked glands.

40a. Staminate part of inflorescence elongated; seeds with small caruncle.

41a. Spikes terminal or opposite the leaves; staminate calyx 3-lobed; ovary 6-cornute; fruiting pedicels less than 5 mm long .... 35. *Sebastiania*

41b. Spikes axillary; staminate calyx of 1 segment or absent; ovary smooth; fruiting pedicels more than 10 mm long .... 36. *Gymnanthes*

40b. Staminate part of inflorescence contracted, subglobose; stamens and styles distinctly connate; seeds foveolate, with large calyptrate caruncle .... 37. *Maprounea*

39b. Columella with persistent 3-pronged gynobase; milky latex usually copious; leaves with paired basal cyathiform glands; seeds (in ours) with small caruncle .... 38. *Stillingia*

38b. Seeds ecarunculate, the coat fleshy; petioles usually with a pair of projecting or stipitate glands; calyces distinctly gamophyllous; stamens 2 .... 39. *Sapium*

37b. Ovary 6–9-locular; fruits drupaceous; seeds ecarunculate; pistillate calyx 3-parted .... 40. *Hippomane*

36b. Stylar column at least 2.5 cm long, terminating in a lobed, fleshy disk 2–3 cm wide; staminate flowers aggregated into a fleshy cone; carpels more than 5 .... 41. *Hura*

33b. Inflorescences pseudanthial, i.e., the 5 involucral bracts fused into a cupular cyathium; pistillate flower solitary, terminal, the staminate flowers each with a single stamen, in 5 lateral cymes; styles usually bifid; milky latex copious; seeds (in Panamanian taxa) ecarunculate or minutely carunculate.
  42a. Cyathia more or less radially symmetrical, with glands alternating with bract tips (lobes) around rim; styles free or nearly so.
    43a. Leaves alternate, opposite, or whorled (but if opposite then not inequilateral at base); stipules (in Panamanian taxa) obsolete or glanduliform; veins not chlorenchyma-sheathed; main axis not precociously aborting .... 42. *Euphorbia*
    43b. Leaves opposite, stipulate, inequilateral at base, the veins with chlorenchyma sheaths; main axis aborting just above the cotyledons .... 43. *Chamaesyce*
  42b. Cyathia reddish, bilaterally symmetrical, the involucral glands hidden within the nectar spur; styles connate into a long column .... 44. *Pedilanthus*

ENUMERATION OF TAXA

Subfamily I. PHYLLANTHOIDEAE Asch.

1. *Astrocasia*

Astrocasia Robinson & Millsp., Bot. Jahrb. Syst. 36, Beibl. 80: 19. 1905. TYPE: *Astrocasia phyllanthoides* Robinson & Millsp. = *Astrocasia tremula* (Griseb.) Webster.

Dioecious, glabrous *trees* or shrubs. *Leaves* alternate, petiolate; stipules ribbed, deciduous; blades entire, pinnately veined. *Inflorescences* axillary; flowers in clusters. *Staminate flowers* pedicellate; sepals 5, sometimes unequal; petals 5, longer than the sepals; disk annular; stamens 3 or 5, the filaments connate into a column, anthers extrorse in bud, dehiscing horizontally; pollen grains tricolporate, reticulate; pistillode dilated at tip into a peltate disk capping the staminal column. *Pistillate flowers* long-pedicellate; sepals 5, articulated, deciduous; petals 5, longer than sepals; disk cupuliform, surrounding the ovary; ovary of 3 or 5 carpels; ovules 2 per locule, anatropous; styles free, bifid. *Fruits* capsular; columella slender, persistent; seeds 1 or 2 per locule, ecarunculate; seed coat dry, thin, smooth; raphe conspicuous; endosperm copious; embryo straight; cotyledons thin, flat, much longer and broader than the radicle.

This neotropical genus of four species was not reported from Panama in the original treatment. *Astrocasia* is one of the more primitive genera of Euphorbiaceae and has its closest relatives in Africa and Madagascar (*Heywoodia* Sim, *Wielandia* Baillon).

1.1. Astrocasia tremula (Griseb.) Webster, J. Arnold Arbor. 39: 208. 1958. *Phyllanthus tremulus* Griseb., Fl. Brit. W.I. 34. 1859. TYPE: Jamaica: *Purdie, Wullschlaegel* (syntypes, K).

Astrocasia phyllanthoides Robinson & Millsp., Bot. Jahrb. Syst. 36, Beibl. 80: 19. 1095. TYPE: Mexico. Yucatán: Mérida, *Seler 3943* (holotype, F).

Shrub or tree 2–10 m high; branches terete or obscurely angled, pale; foliage deciduous. *Leaves* with slender petioles 2–6 cm long; stipules lanceolate, chartaceous, 4–6 mm long; blades chartaceous, ovate, acute or obtuse at tip, broadly cuneate at base, 5–12 cm long, 3–7.5 cm broad; major veins 5–8 on a side, ascending, brochidodromous; veinlets prominulous beneath; margins narrowly revolute. *Flower clusters* axillary, staminate and pistillate on separate plants (or on separate branches of the same plant). *Staminate flow-*

ers with pedicels 8–15 mm long; sepals broadly elliptic to obovate, entire, 1.2–1.5 mm long, 1.2–1.8 mm broad; petals elliptic-lanceolate, 2.4–2.7 mm long, 0.8–1.1 mm broad; disk cupuliform, fluted, 0.4–0.5 mm high, 0.9–1 mm broad; androecium 0.7–0.9 mm across; stamens 5; anthers 0.4 mm across; pistillode head circular, 0.5–0.6 mm across. *Pistillate flowers* with slender pedicels becoming 2.5–5.5 cm long; sepals suborbicular to elliptic, 2–2.2 mm long, 1.8–2 mm broad; disk cupuliform, its margin undulate, ca. 1 mm high and 2 mm broad; styles thickened, 0.6 mm long, bifid, the tips clavate. *Fruits* oblate, 3-angled, reticulate-venose, cocci ribbed on back; columella cylindric, 3.2–3.5 mm long; seeds plano-convex, smooth, yellowish, 4.4–5 mm long, 3.8–4 mm broad.

The recent discovery of *Astrocasia* in Panama is one of the most surprising additions to the flora, particularly since it was found near Madden Dam in what is surely one of the most heavily botanized locations in the country. *Astrocasia tremula* has a broad but greatly disjunct distribution from Mexico and Jamaica to Colombia, Venezuela, and Brazil. The Madden Dam locality, however, is the only known station in Central America south of Belize and Guatemala.

Specimens examined. PANAMA. COLÓN: forests along shores of Madden Lake, near Madden Dam, 50 m, *Knapp 1299* (DAV, F, MO), *Witherspoon 8805* (DAV, MO); 6 km N of Chilibre, along Madden Lake, *Knapp 2715* (MO).

2. *Amanoa*

Amanoa Aublet, Hist. Pl. Guiane 256. 1775. TYPE: *Amanoa guianensis* Aublet.

2.1. Amanoa guianensis Aublet, Hist. Pl. Guiane 256. 1775. TYPE: French Guiana: *Aublet* (possibly at BM, not seen).

Additional specimens examined. PANAMA. COLÓN: along Río Chagres and associated tidal channels off side road 9 km from Fort Lorenzo turnoff, 9°40′N, 80°03′W, sea level, *Knapp 1329* (F, MO). SAN BLAS: along Río Armilo, W of Puerto Obaldía, ca. 8°40′N, 77°25′W, sea level, *McPherson 6944* (F, MO).

3. *Croizatia*

Croizatia Steyerm., Fieldiana, Bot. 28: 308, fig. 57. 1952. TYPE: *Croizatia neotropica* Steyerm.

Dioecious *trees* or shrubs; indumentum simple. *Leaves* alternate, petiolate; stipules persistent or deciduous; blades entire, pinnately veined, without embedded glands. *Flowers* in axillary clusters. *Staminate flowers* pedicellate; sepals 5, imbricate; petals 5, much shorter than sepals, pubescent; disk annular; stamens 5, free or connate, the anthers ± introrse; pollen grains 3-colporate, the sexine echinate; pistillode 3-fid. *Pistillate flowers* pedicellate; sepals 5, imbricate; petals 5, much shorter than sepals, pubescent; disk annular; ovary pubescent; styles free, twice bifid; ovules paired in each locule, hemitropous. *Fruits* capsular; columella distally expanded into 3 broad papery wings; seeds paired or solitary in each locule, smooth, not fleshy, ecarunculate; endosperm absent; cotyledons greenish, contortuplicate, much broader than and about as long as the radicle.

LITERATURE

WEBSTER, G. L., L. GILLESPIE & J. STEYERMARK. 1987. Systematics of *Croizatia* (Euphorbiaceae). Syst. Bot. 12: 1–8.

The affinities of this small neotropical genus of three species have remained questionable because of fragmentary material. The recent discovery of staminate flowers of *Croizatia naiguatensis* Steyerm. (Webster et al., 1987) has not made it possible to determine the affinities of the genus more closely. In the protologue to the original description of *Croizatia*, Steyermark proposed a relationship to the Old World genus *Actephila* Blume on the basis of a suggestion by Dr. Leon Croizat. That suggestion seems very perceptive, as there is a clear resemblance to that genus in details of habit, flower, and fruit. On the basis of gross morphology, *Croizatia* can be maintained as a genus distinct from *Actephila*, especially by virtue of its pubescent petals and ovary and its twice-bifid styles. In this latter character it is similar to the African *Pentabrachium* Muell. Arg.; however, in the African genus the seeds have abundant endosperm and the embryo is not contorted as in *Croizatia*. The echinate pollen grains of *Croizatia* are very different from those of *Actephila* or *Pentabrachium* and indicate a possible closer affinity to genera in subfamily Oldfieldioideae.

3.1. Croizatia panamensis Webster, Syst. Bot. 12: 7. 1987. TYPE: Panama. Panamá: primary forest along road from El Llano to Cartí-Tupile, 300–500 m, 30 Mar. 1973, *Liesner 1279* (holotype, MO; isotype, DAV).

Shrub or small tree 1–6 m high, usually with a single main stem. *Leaves* with petioles 0.5–1 cm long, 3–4 mm thick; stipules ± persistent, oblong-lanceolate, acuminate, ribbed, sericeous, 10–20 mm long, 6–7 mm broad; blades chartaceous, glabrous or sparsely strigose-hispidulous beneath, obovate, abruptly short-acuminate, basally attenuate, 22–47 cm long, 5–15 cm broad, with ca. 15 arcuate-ascending lateral nerves connected by intramarginal loops, the veins and (to some extent) veinlets prominulous beneath. *Staminate flowers* with sparsely pubescent pedicels 3–4 mm long; sepals (4–)5, elliptic, entire, 1.7–2.5 mm long, 1–1.5 mm broad; stamens 5, the filaments 2–4 mm long, connate at the base for 0.5–1.5 mm, the column long-pubescent; anthers 0.6–0.8 mm long; pistillode 1.5–2.5 mm long. *Pistillate flowers* with pubescent pedicels ca. 1.5 cm long, becoming 2.5–3.5 cm long in fruit; sepals 5, elliptic-lanceolate, ± acute, 8–12 mm long, 3–4 mm broad, hispidulous without, persistent and becoming reflexed in fruit; ovary 3.5–5 mm diam., densely hirsutulous; styles 3, 3–4 mm long, connate basally into a column ca. 1 mm high, three times bifid. *Fruit* capsular, 10–15 mm broad; columella ca. 8–9 mm high, 10–11 mm broad; seeds trigonous, smooth, brownish, 7.2–10 mm long, 5.3–6.5 mm broad.

Rainforests, Panama and Colombia.

This more complete species description of *Croizatia panamensis* has been made possible by recently collected flowering specimens and data provided by Dr. Gordon McPherson. It is now apparent that *C. panamensis* is clearly different from *C. naiguatensis* in floral characters: staminate flowers with stamens connate in *C. panamensis* (free in *C. naiguatensis*), staminate petals more long-ciliate and styles more divided in *C. panamensis*. Since flowering material of *C. neotropica* is still unknown, it remains difficult to assess its relationships with *C. panamensis*.

Additional specimens examined. PANAMA. SAN BLAS: near road from El Llano to Cartí, beyond Nusagandí, along divide trail to east, 9°15′N, 79°00′W, ca. 300 m (fr), *McPherson 11037* (DAV, MO), (fl, pistillate), *11040* (DAV, MO), (fl, staminate), *11041* (DAV, MO).

4. *Richeria*

Richeria Vahl, Eclog. Amer. 1: 30, tab. 4. 1797. TYPE: *Richeria grandis* Vahl.

Trees or shrubs; dioecious; indumentum simple or absent. *Leaves* alternate, petiolate; stipules deciduous; blades entire or distantly crenulate, pinnately veined, sometimes with basal laminar glands. *Inflorescences* axillary, racemose or spicate; staminate flowers several per bract in sessile or pedunculate glomerules; pistillate bracts subtending solitary flowers; flowers apetalous. *Staminate flowers* sessile; calyx 3–5-lobed, the lobes imbricate; disk segments 3–5; stamens 3–6, free; filaments exserted from calyx; anthers introrse, ± versatile, dehiscing longitudinally; connective not enlarged; pollen grains prolate, 3-colporate, semitectate, reticulate; pistillode present. *Pistillate flowers* pedicellate; calyx 3–5-lobed, the lobes imbricate; disk cupulate; ovary 3-locular, glabrous or pubescent; styles short, bifid; ovules 2 per locule, anatropous. *Fruits* capsular (somewhat fleshy and tardily dehiscent); columella slender, upwardly dilated, with papery wings; seeds solitary in each locule, ecarunculate, the outer testa fleshy; endosperm present; cotyledons broad, plane, basally cordate.

A neotropical genus of five closely related species, previously unreported from mainland North America. *Richeria* appears to be most closely related to the African genus *Maesobotrya* Benth. and to *Aporusa* Blume of southeastern Asia and Malaysia. The circumscription of the genus adopted here differs from that of Mueller (1866) and Jablonski (1967), since section *Podocalyx* (Klotzsch) Muell. Arg. (based on *Richeria loranthoides* (Klotzsch) Muell. Arg.) should be segregated as the monotypic genus *Podocalyx* Klotzsch, which, in fact (as indicated by the spinose pollen), belongs in the subfamily Oldfieldioideae rather than the Phyllanthoideae.

There are two species of *Richeria* in Panama, neither previously reported.

KEY TO THE SPECIES OF *RICHERIA* IN PANAMA

1a. Carpels 3; capsules glabrous; styles suppressed (stigmas sessile); leaves obtuse or rounded at tip, glabrous or nearly so; stipules less than 1 cm long, lanceolate .... 1. *R. obovata*
1b. Carpels 2; capsules distinctly puberulent; styles ca. 1.5 mm long; leaves acuminate at tip, pubescent abaxially; stipules over 1 cm long, foliaceous .... 2. *R. dressleri*

4.1. Richeria obovata (Muell. Arg.) Pax & K. Hoffm., Pflanzenreich IV. 147. XV(Heft 81): 29. 1922; Jablonski, Mem. New York Bot. Gard. 17(1): 126. 1967. *Richeria grandis β obovata* Muell. Arg. in DC., Prodr. 15(2): 468. 1866; Fl. Bras. 11(2): 16. 1873. TYPE: "Brazil," Rio Casiquiari, *Spruce 3526* (not seen).

A species description is not offered here, since the Panamanian specimens are incomplete, and it is not possible to expand the description of Pax & Hoffmann. In the absence of flowers, it is not entirely certain that the Panamanian specimens belong with those cited by Jablonski from montane rain forests in the states of Bolívar and Amazonas, Venezuela.

Specimens examined. PANAMA. PANAMÁ: ca. 5–6 mi. N of El Llano, 1,300 ft., *Gentry 5796* (GH, MO, SCZ). VERAGUAS: cloud forest, Cerro Tute, NW of Santa Fe, *Mori & Kallunki 5264* (DAV, MO).

4.2. Richeria dressleri Webster, sp. nov. TYPE: Panama. Panamá: Santa Rita Ridge, road to Estación Calibrar el Agua Clara, 9°22′N, 79°42–45′W, 1,000–1,500 ft., 26 June 1971, *Webster & Dressler 16744* (holotype, DAV; isotype, MO).

Species haec ab congeneribus differt stylis elongatis, capsulis 2-locularis; foliis acuminatis eglandulosis, integris, subtus puberulis; ovario sericeo-hispido.

Tree to 15 m high, 3.5 dm thick; twigs terete, mostly densely appressed-hirtellous when young, eventually glabrate; foliage evergreen. *Leaves* with hirtellous petioles 1.5–5 cm long; stipules lanceolate, 1–1.5 cm long, densely sericeous, caducous; blades chartaceous, obovate, mostly abruptly acuminate, at base narrowly cuneate and decurrent on the petiole, 10–30 cm long, 4–14 cm broad; major veins mostly 10–12 on a side, straight, brochidodromous, the midrib saliently raised beneath; secondaries archingly and irregularly scalariform; ultimate veinlets fine, scarcely prominulous; surface of blade above glabrous and flecked or pitted with minute colored spots, beneath bronze-colored and densely to sparsely hirtellous (becoming glabrate in age except along midrib and larger veins); margins entire, plane or recurved. *Inflorescences* spiciform; staminate spikes 1.5–5.5 cm long, pistillate spikes 1.5–7 cm long; axes densely hirsutulous without. *Staminate flowers* sessile; calyx deeply 4–5-lobed, densely hirsutulous without; calyx lobes oblong to obovate or suborbicular, unequal, the larger ones 1.4–1.8 mm long, 1.2–1.5 mm broad, the smaller ones 1.2–1.5 mm long, ca. 1 mm broad; disk segments 5, erect, cylindric-prismatic, apically hirtellous, 0.2–0.3 mm high; stamens 5(–6); filaments free, 2–3 mm long; anthers ellipsoid, ca. 0.4 mm long; pistillode cylindrical, densely hirtellous, 1–1.2 mm high, 0.6–0.9 mm broad. *Pistillate flowers* subsessile; sepals mostly 4(–5), elliptic, tomentulose outside, sericeous within, 1.5–2 mm long, 0.8–1.3 mm broad; disk entire, adnate, ciliate-margined, ca. 1.5 mm across; ovary of 2 carpels, sericeous; styles stout, 2- or 3-fid, 1.5–1.7 mm long. *Capsules* ellipsoid, reddish, smoothish (not venose), ca. 10–13 mm long, 6–9 mm broad; columella flattened, papery-winged, 11–12 mm long; seeds somewhat asymmetrically ovoid-ellipsoid, tapering to an obtuse beak, with reddish, fleshy ribbed-striate exotesta, 8.3–9 mm long, 4.8–5.3 mm broad.

This species is sharply characterized within *Richeria* by its 2-carpellate densely sericeous gynoecium with distinct styles; the staminate flowers are similar to those of *Richeria grandis* but differ in the more slender cylindrical pistillode. The acuminate leaves often copiously hirtellous beneath and the large foliaceous stipules also appear distinctive. The collections from Costa Rica are morphologically divergent but may tentatively be grouped with the Panamanian plants. It seems appropriate to name this species in honor of the co-collector of the type specimen, Dr. Robert Dressler, formerly of the Smithsonian Tropical Research Institute, since he has made a significant contribution to our knowledge of Mesoamerican Euphorbiaceae through his many collections and his monographs of *Pedilanthus* (Dressler, 1957) and *Euphorbia* subgenus *Poinsettia* (Dressler, 1961).

Additional specimens examined. COSTA RICA. HEREDIA: Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, 100–450 m, *Grayum & Perry 1447* (F), *Hammel 8689, 8833* (F), *Jacobs 2179* (F). PUNTARENAS: on road to radio and telecommunications tower 6 km N of Golfito, 300–400 m, *Utley & Utley 4902* (F). PANAMA. COCLÉ: near El Valle de Antón, ca. 8°37′N, 80°07′W, ca. 550 m, *McPherson 7616* (F). COLÓN: Santa Rita lumber road, 15 km E of Colón, *Dressler & Williams 3968* (MO). PANAMÁ: rainforest along El Llano–Cartí road, 4.6–8.2 mi. N of Panamerican Highway, 350–450 m, *D'Arcy 11496* (MO, dupl. at SCZ seen by M. Huft), *Gentry 5076* (MO), *Hammel 7350* (MO), *Knapp 5929* (DAV, F, MO), *McPherson 9959* (F, MO), *Mori & Kallunki 5607* (DAV, MO). SAN BLAS: Cerro Brewster, 9°18′N, 79°16′W, 850 m, *de Nevers et al. 5414* (F).

5. *Hyeronima*

Hyeronima Allemão, Pl. Novas Brasil 1. 1848. TYPE: *Hyeronima alchorneoides* Allemão.

A number of collections made in cloud forests in Panama indicate that there is at least one additional taxon of *Hyeronima* besides the lowland *H. laxiflora*. However, as often happens, these additional specimens have increased the difficulties taxonomically; the following revised treatment is highly tentative pending revisionary studies of this poorly understood genus.

KEY TO THE SPECIES OF *HYERONIMA* IN PANAMA

1a. Stamens 4; pistillode slender, bifid, 0.7–0.8 mm high; leaves sparsely lepidote; blades mostly 10–30 cm long with petioles of 3–9 cm; stipules

5–15 mm long; ovary densely lepidote; endocarp of fruit not over 3.5 mm long .... 1. *H. laxiflora*

1b. Stamens 5; pistillode stout, not bifid, to 0.5 mm high; leaves sparsely to densely lepidote beneath; blades mostly 5–10 cm long with petioles of 1–2 cm; stipules apparently obsolete; ovary glabrous to lepidote; endocarp of fruit at least 4 mm long .... 2. *H. oblonga*

5.1 Hyeronima laxiflora (Tul.) Muell. Arg., Linnaea 34: 67. 1865. *Stilaginella laxiflora* Tul., Ann. Sci. Nat. Bot. III, 15: 244. 1851. TYPE: Guyana: "British Guiana," *Schomburgk 879, Hostmann 391* (syntypes, P).

The specimens originally cited under this name were correctly referred to *H. laxiflora*, which is apparently widespread in lowland rain forests in northern South America. All of the lowland populations of *Hyeronima* in Panama belong to this species.

5.2 Hyeronima oblonga (Tul.) Muell. Arg., Linnaea 34: 66. 1865; in DC., Prodr. 15(2): 271. 1866. *Stilaginella oblonga* Tul., Ann. Sci. Nat. Bot. III, 15: 248. 1851. TYPE: Guyana: "British Guyana," *Schomburgk 805* (P, not seen).

Stilaginella benthamii Tul., Ann. Sci. Nat. Bot. III, 15: 247. 1851. *H. oblonga* (Tul.) Muell. Arg. var. *benthamii* (Tul.) Muell. Arg., Linnaea 34: 66. 1865. SYNTYPES: Mexico. Oaxaca: *Hartweg 513* (P), *Galeotti 7240* (P).

Hieronyma guatemalensis J. D. Smith, Bot. Gaz. (Crawfordsville) 54: 241. 1912. TYPE: Guatemala. Alta Verapaz: *Tuerckheim 423, II 2228* (not seen).

Tree to 10 m high; young twigs angled, densely lepidote (scales ca. 0.15–0.25 mm across). *Leaves* with petioles mostly 10–15 mm long; stipules apparently absent; blades mostly obovate, abruptly cuspidate or short-acuminate, cuneate at base, generally 4–8 cm long, 2.5–5 cm broad; major veins ca. 5–7 on a side, divergent, straight, brochidodromous; midrib and veins raised beneath and ± hirsutulous, the veins and veinlets distinctly prominulous above (upper surface scabrous to the touch); lepidote scales on upper surface scattered to absent, ca. 0.1–0.2 mm across, with reddish center, beneath sparse to dense and overlapping, ca. 0.2–0.25 mm across, with pale center (lower leaf surface much paler than upper). *Panicles* densely lepidote with whitish scales; lateral axes mostly 2–4, the staminate ones 5–10 cm long, the pistillate ones ca. 1.5–2.5 cm long; bracts densely lepidote, acute, ca. 0.7–1 mm long. *Staminate flowers* with rigid stout pedicels ca. 0.4–1.2 mm long; calyx cupulate, shallowly 5-lobed, 1–1.4 mm high, densely lepidote; disk massive, 0.6–0.8 mm high, densely lepidote on top. *Pistillate flowers* subsessile (pedicels equaling or shorter than the bracts); calyx cupulate, shallowly 5-lobed, densely lepidote, 1–1.3 mm high; disk cupulate, subentire, glabrous, ca. 0.4–0.5 mm high; ovary ovoid, ca. 1.5 mm high, glabrous or nearly so; stigmas punctiform. *Fruits* ellipsoid, acute at both ends, coarsely bullate-rugose, 5–6 mm long (endocarp 4–5.5 mm long).

Montane rainforests, Guatemala to Panama and South America.

With some reluctance we are referring all of the high-elevation (cloud forest) populations of *Hyeronima* in Panama to a single species. There is a striking amount of variation in pubescence, and the literature might lead one to recognize two, three, or even more species. Plants with densely lepidote leaves, pale inflorescence axes, and the ovary glabrous or nearly so could be referred to *H. scabrida* (Tul.) Muell. Arg., and plants with sparsely lepidote leaves and densely lepidote ovary to *H. oblonga* s. str. However, specimens from Darién in particular have the pale inflorescence axes of *H. scabrida* combined with the sparsely lepidote leaves of *H. oblonga*. Both "species" occur in the vicinity of El Valle. Plants from the vicinity of Cerro Campana, divergent in having densely lepidote leaves (with prominulous venation above) and larger flowers, appear to match the descriptions of *H. oblonga* var. *benthamii* (Tul.) Muell. Arg. However, it is not clear whether that variety can be satisfactorily delimited from other populations. Only critical field studies can establish whether the broad delimitation of *H. oblonga* adopted here is correct.

Representative specimens examined. PANAMA. BOCAS DEL TORO: between Criollo and Quebrada Higuerón on Chiriquí Trail, *Kirkbride & Duke 783* (MO). CHIRIQUÍ: Cerro Hornitos, ca. 40 km NW of Gualaca, 2,238 m, *Mori & Bolten 7505, 7514* (DAV, MO); Cerro Pate Macho, 4 km NE of Boquete, *Sytsma et al. 4868* (MO). COCLÉ: La Mesa, 2.5 km N of El Valle, 850 m, *Mori et al. 6610* (DAV, MO); hill 3 km E of El Valle, 2,500 ft., *Hammel 4776* (MO); swampy area 5 mi. from El Valle, *Gentry & Dwyer 3622* (DAV, MO); foothills of Cerro Pilón, *Duke & Correa 14675* (MO). DARIÉN: Cerro Mali, 1,400 m, *Gentry & Mori 13629* (DAV, MO); Cerro Tacarcuna, 1,800–1,850 m, *Gentry & Mori 13989, 14025* (DAV, MO). PANAMÁ: Cerro Campana, *Webster & Breckon 16490* (DAV). VERAGUAS: 3–4 km W of Santa Fe, 2,500 ft., *Nee 11315* (DAV, MO); summit of Cerro Arizona, N of Santa Fe, 4,700 ft., *Hammel 4741* (MO); Cerro Tute, just W of Santa Fe, *Knapp & Dressler 5390* (MO).

6. *Drypetes*

Drypetes Vahl, Eclog. Amer. 3: 49. 1807. TYPE: *Drypetes glauca* Vahl.

Trees or shrubs, dioecious; indumentum absent or of simple hairs. *Leaves* alternate, short-petiolate, stipulate; the blades often coriaceous, entire to serrate. *Inflorescences* axillary; flowers in axillary clusters, sometimes cauliflorous. *Flowers* apetalous; sepals usually 4 or 5, imbricate, deciduous. *Staminate flowers* sessile to pedicellate, with intrastaminal disk; stamens mostly 4–5(–50), filaments free; anthers basifixed, extrorse to introrse; pollen grains tricolporate, reticulate; pistillode present or absent. *Pistillate flowers* pedicellate; disk cupuliform; ovary of 1 or 2 (rarely 3 or 4) carpels; styles obsolete or nearly so, dilated stigmas capping the ovary; ovules 2 in each locule, anatropous. *Fruits* indehiscent, ± drupaceous, the exocarp fleshy or leathery, the endocarp crustaceous or bony; seeds usually solitary in each locule, ecarunculate, the testa smooth; endosperm copious; embryo straight, the cotyledons broad and flat.

A large circumtropical genus of about 150 species, best represented in the Old World; about 20 neotropical species have been described. The single Panamanian species was discovered on Barro Colorado Island shortly after the publication of our original treatment.

LITERATURE

WEBSTER, G. L. 1977. A new species of *Drypetes* (Euphorbiaceae) from Panama. Madroño 24: 65–68.

6.1. **Drypetes standleyi** Webster, Madroño 24: 65, fig. 1. 1977; Croat, Fl. Barro Colorado I. 529, fig. 321. 1978. TYPE: Panama. Canal Zone: Barro Colorado I., Armour Trail, *Foster & Croat 2307* (holotype, DAV; isotypes, DUKE, F, F neg. 62358, MO).

Recent collections indicate that *Drypetes standleyi* may occur over a broad area in Panama. A barren collection from the Burica Peninsula, Chiriquí Province (*Busey 602*, MO) may possibly represent *D. standleyi*, although it differs from the other collections in its stiffer leaves with a more prominent veinlet reticulum. The species may also occur in Costa Rica; a specimen from La Selva (*Hartshorn 1009*, DAV) resembles *D. standleyi*, although it is divergent in having more slender pistillate pedicels.

Additional specimens examined. PANAMA. PANAMÁ: Barro Colorado I., Armour Trail, *Foster & Croat 2308* (DAV); vicinity of Armour Trail, *Croat 14843, 14849, 16516* (DAV, MO); S of Zetek 11, *Foster 1122* (DAV, DUKE, MO). COLÓN: Santa Rita lumber road, 9.4 km from Transisthmian Highway, *Dressler 3810* (MO). VERAGUAS: Alto Piedra Santa Fe, *Lao & Maasola 480* (MO); Cerro Tute, *Mori et al. 7541* (MO).

7. *Margaritaria*

Margaritaria L. f., Suppl. Pl. 66. 1782. TYPE: *Margaritaria nobilis* L. f.

RECENT LITERATURE

WEBSTER, G. L. 1979. A revision of *Margaritaria* (Euphorbiaceae). J. Arnold Arbor. 60: 403–444.

8. *Phyllanthus*

Phyllanthus L., Sp. Pl. 981. 1753. LECTOTYPE: *Phyllanthus niruri* L. (chosen by Small in Britton & Brown, Ill. Fl. N. U.S. edition 2, 2: 453. 1913).

RECENT LITERATURE

BANCILHON, L. 1971. Contribution à l'étude taxonomique du genre *Phyllanthus* (Euphorbiacées). Boissiera 18: 1–81.

8.11. **Phyllanthus anisolobus** Muell. Arg. in DC., Prodr. 15(2): 382. 1866. TYPE: Peru: *Pavón* (holotype, G).

The collection from La Palma, Darién (*Pittier 6600*, US) mentioned with doubt in 1968 now appears to represent *Phyllanthus anisolobus* on the basis of its resemblance to the Darién specimens cited below.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Río Teribe, below Puerto Palenque, *Kirkbride & Duke 553* (MO). DARIÉN: Manené, *Kirkbride & Bristan 1592* (MO); Río Balsa, between Manené and Guayabo, *Duke & Nickerson 14958* (MO); Río Pucuro, between Cerro Mali and Cerro Tacarcuna, *Gentry & Mori 13861* (MO). VERAGUAS: 2–5 km NW of Santa Fe on road to Río Calovébora, 500–700 m, *Hernández et al. 744* (F).

8.12. **Phyllanthus gentryi** Webster, sp. nov. TYPE: Panama. Darién: lower slopes of Cerro Pirre, 200–500 m, *Gentry & Clewell 7017* (holotype, F, F neg. 62354; isotypes, DAV, MO). Figure 1.

Species haec aff. *P. juglandifolio* sed ab subsp. *juglandifolio* differt foliis seminibus grandioribus, ab subsp. *cornifolio* differt staminibus 3, stipulis longioribus, ab ambibus differt disco non rugoso, columna stylari breviore.

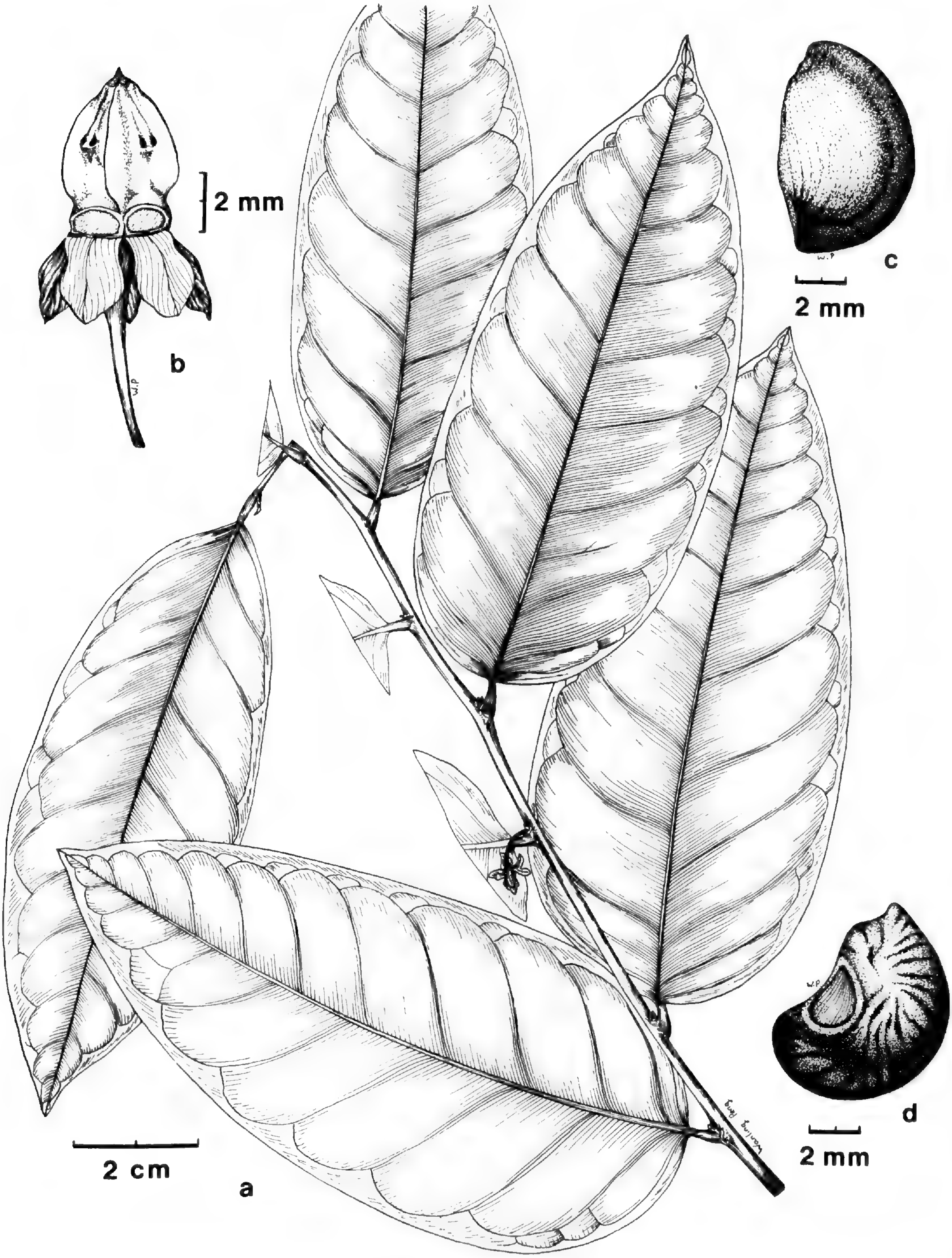

FIGURE 1. Phyllanthus gentryi. —*a. Habit.*—*b. Columella of fruit, showing seed scars and persistent calyx.*—*c. Seed, dorsal view.*—*d. Seed, ventral view. Based on* Gentry 4589. *Illustration by Wan-Ling Peng.*

Shrub or small tree to 5 m high; monoecious; deciduous branchlets pinnatiform, at least 5 dm long, obtusely angled, brownish, minutely scabridulous. *Leaves* with petioles 5–8 mm long; stipules cordate, acuminate, brownish, scarious, ca. 3.5 mm long; blades chartaceous, elliptic-lanceolate, 12–28 cm long, 6–7.5 cm broad, acuminate, rounded to cuneate at base, glabrous on both faces. *Cymules* each of 1 pistillate and several staminate flowers. *Staminate flowers* with pedicels 15–20 mm long; sepals 5, broadly elliptic or oblong; 2.5–3 mm long, 2.2–2.7 mm broad; disk entire, angled, not pitted, 1.8–2.2 mm across; stamens 3, the filaments connate into a column 0.7–0.8 mm high and ca. 0.5 mm broad; anthers suborbicular, flattened, dehiscing horizontally, 0.8–0.9 mm long and broad. *Pistillate flowers* with pedicels 8–13 mm long; sepals 5, elliptic-oblong, blunt, mostly 3–4 mm long, 2.5–3 mm broad; disk massive, angled, not pitted, 2.2–2.5 mm across; ovary smooth, of 3 carpels; styles nearly free, dilated, 1–1.2 mm long, 0.7–1 mm across. *Capsules* reddish, valves 12.5–13 mm long; columella massive, 4.5–5 mm long, 4.2–4.5 mm broad; seeds trigonous-umbonate, 6.5–7.1 mm long, 5.2–5.3 mm broad, smooth, with irregular wavy horizontal dark brown bands on a light brown background, the apex sometimes with a small whitish caruncular outgrowth (ca. 0.5 mm across); hilum triangular, broad, ca. 3 mm long and broad.

Additional specimens examined. PANAMA. DARIÉN: trail up Cerro Pirre, *Gentry 4589* (MO); razorback ridge on Cerro Pirre, *Duke 6556* (MO); Serranía de Pirre, trail from Q. Perecingo to Cerro Pirre, ca. 10 km airline SSE of El Real, in subtropical moist-to-wet forest, 300–750 m, *Reveal & Duke 4919* (MARY, MO); around Rancho Frío, halfway up slope of Cerro Pirre from Piji Vasal, *Folsom 6245* (F, MO); S of El Real on trail up Cerro Pirre, ca. 8°00′N, 77°45′W, 550–1,030 m, *McPherson 7051* (F, MO).

Phyllanthus gentryi is the first representative of subgenus *Xylophylla* (L.) Pers. discovered in Panama. It clearly belongs in section *Asterandra* (Klotzsch) Muell. Arg. by virtue of its confluent staminate disk and dilated styles, and it resembles *P. juglandifolius* Willd. in general aspect. Although it could be interpreted as a subspecies of *P. juglandifolius*, it is distinctive in its large seeds, smooth (nonpitted) disk, and nearly free styles.

In order to accommodate this species in the *Flora of Panama* treatment, the key on p. 221 must be revised as follows:

e. Branchlets pinnatiform.
  e′. Plants (in Panama) herbaceous; leaves less than 3 cm long; seeds less than 3 mm long; pollen grains prolate, 3–4-colporate (subg. *Phyllanthus*).
  ee′. Plants woody; leaves more than 3 cm long; seeds over 3 mm long; pollen grains globose, areolate (subg. *Xyllophylla*) .... 12. *P. gentryi*

Subfamily II. ACALYPHOIDEAE Asch.

9. *Caperonia*

Caperonia A. St. Hil., Hist. Pl. Remarq. Bresil 244. 1826. LECTOTYPE: *Caperonia castaneifolia* (L.) A. St. Hil. (*Croton castaneifolius* L.) (chosen by Britton & Wilson, Bot. Porto Rico 6: 486. 1925).

No additional Panamanian species have been discovered. However, examination of additional specimens indicates that we may not have gone far enough in reducing the taxa proposed under *C. paludosa* Klotzsch. It is extremely difficult to separate that species from *C. castaneifolia* (L.) A. St. Hil., and we now believe that our Panamanian specimens of *C. paludosa* probably represent only forms of that more wide-ranging species. However, the narrower leaves of plants referred to *C. paludosa* are distinctive, and further study in the field is required to establish whether that species concept can be upheld.

10. *Argythamnia*

Argythamnia P. Browne, Civ. Nat. Hist. Jamaica 338. 1756. TYPE: *Argythamnia candicans* Sw.

11. *Alchorneopsis*

Alchorneopsis Muell. Arg., Linnaea 34: 156. 1865: TYPE: *Alchorneopsis floribunda* (Benth.) Muell. Arg. (*Alchornea glandulosa* var. ?*floribunda* Benth.).

11.1 Alchorneopsis floribunda (Benth.) Muell. Arg., Linnaea 34: 156. 1865; in DC., Prodr. 15(2): 765. 1866. *Alchornea glandulosa* Poeppig var. *floribunda* Benth., Hooker's J. Bot. Kew Gard. Misc. 6: 331. 1854. TYPE: Brazil. Amazonas: *Spruce 2681* (holotype, K, not seen).

The single collection of this species cited in the original treatment, from Darién, was the only Central American record known at the time and was likewise a range extension of over 800 miles. The specimens cited below extend the range to western Panama as well as to Costa Rica.

Additional specimens examined. COSTA RICA. CARTAGO: 24 km NE of Turrialba on hwy. to Limón, then E at Tres Equis on jeep road 1.5 km, 9°58'N, 83°34'W, 450–525 m, *Liesner et al. 15354* (MO). HEREDIA: Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, ca. 100 m, *Hammel 9425, 11083* (F, MO); Istarú Farm, Tirimbina, Sarapiquí, 220 m, *Lent 2320* (F, MO). LIMÓN: S end of Lomas de Sierpe, NE of terminus of road from Villa Franca, 10°19'N, 83'34'W, *Grayum et al. 3520* (F, MO). SAN JOSÉ: 2 km N of Dominical along CR 223, 40–100 m, *Utley & Utley 4938* (F). PANAMA. BOCAS DEL TORO: Cerro Pila de Arroz, along road to Chiriquí Grande, 10 road-mi from Continental Divide and 2 mi. along pipeline access road E of highway, ca. 8°55'N, 82°08'W, 350–500 m, *McPherson 8750* (F).

12. *Caryodendron*

Caryodendron Karsten, Fl. Columb. 1: 91, tab. 45. 1860. TYPE: *Caryodendron orinocense* Karsten.

12.1. Caryodendron angustifolium Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 217. 1929. TYPE: Panama. Chiriquí: Progreso, *Cooper & Slater 192* (holotype, F, F neg. 59913).

The collection cited from Darién under this name in the original collection is now known to be *Senefeldera testiculata* Pittier (q.v.). No additional collections of *Caryodendron angustifolium* are known from Panama or elsewhere.

13. *Adenophaedra*

Adenophaedra (Muell. Arg.) Muell. Arg. in Mart., Fl. Bras. 11(2): 385. 1874. *Bernardia* sect. *Adenophaedra* Muell. Arg., Linnaea 34: 172. 1865; in DC., Prodr. 15(2): 918. 1866. TYPE: *Bernardia ?megalophylla* Muell. Arg. = *Adenophaedra megalophylla* (Muell. Arg.) Muell. Arg.

Dioecious *trees* and shrubs; indumentum of simple trichomes. *Leaves* alternate, petiolate, stipulate; blades pinnately veined, without embedded laminar glands, dentate. *Inflorescences* axillary or terminal, spiciform, the staminate often compound; bracts eglandular, subtending 1 pistillate or several staminate flowers. *Staminate flowers* pedicellate; calyx splitting into 3 valvate lobes at anthesis; petals and disk absent; stamens 2(–3); filaments short; anthers with enlarged connectives, dehiscing introrsely and longitudinally; pistillode absent. *Pistillate flowers* pedicellate; calyx lobes 6, biseriate, imbricate; petals absent; disk 3-lobed; ovary of 3 carpels; ovules 1 per locule; styles contracted into sessile stigmas. *Fruits* capsular, 3-lobed; seeds 1 per locule, smooth, ecarunculate.

LITERATURE

CROIZAT, L. 1946. Nomenclatural transfers and corrections in the Euphorbiaceae. Trop. Woods 88: 30–32.

This poorly known genus, hitherto considered to be South American, includes only three species. Croizat (1946) reported *Adenophaedra* from Panama on the basis of *Adenophaedra woodsoniana*; but in the original treatment (Webster & Burch, 1968: 278) it was pointed out that his original generic disposition (J. Arnold Arbor. 24: 167. 1943) of this plant as *Cleidion woodsonianum* was correct, although that species is now known to be synonymous with *C. membranaceum* Pax & K. Hoffm. (q.v.). Several recent collections of *A. grandifolia* from Panama and Costa Rica, however, firmly establish the presence of *Adenophaedra* in southern Central America. In addition, it now appears that the plant called *Bernardia denticulata* in the original treatment is actually *A. grandifolia.*

13.1. Adenophaedra grandifolia (Klotzsch) Muell. Arg. in Mart., Fl. Bras. 11(2): 386. 1874. *Tragia grandifolia* Klotzsch, London J. Bot. 2: 46. 1843. TYPE: Guyana: "British Guiana," *Schomburgk 948* (presumably K, not seen). *Bernardia ?grandifolia* (Klotzsch) Muell. Arg., Linnaea 34: 173. 1865; in DC., Prodr. 15(2): 918. 1866.

Cleidion denticulatum Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 218. 1929. *Bernardia denticulata* (Standley) Webster, Ann. Missouri Bot. Gard. 54: 200. 1967. TYPE: Panama. Bocas del Toro: Chiriquí Trail, Buena Vista Camp, 1,250 ft., *Cooper 606* (holotype, F, F neg. 52608; isotypes, NY, Y).

Shrub or small tree to 8 m; twigs smooth, reddish, thinly puberulent, tardily glabrate. *Leaves* with petiole 3–6 mm long; stipules lanceolate, ca. 1 mm long, ca. 1 mm broad, caducous; blades chartaceous, oblanceolate, acuminate at the tip, attenuate at the base, 12–35 cm long, 3–12 cm wide, 2.5–4.5 times as long as broad, glabrous, or sometimes thinly villous below on the principal veins, the secondary veins 7–9 per side, arcuate, prominent below, the tertiaries reticulate, prominulous; margins remotely denticulate. *Inflorescences* axillary, densely villous, the bracts deltate, 1–2 mm long, densely villous; staminate spikes slender, flexuous, to 15 cm long, the glomerules widely spaced, to 25; pistillate spikes thicker, not flexuous, 5–12 cm long, with 4–7 solitary flowers. *Staminate flowers* to 12 per glomerule, early dehiscent, leaving persistent pedicels ca. 1 mm long; calyx lobes membranous, deltate, spreading at anthesis, ca. 0.5 mm long. *Pistillate flowers* not seen; pedicels at maturity ca. 4 mm long, reflexed, sericeous. *Capsules* depressed-globose, deeply 3-lobed, 6–8 mm high, 12–18 mm diam., sericeous, glabrate at maturity, the persistent calyx lobes ca. 2 mm long, deltate, sericeous; seeds subglobose to ovoid, ca. 1 mm long, ca. 0.7 mm diam., yellowish, mottled.

Additional specimens examined. COSTA RICA. LIMÓN: 7 km SW of Bribrí, 100–150 m, *Gómez et al. 20422* (F); camino entre la finca de don Calixto Kiamble y el antiguo camino a Katsi, subiendo hasta el Cerro Kikírchabata, *Gómez et al. 23800* (F); camino de Fila Dimat (casa de Hermógenes Pereira) hasta Soki pasando por la quebrada Sha, *Gómez et al. 23859* (F). PANAMA. BOCAS DEL TORO: along road from Fortuna Dam to Chiriquí Grande, ca. 8°45′N, 82°15′W, ca. 700 m, *McPherson 8430* (F); Cerro Pila de Arroz along road to Chiriquí Grande, 10 road-miles from Continental Divide and 2 mi. along pipeline access road E of highway, ca. 8°55′N, 82°08′W, 350–500 m, *McPherson 8752* (F), *8775* (F, distributed as *Cleidion woodsonianum*). VERAGUAS: 5 mi. NW of Santa Fe, 700–1,200 m, *Liesner 976* (GH, MO).

14. *Bernardia*

Bernardia Miller, Gard. Dict. abr. ed. 4, 28. 1754. LECTOTYPE: *Bernardia carpinifolia* Griseb. (see Buchheim, 1962).

Following the reduction of *Bernardia denticulata* to the synonymy of *Adenophaedra grandifolia* (q.v.), this genus is now represented in Panama by a single species.

LITERATURE

BUCHHEIM, G. 1960. Nomenklatorische und systematische Bemerkungen über die Gattung *Bernardia* (Euphorbiaceae). Willdenowia 2: 291–318.

———. 1962. Über die Typusart der Gattung *Bernardia* (Euphorbiaceae). Willdenowia 3: 217–220.

14.1. Bernardia macrophylla Standley, J. Wash. Acad. Sci. 15: 103. 1925. TYPE: Panamá: Río Tocumen, near sea level, 3 Jan. 1924, *Standley 29389* (holotype, US).

No Panamanian specimens of this species have been found in addition to those cited in the original treatment. The recent collection cited below extends the range to Costa Rica. That specimen has somewhat more acuminate leaf apices than the Panamanian collections and was taken at a considerably higher altitude but seems otherwise identical. As indicated in the original treatment, the closest relative of *Bernardia macrophylla* seems to be *B. jacquiniana* Muell. Arg. of Venezuela, but the latter differs in having retrorse rather than ascending pubescence on the stems, more prominent venation on the undersurface of the leaves, and 9–12 vs. 14 stamens.

Additional specimen examined. COSTA RICA. PUNTARENAS: foothills of the Cordillera de Talamanca, around Tres Colinas, 9°07′N, 83°04′W, 1,800–1,850 m, *Davidse et al. 25611* (F).

15. *Adelia*

Adelia L., Syst. Nat. ed. 10, 1298. 1759, nom. cons. TYPE: *Adelia ricinella* L. (typ. cons.).

16. *Alchornea*

Alchornea Sw., Prodr. 98. 1788; Fl. Ind. Occ. 2: 1153. 1800. TYPE: *Alchornea latifolia* Sw.

Several recent collections of *Alchornea* indicate that there are some additional taxa in Panama, but the material is still inadequate for a satisfactory treatment. The taxa that appear to be present may be treated as follows.

LITERATURE

PAX, F. & K. HOFFMANN. 1914. Euphorbiaceae—Acalypheae—Mercurialinae. *In:* A. Engler, Das Pflanzenreich IV. 147. VII(Heft 63): 1–473 (*Alchornea*, pp. 220–253).

KEY TO THE SPECIES OF *ALCHORNEA* IN PANAMA

1a. Pistillate spikes less than 25 cm long; leaves less than 25 cm long (or else copiously stellate-pubescent beneath), with 2 or more basal laminar glands; seeds (where known) not over 7 mm long.
  2a. Leaves (except on sprout shoots) not over ca. 20 cm long, glabrate, the veinlet reticulum only moderately prominulous beneath.
    3a. Leaves chartaceous, abruptly cuspidate-acuminate; vein axils not barbate beneath; basal foliar glands usually 2; staminate spikes unbranched, mostly axillary .... 1. *A. costaricensis*
    3b. Leaves not abruptly cuspidate (or else coriaceous); vein axils often barbate beneath.
      4a. Styles 5–20 mm long, relatively slender.
        5a. Leaves coriaceous, usually with 2–4 basal glands; spikes mostly cauliflorous.
          6a. Leaves mostly 8–20 cm long, acuminate, with mostly 5–8 main lateral veins, entire or crenate-dentate; foliar glands mostly 2(–4); pistillate sepals 2–2.8 mm long .... 2. *A. latifolia*

6b. Leaves mostly 2–7 cm long, acute, with mostly 3 or 4 main lateral veins; foliar glands 2–4; pistillate sepals shorter than 2 mm long .... 3. *A. triplinervia*
5b. Leaves chartaceous, usually with 5–10 basal glands, with 5–8 main lateral veins; spikes mostly axillary; pistillate sepals 1–1.5 mm long .... 4. *A. glandulosa*
4b. Styles 3–7 mm long, thick; leaves coriaceous, acuminate, with 5–7 main lateral veins; foliar glands 2–4; spikes axillary .... 5. *A. grandiflora*
2b. Leaves over 20 cm long, copiously stellate-pubescent beneath, with veinlet reticulum corrugate-impressed above and distinctly raised beneath; spikes cauliflorous .... 6. *A. grandis*
1b. Pistillate spikes mostly 25 cm long or longer, cauliflorous; leaves coriaceous, oblanceolate, ca. 25–40 cm long, glabrescent beneath; basal foliar glands obscure or absent; seeds 9–11 mm long .... 7. *A. megalophylla*

16.1. Alchornea costaricensis Pax & K. Hoffm., Pflanzenreich IV. 147. VII(Heft 63): 235. 1914. TYPE: Costa Rica: Palmar, *Tonduz 6757* (not seen).

Recent collections show that *Alchornea costaricensis* is not confined to western Panama; it extends into South America, where there is at least one record from Colombia (Chocó: *Ordóñez et al. 58*, MO). The plant described from Colombia by Croizat (Caldasia 2: 357. 1944) as *A. umboensis* may prove to be a form of *A. costaricensis.*

Additional specimens examined. PANAMA. CHIRIQUÍ: vicinity of San Bartolo Limite, 11 mi. W of Puerto Armuelles, *Croat 21973a* (MO). COCLÉ: along Río San Juan below its junction with Río Tife, *Hammel 3405* (MO). COLÓN: Río Boquerón near juncture with Río Escandaloso, *Hammel 2743* (MO, determination somewhat dubious); along Río Guanche toward Cerro Bruja, *Huft & Knapp 1789* (MO); 3 mi. from Portobelo, *Correa & Dressler 1749* (GH, MO). DARIÉN: Río Ucurgantí, *Bristan 1137* (MO); Río Tuqueza, below Quebrada Venado, *Bristan 1065* (DAV, MO). LOS SANTOS: Loma Prieta, Cerro Grande, *Duke 11859, Lewis et al. 2208* (MO). PANAMÁ: Chiltepe, *Holdridge 6471* (MO). SAN BLAS: Canagangí, forest upstream of village, 9°24′N, 79°24′W, 100 m, *de Nevers et al. 5720* (F).

16.2. Alchornea latifolia Sw., Prodr. 98. 1788. TYPE: Jamaica: *Swartz* (not seen).

Southern Mexico to Venezuela and Peru.

Further botanical exploration has shown that *Alchornea latifolia* is widely distributed in Panama, including Barro Colorado Island, whence it was correctly recorded by Croat (1978). On several peaks and ridges in central Panama occur montane forms that appear very different from typical *A. latifolia* of lowland Central America and the West Indies. For example, plants with entire leaves and unusually short petioles are found on Cerro Jefe and Santa Rita Ridge (e.g., *Gentry & Dwyer 5536, Croat 15309*). These specimens somewhat suggest the South American *A. pearcei* Britton, but their relatively long petioles and short spikes bring them closer to *A. latifolia.* Specimens with very unusual narrowly obovate leaves have been collected on Santa Rita Ridge (e.g., *Croat 13844, Duke 15264*); however, since plants with this leaf form occur in the same area as plants with more typical leaves, it seems probable that they are merely local variants. At present, it seems best to include all of these variants within *A. latifolia*, but it must be admitted that the species so conceived has an extraordinary amplitude of foliar variation; until critical studies in the field are made, the situation will remain unsatisfactory.

Additional specimens examined. PANAMA. CHIRIQUÍ: San Félix, *Croat 33416* (MO). PANAMÁ: Cerro Campana, *Croat 14673, Duke 10742, Sullivan 434* (MO), *Méndez 19, 49* (F); Cerro Jefe, *Dwyer et al. 5048, 5049, Gentry 4938* (MO), *Gentry & Dwyer 5536* (GH, MO), *Webster & Dressler 16454* (DAV); between Cerro Jefe and Cerro Azul, *Tyson et al. 4325, Mori et al. 6543* (MO); Cerro Azul, *Dwyer 5042* (MO), *Lao & Holdridge 33* (DAV, MO), *Stimson et al. 5158* (GH, MO), *Tyson & Blum 4081* (MO); N of El Llano, *Gentry 5105* (MO); El Llano–Cartí road, 7.8–8.6 mi. from Pan-American Hwy., *Folsom 3572, Mori & Kallunki 6405* (MO).

16.3. Alchornea triplinervia (Sprengel) Muell. Arg. in DC., Prodr. 15(2): 909. 1866; Pax & K. Hoffm., Pflanzenreich IV. 147. VII (Heft 63): 227. 1914. *Antidesma triplinervium* Sprengel, Neue Entdeck. 2: 116. 1821. TYPE: Brazil. Rio de Janeiro: Serra do Mar, *Gardner 617* (neotype, G; chosen here).

This species is tentatively added to the Panamanian flora on the basis of two recent collections from a single locality. The collection of Knapp has only staminate flowers, but the small coriaceous leaves with only three or four main veins and the cauliflorous spikes match those of *Alchornea triplinervia* better than those of any of the species of *Alchornea* previously known from Panama. Another collection that may represent *A. triplinervia* is *Hammel 7252* (MO) from Cerro Sapo, Darién; this has much larger leaves and somewhat resembles some of the aberrant forms here treated as *A. latifolia*; for the present, its assignment must be regarded as dubious.

The collections from Coclé do not fit any of the varieties recognized by Pax & Hoffmann (1914: 228–230), but the variation within *A. triplinervia* has not yet been critically studied, and it would certainly be premature to assign the Panamanian material to a new variety. The typification of *Alchornea triplinervia* requires some comment, since Sprengel apparently left no type specimen. Mueller (1866: 909) designated what may be regarded as the typical element of the species as *Alchornea triplinervia* var. *genuina* forma *psilorhachis*. Since there is a good microfiche image (G, Prodromus Herb.) of *Gardner 617*, probably from the general area of the collection that was available to Sprengel, it seems appropriate to designate that as neotype.

Specimens examined. PANAMA. COCLÉ: hills N of El Valle, E slope of Cerro Gaital, 900–1,000 m, *Knapp 5351* (MO), *McPherson 11242, 11260* (MO).

16.4. Alchornea glandulosa Poeppig var. **pittieri** (Pax) Pax, Pflanzenreich IV. 147. VII(Heft 63): 235. 1914. *Alchornea pittieri* Pax, Bot. Jahrb. Syst. 33: 291. 1903. TYPE: Costa Rica: Cañas Gordas, *Pittier 11101* (isotype, US).

Since the Darién collection of Terry & Terry was reported in our original treatment, a number of additional specimens have accumulated; these confirm the widespread occurrence of *Alchornea glandulosa* in montane forests of Panama. Examination of this expanded suite of specimens now shows that the Panamanian plants represent var. *pittieri*, originally described from Costa Rica. This variety is very similar to var. *glandulosa* of the upper Amazon but differs in the smaller glandular spots at the base of the leaf (mostly 0.5 mm long or less in var. *pittieri*, reaching 1–1.5 mm long in var. *glandulosa*). At present, var. *pittieri* is known only from Costa Rica, Panama, and adjacent Colombia (Chocó).

Additional specimens examined. PANAMA. BOCAS DEL TORO: headwaters of Río Mali, between Q. Gutiérrez and La Zorra, *Kirkbride & Duke 726* (MO); along pipeline road in area of Fortuna Dam, near end of road, ca. 8°48'N, 82°15'W, 900–950 m, *McPherson 8691, 8699* (F). DARIÉN: Cana-Cuasí Trail, *Terry & Terry 1575* (MO); Cerro Pirre, *Bristan 620* (MO); Alto de Nique, Cerro Pirre massif, 1,300–1,520 m, *Gentry et al. 28647* (DAV, MO); Cerro Tacarcuna, lower montane wet forest, 1,500 m, *Gentry & Mori 13793* (DAV, F, MO, PMA). VERAGUAS: lower montane wet forest, 7 km W of Santa Fe, ca. 900 m, *Nee 11183* (MO, US); NW of Santa Fe, 2.8 km from Escuela Agrícola, Alto de Piedra, *Mori & Kallunki 6219* (MO).

16.5. Alchornea grandiflora Muell. Arg., Linnaea 34: 170. 1865; in DC., Prodr. 15(2): 907. 1866. SYNTYPES: Venezuela: *Fendler 1272* (G), *Moritz 1497a* (G). Costa Rica: *Hoffman 530* (G, not seen).

Although it has been confused with *A. glandulosa*, the relatively short thick styles and stiff glandular leaves distinguish *A. grandiflora* from *A. glandulosa* and from *A. latifolia*. Mueller (loc. cit.) reported *A. grandiflora* from Costa Rica and Venezuela, so its occurrence in Panama is not surprising.

Specimens examined. PANAMA. CHIRIQUÍ: Cerro Colorado, 1,690 m, *Croat 37195* (MO). DARIÉN: Cerro Tacarcuna, elfin forest, 1,800–1,850 m, *Gentry & Mori 13995* (DAV, F, MO).

16.6. Alchornea grandis Benth., Bot. Voy. Sulphur 164. 1844. TYPE: Colombia. Nariño: Tumaco, *Barclay & Hinds* (K, not seen).

The specimens cited below, and several collections from Chocó Province, Colombia (*Fernández 206, Killip & Cuatrecasas 39076*, both UC) furnish previously unknown characters for the staminate plant: staminate spikes mostly compound, 4–12 cm long, with 1–6 lateral axes; staminate calyx glabrous, sepals ca. 1.2 mm long; stamens 8, anthers 0.7–0.8 mm long, blunt.

Specimens examined. PANAMA. VERAGUAS: Isla de Coiba, road from Campamento Juncal to Colonia Penal, *Antonio 2417* (MO); Playa Hermosa, *Antonio 2342* (MO).

16.7. Alchornea megalophylla Muell. Arg., Flora 47: 343. 1864; in DC., Prodr. 15(2): 911. 1866. TYPE: Colombia. Antioquia: *Purdie* (K, not seen).

Tree to ca. 10 m high; trunk 1.5 dm diam.; twigs subterete, smooth, glabrous. *Leaves* with stout petioles 0.5–1.5 cm long, glabrous, plicate; stipules inconspicuous, ca. 1.5 mm long or shorter, dark, triangular, pubescent; blades becoming subcoriaceous or coriaceous, elliptic to obovate, abruptly short acuminate at apex (the acumen ca. 1–2 cm long), ca. 25–40 cm long, 7–15 cm broad, glabrous or glabrescent (minute scattered stellate hairs on underside of lamina or confined to midrib); basal foliar glands obscure or absent; major lateral veins ca. 10–15 on a side, straight, ascending, raised beneath, connected by ladderlike prominulous veinlets, contracted to an obtuse base; margins distantly crenulate-dentate (ca. 10–15 glandular teeth on a side), apex abruptly short-acuminate (acumen ca. 1–2 cm long). *Spikes* cauliflorous, pendulous, stellate-pubescent; staminate spikes not seen; pistillate spikes ca. 50–75 cm long, with ca. 20–30 flowers. *Staminate flowers* not seen. *Pistillate flowers* subsessile; calyx ca. 3.5 cm broad, 4-lobed, pubescent; ovary copiously pubescent with minute stellate hairs; styles slender, unlobed, ca. 20–25 mm long, basally connate for 2–4 mm, basally stellate, apically smooth and long-attenuate. *Capsules* reddish brown, stellate-pubescent, not seen entire; seeds elliptic, plump, pale brown, coarsely tuberculate, 9–11 mm long.

Rainforests, Panama and Colombia.

This striking species stands out from all other Panamanian taxa by virtue of its long, pendulous, cauliflorous inflorescences and its large, coriaceous, more or less oblanceolate leaves. It resembles *A. grandis* in a number of respects but differs in leaf shape and sparseness of the laminar pubescence.

Specimens examined. PANAMA. DARIÉN: La Laguna, ridge between Pucuro and Tapalisa rivers, 820–840 m, *Gentry & Mori 13560* (DAV, MO); top of Cerro Mali, 1,400 m, *Gentry & Mori 13693* (DAV, MO); Cerro Tacarcuna, *Gentry & Mori 13938* (MO); Alturas de Nique, S of El Real, 900–1,250 m, *McPherson 11614* (MO).

17. *Cleidion*

Cleidion Blume, Bijdr. Fl. Ned. Ind. 612. 1826. TYPE: *Cleidion javanicum* Blume.

Recent collections in Panama and further study of the South American species have greatly altered the picture of *Cleidion* in Panama. Largely as a result of problems encountered in the preparation of this account, the junior author has undertaken a revisionary study of the neotropical species of *Cleidion*, and until its completion, some of the conclusions expressed here must remain tentative.

In addition to the two species treated here, a recent collection in Darién by Dr. Gordon McPherson may belong to *Cleidion prealtum* Croizat (J. Arnold Arbor. 24: 167. 1943), a species otherwise known only from material collected in the basin of the upper Rio Madeira in Amazonian Brazil. The poorly known *Polyandra bracteosa* Leal (Arch. Jard. Bot. Rio de Janeiro 11: 64. 1951), described from staminate material, also from the Rio Madeira, now appears to be synonymous with *C. prealtum.*

LITERATURE

VAN DER WERFF, H. & A. R. SMITH. 1980. Pteridophytes of the State of Falcon, Venezuela. Opera Bot. 56: 1–34.

KEY TO THE SPECIES OF *CLEIDION* IN PANAMA

1a. Fruiting spikes slender, (5–)8–18 cm long; capsules 3–6, remote, 5–8 mm in diameter; leaves up to 13 cm long; leaf vein axils barbate beneath; veins 7 or 8 on a side; staminate thyrses ca. 1 cm long .... 1. *C. membranaceum*

1b. Fruiting spikes thick, 2–3 cm long; capsules 1–3, 13–15 mm in diameter; leaves over 15 cm long; leaf vein axils not barbate beneath; veins 8–10 on a side; staminate thyrses 5–9 cm long .... 2. *C. castaneifolium*

17.1. **Cleidion membranaceum** Pax & K. Hoffm. in Engler, Pflanzenreich IV. 147. XIV(Heft 68): 23. 1919. TYPE: Venezuela. Lara: around Palmosola, in forest along Río Aroa, near sea level, 26–28 June 1913, *Pittier 6375* (US, photo F neg. 44609).

Cleidion woodsonianum Croizat, J. Arnold Arbor. 24: 167. 1943. TYPE: Panama. Panamá: vicinity of Salamanca Hydrographic Station, Río Pequení, ca. 80 m, *Woodson et al. 1587* (holotype, A; isotypes, F, F neg. 62417, MO, F neg. 62356, NY).

There appear to be no differences between the Panamanian plants and the Venezuelan collections of *Cleidion membranaceum.* The three known Venezuelan collections are all from a restricted area near the junction of the provinces of Falcón, Yaracuy, and Lara. No substrate is indicated on the labels of these collections, but it is known that much of this area is underlain by limestone (van der Werff & Smith, 1980), which is also true of the Panamanian collections. The recent disjunct collection from Peru strengthens the probability that this species is restricted to limestone, and that this accounts for the peculiar disjunctions in its range.

Further study may show that *Cleidion membranaceum* is synonymous with *C. tricoccum* (Casar.) Baillon, of eastern Brazil from Bahia to São Paulo, which has leaves similar in shape and size to those of the Panamanian plant, similar long, nearly filiform pistillate inflorescences, and similar capsules.

Additional specimens examined. PANAMA. PANAMÁ: Majé, second growth on limestone hillsides, along Chocó Indian trail, ca. 5 mi. up from village of Majé, *Foster & Kennedy 2021* (MICH, MO, PMA). PERU. HUÁNUCO. LEONCIO PRADO: Distrito Rupa Rupa, Tingo María, ca. 9°18′S, 75°59′W, limestone hills opposite airport, *Plowman et al. 11246* (DAV, F, K). VENEZUELA. FALCÓN: Parque Nacional Quebrada de la Cueva El Toro, steep wet valley along river, 10°50′N, 69°07′W, *Liesner et al. 7722* (F, MO). YARACUY-FALCÓN: Reserva Forestal "Rio Tocuyo," a 4 km del Campto. "Canelon," via Tucacas, *Blanco 895* (MO).

17.2. **Cleidion castaneifolium** Muell. Arg., Linnaea 34: 184. 1865. TYPE: Peru: *Pavon* (holotype, G, F neg. 7159).

Alchornea oblongifolia Standley, Carnegie Inst. Wash. Publ. 461(Botany of the Maya Area 4): 66. 1935. *Cleidion oblongifolium* (Standley) Croizat, J. Arnold Arbor. 24: 166. 1943. TYPE: Guatemala. Petén:

Camp 35, boundary with Belize, 750 m, *Schipp S-279* (holotype, F, F neg. 52594).

Trees to 10 m high; dioecious; twigs glabrous. *Leaves* with petioles 1.5–4 cm long, glabrous or sparsely pubescent with short, white, appressed hairs, swollen toward apex; stipules not evident; blades membranous or thinly chartaceous, elliptic, abruptly caudate-acuminate at tip, acute or cuneate at the somewhat inequilateral base, 15–26 cm long, 6.5–9.5 cm broad, minutely pustulate, glabrous, the veins 8–10 on a side; margins shallowly dentate, the teeth callose, 15–28 on a side. *Inflorescences* unisexual, axillary; pistillate racemes to 16 cm long, widely divergent from the stem, the rachis glabrous, or puberulent toward the apex, with ca. 3 flowers occurring singly (3 fruits on only complete pistillate raceme seen); staminate thyrses 5–9 cm long, with 7–12 flowers crowded at each of the 20–50 nodes, the rachis densely puberulent. *Staminate flowers* on pedicels to 1 mm long; calyx lobes cucullate, reflexed, 1.5–2 mm long, glabrous, ovate, the apex acute or acuminate; stamens ca. 60–80. *Pistillate flowers* not seen; bracts narrowly lanceolate, rigid, divergent, ca. 2 mm long, puberulent; fruiting pedicels 10–12 mm long, slightly clavate, puberulous, jointed; calyx lobes (in fruit) 3–5, somewhat reflexed, deltate, 2–3 mm long, acute, canescent below, ciliate on the margins; styles (persistent on mature fruits) 7–12 mm long, deeply bifid, densely strigose. *Capsules* 3-locular (of which often only 2 fully developed), deeply lobed, dorsally carinate, ca. 1 cm high, 14–18 mm diam., densely puberulent, drying black; columella 6–8 mm long, trigonous, narrowly winged, the seed scars elongate, conspicuous; seeds globose, smooth, not beaked, ca. 9 mm long, mottled light and dark brown.

Rainforests, southern Mexico to Panama, Ecuador.

The Panamanian collections of *Cleidion castaneifolium* match perfectly the type photograph as well as the original description except for the curious statement in the latter that the capsule is six-lobed. Since all other species of *Cleidion* have three-lobed capsules (as do the Panamanian collections), and since the one capsule on the type photo appears crushed and misshapen (and thus made to appear six-lobed), it seems that Mueller was merely careless in his description. Since these collections are in perfect agreement with all other distinguishing characteristics of this species (large elliptic-ovate leaves, petioles 3–5 cm long and glabrous except for the subpuberulous tips, long undivided pistillate racemes, and large capsules with dorsally carinate lobes), their identification seems certain. The only other Panamanian species of the genus, *C. membranaceum*, and the Peruvian *C. amazonicum* Pax both differ from *C. castaneifolium* in their smaller leaves, much shorter petioles (2–5 mm long), and smaller capsules. *Cleidion prealtum* Croizat of Amazonian Brazil differs from all of these in its obovate and coriaceous leaves.

Cleidion castaneifolium was described from "Peru," but a possible isotype sheet at F (*Ruiz & Pavón s.n.*) is labeled as having been collected at Guayaquil, Ecuador (another Ruiz & Pavón specimen at F has no locality data). The species is not definitely known from Peru, but there are two modern collections from between Santo Domingo and Quinindé in Esmeraldas Province, Ecuador (*Acosta Solís 13649, Little 6196*, both at F, both distributed as *Alchornea*).

There appear to be no salient differences separating *Cleidion castaneifolium* from Panama and South America from the Mexican and Central American populations that have long been referred to *C. oblongifolium*. In addition to the common characters given in the key, these populations all frequently exhibit a characteristic purplish cast to the leaves.

Specimens examined. PANAMA. DARIÉN: Serranía de Pirre, on the NW slope of the mountain range dominated by Cerro Pirre, along Q. Perecingo (Parasénico), a tributary to Río Pirre, ca. 10 air km S of El Real, 8°03'N, 77°43'W, *Reveal & Duke 4875* (MARY, MO); 2–3 mi. SE of Pijibasal on Río Perasénico, ca. 9–10 mi. S of El Real, *Hartman 12038* (F, MO).

18. *Ricinus*

Ricinus L., Sp. Pl. 1007. 1753. TYPE: *Ricinus communis* L.

19. *Acalypha*

Acalypha L., Sp. Pl. 1003. 1753. LECTOTYPE: *Acalypha virginica* L. (chosen by Small in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 457. 1913).

19.10. Acalypha cuneata Poeppig in Poeppig & Endl., Nov. Gen. Sp. Pl. 3: 22. 1841. TYPE: Peru. Maynas: Yurimaguas, *Poeppig* (not seen).

Acalypha obovata Benth. in Seemann, Bot. Voy. Sulphur 163. 1844. TYPE: Ecuador. Esmeraldas: Atacames, *Hinds* (BM, not seen). *A. cuneata* Poeppig var. *obovata* (Benth.) Muell. Arg. in DC., Prodr. 15(2): 816. 1866.

Shrub or small tree 2–5(–8) m high; monoecious; stems nearly glabrous. *Leaves* with petioles 1–7 cm long, glabrous; stipules lanceolate, 4–7 mm long, strongly keeled, caducous; blades obovate or obovate-oblong, cuspidate-acuminate at the tip (the acumen 1.5–3 cm long), acute at the base, 15–30 cm long, 5–13 cm broad, 2–3.2 times as long as broad, glabrous, pinnately veined, the secondary veins 11–15 per side, arcuate, prominent above and below, connected by a prominulous reticulum; margins shallowly crenate-denticulate. *Inflorescences* axillary, spicate, unisexual; staminate spikes to 15 cm long, densely flowered, densely puberulent, solitary and pedunculate or 2–4 and sessile on a slender rachis; pistillate spikes 7–15 cm long, 4–7 mm thick, loosely flowered with 15–50 bracts, the rachis glabrous to densely puberulent. *Pistillate flowers* solitary; bracts ± reniform, 3–4 mm long, 6–7 mm wide, inconspicuously 8–10-lobed, each lobe with a short tuft of bristles, the bracts otherwise glabrous or lightly short-strigose; calyx lobes obscure; ovary densely hispid, the styles free, lightly strigose, pinnatifid along entire length into 8–12 narrow segments. *Capsules* 4–5 mm diam., hispid, verrucose; seeds obovoid-ellipsoid, 3–3.5 mm long, ca. 2.5 mm diam., smooth, brown, the caruncle nearly obsolete.

This is a widespread species of lowland rainforests in northern South America, and its discovery in eastern Panama is not surprising. It is easily recognized by the long-petiolate obovate leaves with pinnate venation and axillary pistillate inflorescences. In order to accommodate this species in the *Flora of Panama* treatment, the key on p. 300 must be revised as follows:

ee. Leaves pinnately veined; pistillate bracts subentire or shallowly dentate.
  e′. Spikes mostly bisexual, 3–8 cm long, with 1 or 2 pistillate bracts at base, these subtending 2 or 3 flowers .... *A. diversifolia*
  ee′. Spikes unisexual, to 15 cm long, the pistillate ones toward the apex of the branch, the staminate below; pistillate bracts subtending a single flower .... *A. cuneata*

Specimen examined. PANAMA. DARIÉN: S of El Real on trail to Cerro Pirre, disturbed forest along Cerro Perrecénega, ca. 8°00′N, 77°45′W, ca. 50 m, *McPherson 6977* (F).

20. *Plukenetia*

Plukenetia L., Sp. Pl. 1192. 1753. TYPE: *Plukenetia volubilis* L.

The discovery of a second species of *Plukenetia* in Panama makes it necessary to provide the following key.

KEY TO THE SPECIES OF *PLUKENETIA* IN PANAMA

1a. Leaves palmately veined; stylar column cylindrical, slender, 10–25 mm long; capsules to 3.5 mm broad .... 1. *P. volubilis*
1b. Leaves pinnately veined; stylar column obovoid, to 2 mm long; capsules to 1.5 mm broad .... 2. *P. penninervia*

20.1. Plukenetia volubilis L., Sp. Pl. 1192. 1753. TYPE: West Indies, *Plumier* (perhaps at BM).

This species is more widespread in eastern Panama than was indicated by the single collection cited in the original treatment. These new collections also confirm the identity of the Panamanian species with *Plukenetia volubilis* of the Antilles and South America. Recent collections have also extended the range to Costa Rica (*Gómez et al. 19184*, F), Nicaragua (*White 5323*, F), and Veracruz, Mexico (*Calzada 1034*, F).

Additional specimens examined. PANAMA. COLÓN: upstream from bridge over Río Guanche, 0–100 m, *Antonio 3351* (F, MO); near Portobelo, *Croat 12969* (MO); Portobelo, along stream running into Río Buena Ventura, S of Portobelo, 0–10 m, *Foster 2060* (F, MO); along Río Guanche, 6 km S of Portobelo, 0–10 m, *Nee & Gentry 8686* (MO). DARIÉN: Cerro Pirre, valley between Pirre and next most southerly peak, *Folsom 4426* (F, MO). PANAMÁ: 4–5 hours walk upriver from Tortí Arriba, 200–300 m, *Folsom et al. 6845* (F, MO).

20.2. Plukenetia penninervia Muell. Arg., Linnaea 34: 158. 1864; in DC., Prodr. 15(2): 770. 1866. TYPE: Venezuela, near Biscaina, *Fendler 2412* (holotype, G, not seen; photo F neg. no. 7110).

Plukenetia angustifolia Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 314. 1929. TYPE: Honduras. Atlántida: Lancetilla Valley, 8 Mar. 1928, *Standley 56708* (holotype, F, F neg. 52742).

Liana; twigs spreading-puberulent, glabrescent. *Leaves* with petioles ca. 1 cm long, puberulent; stipules brownish, glabrous, rigid, deltate-lanceolate, 1–1.7 mm long; blades chartaceous-oblong, oblong-elliptic, or oblong-lanceolate, acute to acuminate at tip, abruptly acuminate-truncate at base, 5–10 cm long, 2–4.5 cm broad, glabrous and shining above, glabrate or with a few hairs along the nerves and paler below, with 2 prominent glands above at the base, often with 1–3 pairs of smaller ones in a row above them, pinnately veined, the midrib and secondary veins (6–11 on a side) prominent below; margins shallowly crenate-denticulate. *Inflorescences* axillary, bisexual or staminate, 0.5–3 cm long; pistillate flowers solitary at lower nodes of bisexual inflorescences, the staminate flowers few at the distal nodes. *Staminate flowers* with pedicels short-pilose, 4–7 mm long; calyx segments generally 3, obovate, acute, 1.2–1.6 mm long; receptacle cylindrical, 1.6–1.8 mm high; disk obsolete; stamens ca. 18–25, inserted spirally on the receptacle, the filaments ca. 0.1 mm long, the anthers 0.1–0.2 mm long. *Pistillate flowers* with pedicels becoming 12–20 mm long, these narrowly clavate, strigose when young, glabrate to sparsely short-pubescent at maturity; calyx lobes lanceolate, 1–1.2 mm long, ca. 0.5 mm broad, strigose in a band along the center; ovary of 4 carinate carpels, strigose on the keels, otherwise glabrous, the stylar column to 2 mm long, obovoid, the stigmas thick, unlobed. *Capsules* deeply 4-lobed, oblate, to ca. 1 cm high, 1.5 cm broad, the cocci thick and rigid; seeds subglobose, only slightly compressed laterally, reticulate-venose, brownish mottled, ca. 5 mm long, 3–4 mm thick.

Lowland evergreen rainforests, Mexico (Oaxaca, Yucatán Peninsula) to Colombia and Northern Brazil (Pará); here reported from Panama for the first time.

The discovery of *Plukenetia penninervia* in Panama is not surprising, although it is still unknown in Costa Rica, and the reason for its apparent scarcity in southern Central America is not clear. The populations from northern Central America, where the species is much better known, were described by Standley as *P. angustifolia*, but no salient differences between these plants and those of South America are apparent.

Specimens examined. PANAMA. COLÓN: Santa Rita Ridge, in ravine bottom near Agua Clara rainfall station, 400–500 m, *Foster & Morton 2222* (F); Santa Rita Ridge, ca. 9°20′N, 79°45′W, ca. 500 m, *McPherson 8461* (F). PANAMÁ: 1–2 mi. S of Pan American Highway, 3.0 mi. E of Cañazas checkpoint, foothills of Serranía de Cañazas, 8°52′N, 78°15′W, 0–50 m, *Knapp 3887* (F, MO).

21. *Acidoton*

Acidoton Sw., Prodr. 84. 1788. TYPE: *Acidoton urens* Sw.

21.1 Acidoton nicaraguensis (Hemsley) Webster, Ann. Missouri Bot. Gard. 54: 191. 1967. *Cleidion ?nicaraguensis* Hemsley, Biol. Cent.-Amer., Bot. 3: 130. 1883. TYPE: Nicaragua. Chontales: *Tate 352, 455* (syntypes, presumably K, not seen).

Additional specimens examined. PANAMA. COLÓN: Santa Rita, *Correa & Dressler 607* (MO); Santa Rita Ridge Rd., 20 km from Transisthmian Hwy., 9°24′N, 79°39′W, *Sytsma 1117* (F, MO). PANAMÁ: along the El Llano–Cartí rd., ca. 10 mi. N of Pan Am Hwy., 500 m, *Gentry et al. 8878* (MO). SAN BLAS: El Llano–Cartí road, km 26.5, 9°19′N, 78°55′W, 300–400 m, *de Nevers et al. 5292* (F); Nusagandí, along trail to Quebrada de Nusagandí, *van der Werff 7029* (F).

22. *Tragia*

Tragia L., Sp. Pl. 980. 1753. LECTOTYPE: *Tragia volubilis* L. (chosen by Small in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 458. 1913).

The discovery of three additional species in Panama makes it necessary to provide a key to the Panamanian species.

LITERATURE

PAX, F. & K. HOFFMANN. 1919. Euphorbiaceae—Acalypheae—Plukenetiinae. *In:* A. Engler, Das Pflanzenreich IV. 147. IX (Heft 68): 1–108 (*Tragia*, pp. 32–101).

KEY TO THE SPECIES OF *TRAGIA* IN PANAMA

1a. Leaf blades 12–25 cm long, 11–18 cm broad, often 3-lobed; stamens ca. 40 .... 1. *T. bailloniana*
1b. Leaf blades 6–16 cm long, less than 10 cm broad, unlobed; stamens 2–12.
    2a. Inflorescence bifurcate, the pistillate flowers 5–10 on lower branch; stamens 8–12 .... 2. *T. fendleri*
    2b. Inflorescence racemose, not bifurcate; pistillate flowers solitary at basal node; stamens 2 or 3.
        3a. Pistillate flower long-pedicellate; styles connate .... 3. *T. volubilis*
        3b. Pistillate flower subsessile; styles free .... 4. *T. correae*

22.1. Tragia bailloniana Muell. Arg., Linnaea 34: 178. 1865; in DC., Prodr. 15(2): 927. 1866. TYPE: Mexico. Tabasco: Teapa, *Linden* (P, not seen). *Zuckertia cordata* Baill., Etud. Euphorb. 496, pl. 4, 1858, not *Tragia cordata* Michx., 1803.

Twining vine; stamens and foliage ± densely covered with stinging hairs. *Leaves* with petioles 8–14 cm long; stipules ovate-lanceolate, acuminate, greenish, 7–10 mm long; blades membranous, broadly ovate, unlobed, with a single lateral lobe, or shallowly 3-lobed, acuminate or caudate at tip, deeply cordate at base, 12–25 cm long, 11–18 cm wide, sparsely beset above and below with stinging hairs, usually 7-veined at the base, the margins remotely denticulate. *Inflorescences* opposite the leaves, bifurcate; peduncle 3–10 cm long; staminate branch to 20 cm long, many-flowered; pistillate branch 15–25 cm long, 7–15-flowered. *Staminate flowers* 1–3 per bract; bracts foliaceous, ovate-lanceolate, acuminate, 3–5 mm long, reflexed; pedicels 8–10 mm long, divergent, glabrate; sepals 5, linear-lanceolate, acuminate, ca. 6 mm long; stamens ca. 40; buds pyriform, acute. *Pistillate flowers* solitary in the axil of each bract; bracts similar to those of the staminate flowers; pedicels 1–4 mm long, hirsute; sepals deltate to lanceolate, acute to acuminate, 4–5 mm long; margins ciliate with long, stiff hairs; ovary densely hirsute with stiff hairs ca. 1 mm long; styles black, 6–8 mm long, fused ca. ⅔ their length, the style branches slightly spreading. *Capsules* deeply 3-lobed (one lobe sometimes abortive), ca. 15 mm diam., ca. 8 mm high, densely hirsute with stiff hairs; columella 6–7 mm long, with 3 prominent, narrow wings at tip; seeds nearly globose, ca. 6 mm diam., smooth, with 8 or 9 light longitudinal striations.

Forests, southern Mexico to western Panama.

This distinctive species is the only member of *Tragia* section *Zuckertia* (Baill.) Muell. Arg., distinguished from all other American species of the genus by its numerous stamens (ca. 40 vs. 2 or 3 or rarely up to 20) and its large, usually lobed leaves. The Panamanian collection represents a considerable range extension, for the species had previously been known only from southern Mexico (Veracruz, Chiapas, Yucatán Peninsula) to Honduras. Earlier reports of *Tragia bailloniana* from Costa Rica (Standley, 1937: 622) are erroneously based on collections of *Dalechampia shankii* (see discussion in Huft, 1984); however, several recent collections establish the presence of the former there.

Specimens examined. COSTA RICA. ALAJUELA: along upper Río Sarapiquí, near Cariblanco and along the road to Colonia Virgen del Socorro, 10°18'N, 84°10'W, ca. 800 m, *Burger et al. 11850* (F); lower NE slope of Arenal Volcano, 10°29'N, 84°42'W, 500 m, *Lent 2947* (F). LIMÓN: hills 2 airline km SSE of Islas Buena Vista in the Río Colorado, 14 airline km SW of Barro del Colorado; 83°40'W, 10°40'N, 10–120 m, *Davidse & Herrera 31023* (F, MO); southwesternmost ridge of Cerro Coronel, NW-facing slope, just S of the Río Colorado, 10°40'30"N, 83°39'30"W, 10–80 m, *Davidse & Herrera 31388* (F, MO); Cerro Coronel, E of Laguna Danto; 10°41'N, 83°38'W, 20–170 m, *Stevens 24383* (F, MO). PANAMA. CHIRIQUÍ: Fortuna Dam site, 1,400–1,600 m, *Folsom et al. 5612* (MO).

22.2. Tragia fendleri Muell. Arg., Linnaea 34: 178. 1865; in DC., Prodr. 15(2): 928. 1866. TYPE: Venezuela: Biscaina, *Fendler 1208* (G).

Twining vine; stems and petioles hirsutulous or strigose with mostly nonstinging hairs. *Leaves* with petioles 4–11 cm long; stipules lanceolate, 5 mm long or more; blades thinly chartaceous, oblong- or elliptic-obovate, rather abruptly short-acuminate at tip, distinctly cordate at base with open to closed sinus, mostly 8–16 cm long, 4–7 cm broad, sparsely hispidulous on both faces with stinging and nonstinging hairs, mostly 5-nerved at base; the margins bluntly and coarsely crenate (teeth 15–25 on a side). *Inflorescences* opposite the leaves, becoming ca. 10–15 cm long, distinctly bifurcate and protogynous, the lower pistillate branch with 5–10 flowers; pistillate bracts entire, 3–4 mm long, the staminate ones entire, 1.5–2 mm long. *Staminate flowers* with minutely hispidulous pedicels ca. 1.5–2 mm long, articulate near the base (stumps remaining after dehiscence of flower much shorter than subtending bract); sepals 3 or 4, obovate, acute, strigose without, 1.5–3 mm long, 1.8–2.2 mm broad; disk glands 5, erect, cylindric, thicker than filaments, 0.5–0.8 mm high; stamens 8–12; filaments free; anthers 1–1.2 mm long. *Pistillate flowers* with hispidulous pedicels up to 2.5 mm long in fruit; sepals 6, lanceolate, asymmetric, green, reflexed in fruit, becoming 3.5–6 mm long, 1–1.5 mm broad; ovary densely hispidulous with stinging hairs; styles basally connate or nearly free, 2–2.5 mm long, distinctly papillate. *Capsules* copiously hispid with stinging hairs, cocci ca. 8 mm long; columella 2.4–2.7 mm long; seeds globose, mottled brownish and gray, 3.6–3.7 mm across.

The single specimen of this species, previously unrecorded from Panama, is in poor condition and without flowers, so there is some doubt regarding its assignment. The Bristan collection matches a photograph of the type specimen from Venezuela, although the basal leaf sinus is not as open in the Panamanian plant. There is also some resemblance to *T. japurensis* Muell. Arg., described from Amazonian Brazil. However, it seems probable that the Brazilian species is synonymous with the one from Venezuela; at least, no convincing differences are given by Pax & Hoffmann (1919: 36).

Specimen examined. PANAMA. DARIÉN: Río Uruceca, *Bristan 1444* (MO).

22.4. Tragia correae Huft, sp. nov. TYPE: Panama. Panamá: Picada da Estrada Panamá–San Blas entre 320–420 m, 9.1.1973, *Sucre, Braga, Dressler & Correa 9832* (holotype, RB-165572, F neg. 62359).

Caulis volubilis lignosus; ramunculi rubelli dense pilosi. Folia alterna elliptica-oblonga 6–12 cm longa septemnervia, infra dense pilosa supra sparsia, basi cordata, margine remote denticulata. Inflorescentia racemosa unico flore femineo infime, ceteris floribus (20–25) masculis; flores masculi calyce trilobo, staminibus 3, filamentis crassis, antheris extrorsis; flores feminei calyce 5-lobo, ovario dense hispiduloso, stylis papillatis.

Twining woody vine; twigs reddish, densely pilose, tardily glabrate, the older twigs with loose, exfoliating bark. *Leaves* with petioles 0.5–4 cm long, densely pilose; stipules deltate-lanceolate, acute, 6–10 mm long, pilose below, glabrous above; blades membranous, elliptic-oblong, acuminate at tip, cordate at base, 6–12 cm long, 3–4.5 cm broad, 2.2–2.7 times as long as broad, sparsely pilose above, more densely so below, usually 7-nerved at base; margins remotely denticulate (teeth 18–22 on a side). *Inflorescences* opposite the leaves, racemose, ca. 3 cm long (immature), with a single basal pistillate flower, the remaining nodes (ca. 20–25) with staminate flowers; bracts trifid; bracts entire. *Staminate flowers* on short, hispidulous pedicels; calyx lobes 3, obovate, acute, ca. 1.3 mm long, ca. 1.2 mm broad, hispidulous without, cucullate; stamens 3, the filaments thick and fleshy, free, ca. 0.8 mm long; anthers elliptic, 0.2–0.3 mm long, extrorse. *Pistillate flowers* with pilose pedicels ca. 2 mm long; calyx lobes 5, lanceolate, acute, ca. 3 mm long; ovary densely hispidulous with stinging hairs, the styles free to the base, spreading, papillate, ca. 2 mm long. *Mature capsules* not seen.

In aspect *Tragia correae* resembles the species that Pax & Hoffmann (1919) placed in section *Bia*, particularly such species as *T. fendleri*, *T. japurensis* Muell. Arg., and *T. fallax* Muell. Arg. The new species is excluded from that affinity, however, by its racemose rather than bifurcate inflorescences and staminate flowers with three (vs. 8–20) stamens. The entire sepals and extrorse anthers dictate its placement in section *Tragia* (section *Eutragia* Muell. Arg. of Pax & Hoffmann, 1919). This species bears some similarity to *T. volubilis* but differs by a much woodier habit, densely pilose leaves, and persistently sessile pistillate flowers.

It is a pleasure to name this distinctive new species for Profesora Mireya Correa of the University of Panama. *Tragia correae* is known only from the type collection. Dra. Correa has kindly searched for a duplicate at the herbarium of the University of Panama (PMA), but so far, unfortunately, none has been found.

23. *Dalechampia*

Dalechampia L., Sp. Pl. 1054. 1753. TYPE: *Dalechampia scandens* L.

LITERATURE

ARMBRUSTER, W. S. 1984. Two new species of *Dalechampia* (Euphorbiaceae) from Mesoamerica. Syst. Bot. 9: 272–278.

——— & A. HERZIG. 1984. Partitioning and sharing of pollinators by four sympatric species of *Dalechampia* (Euphorbiaceae) in Panama. Ann. Missouri Bot. Gard. 71: 1–16.

HUFT, M. J. 1984. A new combination in *Dalechampia* (Euphorbiaceae). Ann. Missouri Bot. Gard. 71: 341.

PAX, F. & K. HOFFMANN. 1919. Euphorbiaceae—Dalechampieae. *In:* A. Engler (editor), Das Pflanzenreich IV. 147. XII (Heft 68): 1–59.

WEBSTER, G. L. & B. WEBSTER. 1972. The morphology and relationships of *Dalechampia scandens* (Euphorbiaceae). Amer. J. Bot. 59: 573–586.

As a result of additional collecting in Panama, the species of *Dalechampia* are now considerably better understood, and the number of species has increased from five to seven, necessitating a new key. The order of species has been modified to reflect better their systematic relationships (Webster & Armbruster, unpubl. synopsis).

KEY TO THE SPECIES OF *DALECHAMPIA* IN PANAMA

1a. Leaves lobed or unlobed, never compound.

  2a. Stem tips and inflorescences densely golden-hirsute; leaves unlobed to 3-lobed, mostly 15–30 cm long, with broad, open sinus at base; stamens 60–70 (involucral bracts narrowly spathulate and apically trifid, dull yellowish; bracts of staminate involucel free) .... 1. *D. shankii*

  2b. Stem tips and inflorescences with appressed to spreading hairs, these never golden; leaves mostly smaller, variously shaped; stamens 15–45.

    3a. Bracts of staminate involucel free and disarticulating separately; bractlets within staminate involucel apically lacerate; leaves unlobed (occasionally with 1 or 2 small lateral teeth); involucral bracts creamy or pinkish, marginally lacerate; seeds more or less rugulose.

      4a. Stigma asymmetric, slightly dilated, not over 1.2 mm across; involucral bracts creamy or white with greenish veins; hairs of stem spreading at least in part; leaves persistently pubescent beneath, attenuate-acuminate, basal sinus narrow or lobes overlapping .... 2. *D. canescens* subsp. *friedrichsthalii*

      4b. Stigma peltate, 1–3.5 mm across; involucral bracts pink or purple to white with pink veins (rarely white with greenish veins); hairs of stem appressed; leaves glabrate beneath, cuspidate, with broad open sinus .... 3. *D. dioscoreifolia*

    3b. Bracts of staminate involucel more or less connate into a cup, not disarticulating separately; leaves lobed, at least in part; involucral bracts creamy or white, with entire denticulate margins; seeds smooth.

5a. Unlobed leaves often present with lobed leaves; involucral bracts merely 3-dentate at apex, 7–9-nerved, 3–6.5 cm long; bractlets within staminate involucel apically lacerate .... 5. *D. tiliifolia*

5b. Unlobed leaves rare or absent, the leaves all 3- or 5-lobed; involucral bracts 3-lobed at least to the middle, 5-nerved, 1.5–3 cm long; bractlets within staminate involucel entire, laminar .... 7. *D. scandens*

1b. Leaves compound, 3-foliolate (rarely 5-foliolate).

6a. Young stems and lower leaf surfaces spreading-hirsute; leaflet tips cuspidate-acuminate; involucral bracts white; staminate involucel of 4 separate bracts, staminate bractlets lacerate; central fruiting pedicel ca. 3 cm long .... 4. *D. websteri*

6b. Young stems retrorsely pubescent; leaf blades glabrate; leaflet tips acute to evenly acuminate; involucral bracts green; staminate involucel 2-lipped (bracts confluent); staminate bractlets truncate, laminar; central fruiting pedicel ca. 1 cm long .... 6. *D. cissifolia* subsp. *panamensis*

23.1. Dalechampia shankii (A. Molina) Huft, Ann. Missouri Bot. Gard. 71: 341. 1984. *Tragia shankii* A. Molina, Ceiba 11: 68. 1965. TYPE: Costa Rica. Limón: Río Reventazón, 15 m, 23 Oct. 1951, *Shank & Molina 4427* (holotype, F).

This species, originally described from Costa Rica, has now been recorded from Nicaragua to Colombia. It may easily be distinguished from our other Panamanian species by its large and distinctive golden hairs, as well as yellowish, narrowly spathulate, trifid involucral bracts. The free bracts of the staminate involucel and the lacerate staminate bractlets indicate that the species belongs to section *Dioscoreifoliae* in the emended sense (Webster & Armbruster, ined.), along with the two following Panamanian taxa. The collections of Barry Hammel show that *D. shankii* is polymorphic in leaf shape, since leaf blades from the single locality vary from unlobed to having one lateral lobe to three-lobed. Additional collections from Costa Rica, Panama, and Colombia are cited by Huft (1984).

Specimens examined. PANAMA. COCLÉ: near sawmill, 16.7 km N of turnoff to Coclesito from Llano Grande, 700 ft., *Hammel 1811, 1812, 1813* (MO); 12 mi. from Llano Grande, 200 m, *Churchill et al. 4148* (F, MO).

23.2. Dalechampia canescens Kunth subsp. **friedrichsthalii** (Muell. Arg.) Webster & Huft, stat. nov. *Dalechampia friedrichsthalii* Muell. Arg., Flora 55: 45. 1872. TYPE: Nicaragua. Río San Juan: *Friedrichsthal 683* (not seen; locality erroneously cited by Mueller as Guatemala).

Several additional collections of this plant have now been made in Panama.

Specimens examined. PANAMA. COLÓN: along Río Mendosa, 8 km NW of Gamboa *Nee & Smith 11370* (MO); Río Fato, *Pittier 3866* (GH, NY, US); Río Boquerón, 6–8 km upstream from Peluca Hydro Station, *Siri 1005* (DAV). SAN BLAS: Puerto Obaldía, sea level, *Knapp & Mallet 4627* (DAV, MO).

It now appears that *Dalechampia friedrichsthalii* is excessively close morphologically to *D. canescens* Kunth (Nov. Gen. Sp. 2: 98. 1817). The collection from San Blas in particular seems somewhat intermediate, and it makes more sense biologically to treat the two taxa as allopatrically replacing subspecies of a single species. The two subspecies may be keyed out as follows:

1a. Leaf blades mostly attenuate-acuminate, sparsely to moderately pubescent beneath (hairs mostly 0.1–0.2 mm long, not overlapping in sinuses between veinlets) .... subsp. *friedrichsthalii*

1b. Leaf blades mostly abruptly cuspidate, softly pubescent beneath (many hairs over 0.2 mm long, overlapping in sinuses between veinlets) .... subsp. *canescens*

The Colombian taxon, subsp. *canescens*, was described from Tolima Province (Mariquita) and cited from Nariño by Pax & Hoffmann (1919: 52). The additional collections cited below indicate that subsp. *canescens* is widely distributed in the lowlands and foothills of the western Andean region in Colombia.

Specimens examined. COLOMBIA. CALDAS: Quebrada Yeguas, 20 km N of Honda, 300 m, *Gentry et al. 18167* (DAV, MO). CAUCA: Río Patía, 590 m, *Plowman & Vaughan 5354* (DAV). SANTANDER: 29 km W of San Vicente de Chucurí, 200 m, *Gentry & Aguirre 15429* (MO).

23.3. Dalechampia dioscoreifolia Poeppig in Poeppig & Endl., Nov. Gen. Sp. Pl. 3: 20. 1841. TYPE: Peru. Maynas: *Poeppig 2163* (W).

One additional locality merits noting: PANAMA. DARIÉN: near Río Canglón, *Duke & Bristan 378* (MO).

An unusual specimen from Playón Chico, San

Blas (*Gentry 6365*, MO) appears to be intermediate between *D. dioscoreifolia* and *D. canescens* subsp. *friedrichsthalii*, having the broad stigma of the former and the pubescent attenuate-acuminate leaves of the latter.

23.4. Dalechampia websteri Armbruster, Syst. Bot. 9: 272. 1984. TYPE: Costa Rica. Heredia: La Selva, 3 km SE of Puerto Viejo, *Armbruster & Herzig 79-207* (DAV).

This species, recently described from Costa Rica, has been identified from Panama on the basis of the single record that was attributed (with doubt) to *D. cissifolia* in our treatment of 1968.

Specimen examined. PANAMA. BOCAS DEL TORO: Chiriquicito, *Lewis et al. 2123* (MO).

23.5. Dalechampia cissifolia Poeppig subsp. **panamensis** (Pax & K. Hoffm.) Webster, Ann. Missouri Bot. Gard. 54: 193. 1967. *D. panamensis* Pax & K. Hoffm., Pflanzenreich IV. 147. XII (Heft 68): 19. 1919. SYNTYPES: Costa Rica: *Tonduz 8089*, Guatemala: Cubilgüitz, *Tuerckheim II. 244*, *7978*, Mexico. Chiapas: Escuintla, *Donnell Smith 2079*. Panama: *Oersted; Pittier 2311*, *3775*.

This species still requires additional study. A variant with simple, unlobed leaves mixed with the compound ones, to which the name *Dalechampia heteromorpha* Pax & K. Hoffm. has been applied, occurs in Panama and throughout Central America but does not appear to be specifically distinct from the South American subsp. *cissifolia*.

There is one new provincial record for *D. cissifolia* subsp. *panamensis*.

Additional specimen examined. PANAMA. BOCAS DEL TORO: 10 mi. NW of Almirante, *D'Arcy 11204A* (MO).

24. *Omphalea*

Omphalea L., Syst. Nat. ed. 10. 1264. 1759. Nomen conserv. TYPE: *Omphalea triandra* L. (typ. conserv.).

24.1. Omphalea diandra L., Sp. Pl. ed. 2. 1377. 1763. TYPE: Jamaica, *Browne* (presumably BM, not seen).

Additional specimen examined. PANAMA. CHIRIQUÍ: Burica Peninsula, 2–4 mi. SW of Puerto Armuelles, *Croat 22045*, *Liesner 409* (MO).

25. *Pera*

Pera Mutis, Kongl. Vetensk. Akad. Nya. Handl. 5: 299, tab. 8. 1784. TYPE: *Pera arborea* Mutis.

Subfamily III. CROTONOIDEAE Pax

26. *Tetrorchidium*

Tetrorchidium Poeppig in Poeppig & Endl., Gen. Nov. Sp. Pl. 3: 23, tab. 227. 1841. TYPE: *Tetrorchidium rubrivenium* Poeppig.

The discovery of two distinctive new species in western Panama makes it necessary to provide a revised key. New province records are also recorded.

KEY TO THE SPECIES OF *TETRORCHIDIUM* IN PANAMA

1a. Stems knobby, the apex densely hirsute or strigose.
  2a. Stems with persistent swollen stipules; leaves less than 7 cm long, the paired glands toward the apex of the petiole .... 1. *T. microphyllum*
  2b. Stems with raised leaf scars, the stipules persistent or not, rarely swollen; leaves usually over 10 cm long, the paired glands near the middle of the petiole .... 2. *T. costaricense*
1b. Stems smooth, the apex appressed-pubescent or glabrescent; leaves mostly more than 7 cm long; staminate inflorescence usually more than 4 cm long.
  3a. Basal foliar glands ca. 0.5–0.6 mm thick, definitely attached on laminar tissue; leaves mostly 15 cm long or more, with 6 or 7 prominent lateral veins; pistillate flowers sessile .... 3. *T. euryphyllum*
  3b. Basal foliar glands ca. 0.15–0.3 mm thick, attached at junction of lamina and petiole or well down on petiole; leaves 7–12 cm long, mostly with only 4 or 5 prominent lateral veins; pistillate flowers with distinct pedicels mostly 1.5–2 mm long .... 4. *T. gorgonae*

26.1. Tetrorchidium microphyllum Huft, sp. nov. TYPE: Panama. Chiriquí: 3.5 mi. NE of Boquete, end of road along Río Alto, 6,200 ft., 18 Nov. 1978, *Hammel 5721* (holotype, MO; isotype, F, F neg. 62357). Figure 2.

Arbor mediocris, gracilis, dioecia; ramulis junioribus fragilibus, praeter apicem dense hirsutum, glabris; foliis oblanceolatis, 2.5–7 cm longis, sparsim pubescentibus utrinque pilis malpighiaceis vel glabratis, margine integris, apice acuminatis; petiolis brevibus, dense appressis pubescentibus pilis malpighiaceis; stipulis glanduliformibus, tumidis, persistentibus; floribus masculis in thyrsis axillaribus ad 3 cm longis; floribus femineis et capsulis ignotis.

Dioecious *tree* to 10 m; branches brittle, glabrous except at tips where densely hirsute, appearing warty by the presence of persistent, swollen

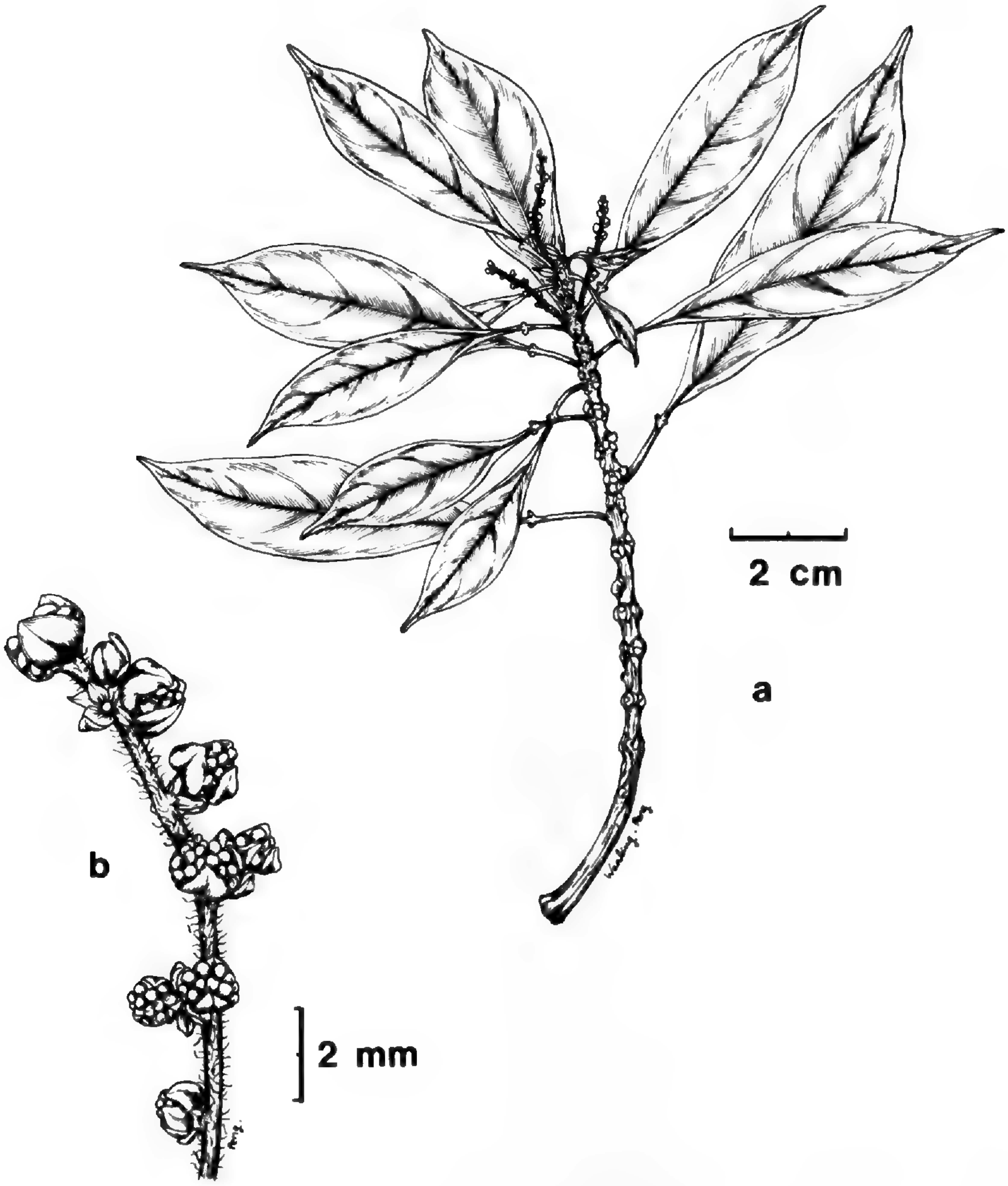

FIGURE 2. Tetrorchidium microphyllum.—*a. Habit.—b. Detail of staminate inflorescence. Based on* Hammel 6039. *Illustration by Wan-Ling Peng.*

stipules. *Leaves* short-petiolate, crowded near ends of branches; petioles 0.5–1.2(–1.5) cm long, densely appressed-pubescent with malpighiaceous hairs to glabrate, with massive, paired, thick-stalked, opposite or subopposite glands near the tip, these 0.6–0.8 mm long, 0.8–1 mm thick, stipules glanduliform, tumid, broadly triangular, 1.5–2 mm long, densely pubescent, persistent, glabrate soon after leaf-fall; blades chartaceous, oblanceolate, acuminate at tip, cuneate at base, (2.5–)4–5.5(–7) cm long, (0.9–1)1.2–2 cm broad, sparsely pubescent with malpighiaceous hairs to glabrate on both sides, the midrib and primary veins (3–4 on a side) prominently raised below, the veinlets forming a prominent reticulum; margins entire. *Inflorescences* axillary; staminate thyrses unbranched, 1.5–3 cm long, the rachis densely strigose; pistillate inflorescences unknown. *Staminate flowers* subsessile; calyx lobes 3, triangular, glabrous, ca. 1–1.2 mm long; petals lacking; anthers subsessile, 0.8–0.9 mm long. *Pistillate flowers* unknown. *Fruits* unknown.

Cloud forests, western Panama.

This distinctive new species of *Tetrorchidium* appears to be most closely related to *T. brevifolium* Standley & Steyerm., described from the province of Alta Verapaz, Guatemala (Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 126. 1944), from which it differs by the smaller leaves (7–12 cm long in *T. brevifolium*), densely pubescent shoot apices and inflorescences (both glabrous in *T. brevifolium*), and shorter inflorescences (4–7 cm long in *T. brevifolium*). The type specimen of the Guatemalan species (Rubelpec, Finca Seamay, *Wilson 188*, F) lacks the persistent tumid stipules that are so characteristic of *T. microphyllum*, but these are present on several collections of the former species made in 1974 and 1975 from Baja Verapaz, Guatemala (*Lundell & Contreras 19173, 19436* (both

F, LL); *Williams et al. 43277*, F). The type specimen consists only of branchlet tips with a few leaves and staminate inflorescences that appear to have been taken from rapidly growing long shoots. *Tetrorchidium molinae* L. Williams, described from cloud forests in the mountains above San Juancito, Honduras (Fieldiana, Bot. 29: 348. 1961, based on *Williams & Molina 17068*, F), is similar in all respects to *T. brevifolium* and should be relegated to the synonymy of that species. A paratype specimen of *T. molinae* from the same area, *Williams & Molina 13980* (F), has long shoots without stipules attached to a normal shoot with persistent stipules. This matches the pattern of the type collection of *T. brevifolium*, thus confirming the suspicion voiced above concerning the nature of that collection.

Additional specimen examined. PANAMA. CHIRIQUÍ: end of road past Palo Alto NE of Boquete in forest along ridge, 6,200–6,800 ft., *Hammel 6039* (F, MO).

26.2. Tetrorchidium costaricense Huft, sp. nov. TYPE: Costa Rica. Puntarenas: Cordillera de Tilarán, Monteverde Reserve, near Continental Divide on Pacific side, 1,520–1,580 m, *Dryer 1403* (holotype, CR, F neg. 62351; isotypes, F, F neg. 62350, MO, F neg. 62349).

Arbor ad 16 m alta, dioecia; ramulis junioribus dense strigosis; foliis anguste oblongis, 8–16 cm longis, apice abrupte cuspidatis; petiolis longis, prope medium glandibus binatis; floribus masculis sessilibus, in thyrsis axillaribus 4–9 cm longis; floribus femineis subsessilibus, ad fructus maturitatem brevipedicellatis, segmentis disci discretis ligulatis; ovariis 2-locularibus; seminum ovoideis, grosse reticulatis.

Dioecious *tree* to 16 m; branches densely strigose toward tip, appearing knobby from the raised leaf scars and occasionally from persistent, indurate stipules. *Leaves* long-petiolate, not crowded toward ends of branches; petioles 2.5–6 cm long, glabrous or minutely strigose, with paired, subopposite, sessile, patelliform glands near the middle, these ca. 1 mm (rarely to 2.2 mm) diam.; stipules oblong, 1.5–2.5 mm long, 1–1.5 mm broad, densely strigose, persistent, sometimes indurate after leaf-fall; blades membranous, narrowly oblong, 8–16 cm long, 3–7 cm broad, 2.2–3.3 times as long as broad, abruptly cuspidate at tip with an acumen 5–10 mm long, acute to attenuate at base, minutely puberulent below with scattered short malpighiaceous hairs, glabrous or nearly so above, the midrib prominent below, the secondary veins 6–8 on a side, arcuate, prominent below, obscure above; margin entire, eglandular. *Inflorescences* axillary, the axes densely strigose with short malpighiaceous hairs; staminate thyrses 4–9 cm long, freely branched, the lateral branches to 3.5 cm long; pistillate racemes to 5 cm long. *Staminate flowers* in glomerules of 2–5, sessile; sepals 3, obovate, cucullate, glabrous without, pilose within; anthers subsessile, 1.3–1.5 mm broad. *Pistillate flowers* subsessile, the pedicels becoming 0.5–3 mm long in fruit; sepals broadly ovate, obtuse, 3–3.5 mm long, glabrous or sparingly short-strigose without, densely hispid toward base within; disk segments free, narrowly ligulate, ca. 2 mm long; ovary smooth, 2-locular, glabrous above, densely long-strigose below; style cap at maturity 0.5–0.8 mm high, 1.5–1.8 mm diam. *Capsule* 3–5 mm high, 5–6 mm diam., glabrous, oblate to globose; seeds ovoid-lenticular, 5–6 mm long, prominently and coarsely reticulate, the caruncle an irregular yellow papery keel running halfway from the hilum to the apex.

Known only from Costa Rica and extreme western Panama, this distinctive species is easily distinguished by the large, dark green, lanceolate leaves that are conspicuously venose, the paired glands near the middle of the rather long petioles, and the densely and minutely strigose branchlet tips, petioles, and leaves.

Tetrorchidium costaricense belongs to the group of species with free ligulate disk segments in the pistillate flower that includes *T. rotundatum* Standley and *T. brevifolium* Standley & Steyerm. in northern Central America. Like *T. costaricense*, *T. rotundifolium* has paired glands near the middle of long petioles, but differs in its completely glabrous stems and leaves, mostly unbranched staminate thyrses that have larger glomerules, densely pubescent pistillate calyces, and distinctly pedicellate fruits. *Tetrorchidium brevifolium* differs in its glabrous stems, leaves, and calyces, short petioles with paired glands near the tip, and unbranched staminate thyrses. The widespread South American species *T. rubrivenium* Poeppig also belongs to this group but has glabrous stems and leaves, crenate or denticulate leaf margins, sometimes long petioles with the paired glands near the tip, densely pubescent pistillate calyces, uniformly puberulent ovary and capsule, and pedicellate fruits.

Additional specimens examined. COSTA RICA. ALAJUELA: Cordillera de Tilarán, Monteverde Reserve, Atlantic side, 1,500–1,580 m, *Dryer 1071* (CR, F). CARTAGO: Reserva de Tapantí, 1,300–1,800 m, *Gómez 18752* (F). PUNTARENAS: Cordillera de Tilarán, Monteverde Reserve, Pacific side, en orilla de Pantano Chomogo, 1,600–1,620 m, *Dryer 659* (CR), *887* (CR, F); Monteverde Reserve, at field station, 1,500 m, *Haber 491* (F); Monteverde Reserve, 1,570 m, *Haber & Bello 1640* (F), 1,500 m, *Haber & Bello 2457* (F). ALAJUELA/PUNTARENAS: on and near the Continental Divide, ca. 2–5 km

E and SE of Monteverde, 10°18′N, 84°46′W, 1,580–1,700 m, *Burger & Gentry 8608* (F); Monteverde, *Dryer 1731* (F). SAN JOSÉ: bajo de La Hondura, *Poveda 862* (CR, USJ). PANAMA. BOCAS DEL TORO: along Continental Divide, trail to headwaters of Río Mali, to W of Oleoducto Road, 8°47′N, 82°13′W, 1,200 m, *Churchill 5276* (F); Fortuna Dam region, along Continental Divide W of highway pass, ca. 8°45′N, 82°15′W, ca. 1,200 m, *McPherson 9695* (F).

26.3. **Tetrorchidium euryphyllum** Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 219. 1929. TYPE: Panama. Bocas del Toro: vicinity of Almirante, 1928, *Cooper 621* (holotype, F).

When the original treatment was written, this species was known only from Costa Rica and extreme western Panama, but recent collections in Panama have now extended its range eastward to Darién.

Additional specimens examined. PANAMA. BOCAS DEL TORO: between Quebrada and Buena Vista, *Kirkbride & Duke 662* (MO). CHIRIQUÍ: Fortuna Dam region, along Quebrada Arena, ca. 8°45′N, 82°15′W, ca. 1,100 m, *McPherson 8394* (F). COCLÉ: slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12196* (MO, 2 sheets); Cerro Pilón, *Dwyer 8330* (MO); La Mesa, 8.5 mi. from Club Campestre (El Valle), *Dwyer 10515* (MO); Margarita near chicken farm, *Dwyer & Duke 8280* (MO); La Mesa, above El Valle, *Dwyer & Nee 11938* (MO); La Mesa, 4 km N of El Valle, 850–875 m, *Nee & Dwyer 9212* (MO). DARIÉN: Cerro Sapo, ca. 2,500 ft., *Hammel 1240* (MO). SAN BLAS: Cerro Brewster, 9°18′N, 79°16′W, 850 m, *de Nevers et al. 5408* (F). VERAGUAS: Caribbean slope above Río Primero Brazo, 5 mi. NW of Santa Fe, 700–1,200 m, *Croat 23233* (MO); NW of Santa Fe, 4.2 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 4831* (MO); ca. 2.7 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 5359, 6208* (MO); 7 km W of Santa Fe on road past agricultural school, 2,900 ft., *Nee 11216* (MO).

26.4. **Tetrorchidium gorgonae** Croizat subsp. **robledoanum** (Cuatrec.) Webster, Ann. Missouri Bot. Gard. 54: 199. 1967. *T. robledoanum* Cuatrec., Brittonia 9: 81. 1957. TYPE: Colombia. Antioquia: 23 Jan. 1947, *Gutiérrez 35556* (holotype, CAL, not seen).

This species is still unknown in Central America outside of Central Panama. Several recent collections allow a description of the fruit to be made for the first time. They are on densely strigose pedicels 7–10 mm long and jointed below the middle. The capsule is green, drying to brown, globose, shallowly 3-lobed, rugulose, 4–6 mm high, 4.5–7 mm in diameter, more or less densely strigose with short (0.2–0.6 mm) malpighiaceous hairs. The 3 styles are deeply bifid, 0.6–0.7 mm long, and tumid. The seeds are ovoid, 4–5 mm long, 3–4 mm in diameter, black, coarsely and shallowly pitted, and completely surrounded by bright red, juicy arils.

Additional specimens examined. PANAMA. COLÓN: Santa Rita Ridge Road 1.5 mi. from Transisthmian Hwy., *Dwyer & Gentry 9338* (MO, 2 sheets); Santa Rita Ridge Road 4 mi. from Transisthmian Hwy. to Agua Clara weather station, ca. 500 m, *Gentry et al. 8841* (MO, 2 sheets); in forest along Río Guanche 3–7 km above bridge, 300–700 ft., *Hammel 4894* (MO). PANAMÁ: El Llano–Cartí highway, 17–20 km N of El Llano, *Dressler 4629* (F, MO); 10 km N of Margarita on road to Madroño, then 3 km W on ridgetop road, 1,800 ft., *Hammel 6014* (MO); Cerro Jefe region 2.5 mi. N of turnoff to radio tower along road, 2,400 ft., *Hammel 6300* (MO); El Llano–Cartí road, 9.6–11 km from Inter-American Hwy., 350 m, *Mori & Kallunki 3531* (MO); 5–10 km NE of Altos de Pacora on trail at end of road, 700–800 m, *Mori & Kallunki 6058* (MO); El Llano–Cartí road, 8 km N of Pan Am. Hwy. at El Llano, ca. 450 m, *Nee & Warmbrodt 10391* (MO).

27. *Manihot*

Manihot Miller, Gard. Dict. abr. ed. 4. 1754. TYPE: *Manihot esculenta* Crantz (*Jatropha manihot* L.).

RECENT LITERATURE

ROGERS, D. J. & S. G. APPAN. 1973. *Manihot; Manihotoides.* Fl. Neotropica 13: 1–272.

——— & H. S. FLEMING. 1973. A monograph of *Manihot esculenta*—with an explanation of the taximetric methods used. Econ. Bot. 27: 1–113.

The discovery of an additional *Panamanian* species necessitates a revised key and enumeration.

KEY TO THE SPECIES OF *MANIHOT* IN PANAMA

1a. Leaves glabrous, mostly with 7–9 lobes; calyx glabrous within (12–14 mm long; disk entire; anthers glabrous; ovary not sharply ribbed or winged) .... 1. *M. aesculifolia*
1b. Leaves pubescent or with fewer lobes; calyx pubescent within.
  2a. Leaves pubescent, mostly with 5 or more lobes; ovary distinctly ribbed or winged; staminate calyx 3–4.5 mm long; anthers pubescent; shrubs with erect stems .... 2. *M. esculenta*
  2b. Leaves glabrous, strictly 3-lobed; ovary not ribbed or winged; staminate calyx 10–20 mm long; anthers glabrous; clambering vine .... 3. *M. brachyloba*

27.1. **Manihot aesculifolia** (Kunth) Pohl, Pl. Bras. Icon. Descr. 1: 55. 1827. *Janipha aesculifolia* Kunth, Nov. Gen. Sp. 2: 85, tab. 109. 1817. TYPE: Mexico. Campeche: *Humboldt & Bonpland* (P, not seen).

This plant was called *M. gualanensis* Blake in our original treatment, but that name has been reduced to a synonym of *M. aesculifolia* in the recent monograph of the genus by Rogers & Appan cited above.

27.3. Manihot brachyloba Muell. Arg., Fl. Brasil 11(2): 451. 1874; Rogers & Appan, Fl. Neotrop. 13: 190–192. 1973. TYPE: Brazil. Pará: *Martius* (syntype, G; microfiche seen).

The Bristan specimens have very young inflorescences but vegetatively match the description and illustration given by Rogers & Appan. However, contrary to their description and that of Mueller, the staminate buds in the Panamanian specimens are pubescent externally.

Specimens examined. PANAMA. DARIÉN: headwaters of Río Tuqueza, between Quebrado Venado and Peje Swamp, *Bristan 1001* (DAV, MO); between Manené and Río Coasí, *Hartman 12127* (MO).

28. *Cnidoscolus*[4]

Cnidoscolus Pohl, Pl. Brasil. Icon. Descr. 1: 56. 1827. LECTOTYPE: *Cnidoscolus hamosus* Pohl (chosen by Small in Britton & Brown, Illust. Fl. N. U.S. ed. 2, 2: 462. 1913).

28.1. Cnidoscolus urens (L.) Arthur, Torreya 21: 11. 1921. *Jatropha urens* L., Sp. Pl. 1007. 1753. TYPE: "America calidiori, in Brasilia & c." (not seen, possibly in Hortus Cliffortianus Herbarium, BM).

Since the treatment of 1968, further study of the Panamanian specimens of *C. urens* leads to the conclusion that the two variants discussed there merit taxonomic recognition. Pending a more detailed revision of the *C. urens* complex (Breckon, ined.), the Panamanian plants may be disposed of as follows.

28.1a. Cnidoscolus urens (L.) Arthur subsp. **urens.**

Specimens examined. PANAMA. PANAMÁ: Farfan Beach area, *Correa et al. 1586, Dwyer 3065, Tyson 1803* (MO). COCLÉ: between Aguadulce and San Antón, *Woodson et al. 1226a* (MO); between Antón and Natá, *D'Arcy & Croat 4117* (MO); banks of Río Grande, *Burch et al. 1157* (MO). HERRERA: Chitré to Divisa, *Burch et al. 1357* (MO); Sal Salinas de Chitré, *Croat 9692* (MO). PANAMÁ: San Carlos, *de McPherson 11* (MO).

28.1b. Cnidoscolus urens subsp. **adenophilus** (Pax & K. Hoffm.) Breckon, stat. nov. *Jatropha adenophila* Pax & K. Hoffm., Pflanzenreich IV. 147. VII(Heft 63): 409. 1914. *Cnidoscolus adenophilus* (Pax & K. Hoffm.) Pax & K. Hoffm., Nat. Pflanzenfam. ed. 2, 19c: 166. 1931. TYPE: Panama. Panamá: Chepo, *Pittier 4740* (isotype, US).

Specimens examined. PANAMA. CANAL ZONE: Miraflores Locks, *Stern et al. 81* (MO); Pipeline Road, *Croat 12732* (MO); Curundú, *McDaniel 5180* (MO), *Tyson 1045* (MO); Ft. Amador Islands, *Tyson 5413* (MO). DARIÉN: El Real, *Lazor & Correa 3364* (MO), *Stern et al. 454* (MO). LOS SANTOS: 5 mi. NW of Guararé, *Wilbur et al. 12054* (MO); Monagre Beach, *Lewis et al. 1673* (MO). PANAMÁ: Jenine, Río Cañita, *Duke 3821* (MO); between Las Margaritas and Río Mamoní, *Duke 5867* (MO); Puente de Pacora, *De Hoyos 18* (MO). VERAGUAS: 2–4 mi. E of Santiago, *Duke 12354* (MO); 12 km E of Santiago, *Dwyer & Kirkbride 7450* (MO).

28.2. Cnidoscolus aconitifolius (Miller) I. M. Johnston, Contr. Gray Herb. 68: 86. 1923. subsp. **aconitifolius.** *Jatropha aconitifolius* Miller, Gard. Dict. ed. 8. 1768. TYPE: *Herb. Miller* (presumably at BM, not seen).

In the present interpretation, the Panamanian specimens of *Cnidoscolus aconitifolius* all belong to the nominate subspecies, which is not native to Panama.

29. *Jatropha*

Jatropha L., Sp. Pl. 1006. 1753. LECTOTYPE: *Jatropha gossypiifolia* L. (see McVaugh, 1944: 459).

RECENT LITERATURE

DEHGAN, B. 1982. Comparative anatomy of the petiole and infrageneric relationships in *Jatropha* (Euphorbiaceae). Amer. J. Bot. 69: 1283–1295.

———. 1984. Phylogenetic significance of interspecific hybridization in *Jatropha* (Euphorbiaceae). Syst. Bot. 9: 467–478.

——— & G. L. WEBSTER. 1979. Morphology and infrageneric relationships of the genus *Jatropha* (Euphorbiaceae). Univ. Calif. Publ. Bot. 74: 1–73.

MCVAUGH, R. 1944. The genus *Cnidoscolus*: generic limits and intrageneric groups. Bull. Torrey Bot. Club 71: 457–474.

30. *Pausandra*

Pausandra Radlk., Flora 53: 92, tab. 2. 1870. TYPE: *Pausandra morisiana* (Casar.) Radlk. (*Thouinia morisiana* Casar.).

Dioecious *trees* or shrubs; stems with reddish latex; indumentum malpighiaceous. *Leaves* alter-

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[4] Contributed by Dr. Gary Breckon, University of Puerto Rico, Mayagüez.

nate, simple; petioles swollen distally; blades pinnately veined, biglandular at base, the margins serrate. *Inflorescences* axillary, spiciform; staminate flowers in glomerules; pistillate flowers solitary at each node; bracts inconspicuous, eglandular. *Staminate flowers* subsessile; calyx lobes 5, imbricate; petals 5 or rarely 6, connate (at least below), adaxially villous; disk extrastaminal, urceloate, lobate, glabrous; stamens (3–)5–7; filaments free; anthers dehiscing introrsely and longitudinally, the connective not enlarged; pollen grains globose, inaperturate, clavate; pistillode absent. *Pistillate flowers* subsessile; sepals 5, imbricate; petals 5, free, adaxially villous; disk urceolate, sometimes lobate, glabrous; ovary of 3 carpels; ovules 1 per locule; styles free, bifid. *Fruits* capsular; seeds smooth, carunculate; endosperm copious; embryo straight, cotyledons palmatinerved, much longer than radicle.

This primarily South American genus is here reported from Panama for the first time.

LITERATURE

BAILLON, H. 1873. Nouvelles observations sur les Euphorbiacées. Adansonia 11: 72–138.

LANJOUW, J. 1936. The genus *Pausandra* Radlk. Recueil Trav. Bot. Néerl. 33: 758–769.

30.1. Pausandra trianae Baillon, Adansonia 11: 92. 1873, proposed without reference to *Pogonophora trianae* Muell. Arg. TYPE: Colombia: Bogotá, plains of San Martín, Río Meta, *Triana 2597* (holotype, P, not seen; isotypes, G, not seen, photo F neg. 24574, K, not seen, holotype of *Pogonophora trianae* Muell. Arg.).

Pogonophora trianae Muell. Arg., Flora 47: 434. 1864. TYPE: Colombia. Bogotá: plains of San Martín, Río Meta, *Triana 2597* (holotype, K, not seen, isotypes, G, not seen, photo F neg. 24574, P, not seen, holotype of *Pausandra trianae* Baillon).

Pausandra quadriglandulosa Pax & K. Hoffm., Pflanzenreich IV. 147. XIV(Heft 68): 43. 1919. TYPE: Brazil: Rio Acre, Seringal S. Francisco, *Ule 9538* (holotype, B, not seen, photo F neg. 5406).

Pausandra extorris Standley, Trop. Woods 17: 24. Mar. 1929; Publ. Field Columbian Mus., Bot. Ser. 4: 219. Oct. 1929. TYPE: Nicaragua: Bragman's Bluff, *Englesing 216* (holotype, F, F neg. 52719; wood sample, Y no. 13301).

Clavija septentrionalis L. O. Williams, Fieldiana, Bot. 32: 205. 1970. TYPE: Nicaragua: Cabo Gracias a Dios, Laimos Creek, ca. 15 km SW of Waspam, 7 Mar. 1961, *Bunting & Licht 390* (holotype, F; isotypes, NY, US).

Tree to 30 m; branching pagodiform; sap dark red-brown; twigs and buds ± densely brown-puberulent with malpighiaceous hairs; leaf scars prominent. *Leaves* horizontally aligned; petiole 1.5–3.5 cm long, 2–4 mm thick, terete, strigose with short (to 0.5 mm long) malpighiaceous hairs; glands at apex of petiole (3–)4, cylindrical, 1–1.5 mm long, ca. 1 mm thick; blade chartaceous, obovate to oblanceolate, rounded, obtuse, or abruptly short-cuspidate at tip, long-attenuate at base, 20–50 cm long, 7–18 cm broad, 2.6–4 times as long as broad, glabrous above, glabrate or thinly puberulent with short malpighiaceous hairs below, the secondary veins prominent, 15–23 per side; margin remotely denticulate. *Inflorescences* spicate, arising singly in the upper axils, 10–25 cm long, the rachis densely puberulent. *Staminate flowers* 6–12 per glomerule, these sessile, widely spaced; sepals 5, imbricate, densely puberulent, obovate, ca. 1.5 mm long, ca. 1.5 mm broad, rounded at apex; petals 5, white, narrowly obovate, ca. 6 mm long, glabrous without, densely hirsute toward base within; stamens 6, exserted, the filaments 5–6 mm long; disk cupulate. *Pistillate flowers* not seen. *Capsule* smooth, strigose with short malpighiaceous hairs, apparently subglobose, ca. 1 mm diam. (fragments only seen); columella 7–8 mm long; seeds subglobose, brown with irregular white striations, 8–9 mm long, ca. 6 mm diam.; caruncle a flattened irregular mass near hilum.

Rainforests, Honduras to western Brazil.

The description is based on the Panamanian specimens cited below and supplemented by collections at F from Costa Rica and Nicaragua.

The genus *Pausandra* remains poorly understood. The most recent revision (Lanjouw, 1936) was based upon only 33 collections and resulted in the recognition of nine species, most known from only a single sex. Lanjouw admitted that several of the species might need to be united as more material became available. *Pausandra trianae* does appear, however, to be one of the better-delimited species in the genus and is certainly the most widespread. The Central American plants readily key to that species in Lanjouw's revision, where *P. extorris* and *P. quadriglandulosa* are reduced to synonymy. The identity of *Clavija septentrionalis* as *P. trianae* was first pointed out by R. L. Liesner of the Missouri Botanical Garden (pers. comm.).

The author citation for *Pausandra trianae* has been almost universally given for the last century as *Pausandra trianae* (Muell. Arg.) Baillon, carrying the implication that Baillon had transferred *Pogonophora trianae* Muell. Arg. to its correct place in *Pausandra*. It is clear from Baillon's text, however, that he intended to describe a new species; there is no indication that he was aware of Mueller's name. Baillon's paper (1873) is a series of miscellaneous notes on the Euphorbiaceae. Under *Pausandra* (pp. 92–93), he stated that the genus was described in 1870 and was known by a single species, *P. morisiana*. He then indicated that a collection from Colombia (*Triana 2597*) represented an additional species in the genus, which may be given the name *P. trianae*. ("Ce genre est aussi représenté à la Nouvelle-Grenade, par une plante qui est bien voisin de celle de Brésil, qui n'en est peut-être même qu'une forme; je lui donnerai provisoirement le nom de *P. Trianae*.") No reference whatever was made to Mueller's name, and none would be expected. One would not normally look in *Pogonophora* for species pertaining to *Pausandra*; the genera are too different for that.

The fact that the names of Mueller and of Baillon are both based on the same collection, although on different specimens, is merely a coincidence. That both chose the same epithet is also coincidental, but not very surprising, given the common practice of naming species after the collector of the type.

Thus, although Baillon ideally should have made a transfer of Mueller's name, he was understandably unaware that Mueller had previously described the species at hand, and did not make the transfer. Had the two authors chosen different epithets, then the rules would mandate a transfer of Mueller's epithet to create a new combination in *Pausandra* supplanting Baillon's name. But that solution is closed because it would create a later homonym. Article 63 of the Code (Voss, 1983) might mislead one to reject Baillon's name as superfluous, because it seems to be based on the type of a name whose epithet ought to have been adopted under the rules. A correct reading of the Code, however, makes it clear that a type is a *specimen*, and not a gathering, which usually consists of several duplicate specimens. An isotype has no official standing as long as the holotype exists, although its value is unquestioned. Thus, for a name to be rejected as superfluous, it must be based upon the same specimen as an earlier name whose epithet ought to have been adopted. This is not the case with *Pausandra trianae* Baillon. There is therefore no bar to the acceptance of that name as the correct one for this species.

Additional specimens examined. PANAMA. BOCAS DEL TORO: premontane rainforest between Q. Lugron and Cerro Bonyic, near Terebe, 300–900 ft., *Kirkbride & Duke 647* (MO). SAN BLAS: Río Taindi (Taimdi of maps) 6 km above confluence with Río Mandinga, 9°25'N, 79°11'W, 30–100 m, *de Nevers & Herrera 7674* (F); along newly cut road from El Llano to Cartí-Tupile, near Continental Divide, 300–500 m, *Liesner 1289* (DAV, F, MO), *Mori & Kallunki 5535* (MO); seasonal lowland rainforest on the Aila Tilar (Río Acla), 8°48'N, 77°40'30"W, 25–100 m, *Sugden 424, 588* (MO).

31. *Garcia*

Garcia Vahl in Rohr, Skr. Naturhist.-Selsk. 2: 217. 1792. TYPE: *Garcia nutans* Vahl.

31.1. Garcia nutans Vahl in Rohr, Skr. Naturhist.-Selsk. 2: 217, tab. 9. 1792. TYPE: Colombia. Magdalena: near Santa Marta, *von Rohr* (C, not seen).

Additional specimens examined. PANAMA. CANAL ZONE: Barro Colorado I., *Knight 1090* (MO). LOS SANTOS: between Tonosí and Guánico, *Tyson et al. 3126* (MO).

32. *Croton*

Croton L., Sp. Pl. 1004. 1753. LECTOTYPE: *Croton aromaticus* L. (chosen by Webster, J. Arnold Arbor. 48: 354. 1967).

Seven species new to Panama (including two new species and one new subspecies) are reported here; a few new province records are indicated as well. These additions make it necessary to provide a revised key.

LITERATURE

LANJOUW, J. 1931. The Euphorbiaceae of Surinam. Amsterdam.

KEY TO THE SPECIES OF *CROTON* IN PANAMA

1a. Staminate flowers apetalous; stipules and petiolar glands absent; leaves with stellate-lepidote indumentum above, lepidote beneath (stamens 10–12; filaments hirsutulous; styles usually 3 times bifid; seeds deciduously stellate, 5–6 mm long) .... 20. *C. punctatus*

1b. Staminate flowers petaliferous; leaves stipulate (stipules sometimes early deciduous); indumentum various.

2a. Indumentum lepidote.

3a. Leaves without basal laminar or petiolar glands; petals in flowers not reduced; pistillate calyx lobes valvate but not reduplicate.

4a. Stamens 9–12; filaments glabrous; anthers 0.6–0.8 mm long; petals of staminate flowers not lepidote or with only 1 or 2 scales; seeds mostly 7 mm long or shorter.

5a. Leaves more or less oblong-elliptic, pinnately veined; inflorescences mostly 2 cm long or longer; pedicels of pistillate flowers mostly 10 mm long or longer .... 1. *C. schiedeanus*

5b. Leaves ovate, more or less cordate, (3–)5-veined at base; inflorescences 1 cm long or shorter; pedicels of pistillate flowers 1–2 mm long .... 2. *C. pseudoniveus*

4b. Stamens 14–17, or if fewer, then filaments hirsutulous; anthers 1–1.2 mm long; petals of staminate flowers lepidote; seeds 15 mm long or longer.

6a. Stamens (10 or)11–13; leaves pinnately veined; pistillate flowers mostly 3 or 4 per raceme; seeds 20–22 mm long .... 3. *C. tenuicaudatus*

6b. Stamens 15; leaves 3–5-veined at base; pistillate flowers mostly 1 or 2 per raceme; seeds 15–18 mm long .... 4. *C. pyriticus*

3b. Leaves with basal laminar glands; petals in pistillate flowers reduced; pistillate calyx lobes reduplicate-valvate.

7a. Seeds 3–5 mm long; fruiting pedicels 8–15 mm long .... 5. *C. lanjouwensis*

7b. Seeds 16–17 mm long; fruiting pedicels not over 7 mm long .... 6. *C. pachypodus*

2b. Indumentum not lepidote, the trichomes mostly or entirely stellate or dendritic; petals in pistillate flowers distinctly reduced or absent (sometimes fairly well developed in *C. draco*); petioles with prominent glands at junction with blade (except sometimes in *C. hircinus*); inflorescence (at least in part) terminal.

8a. Leaves deeply 3–5-lobed; staminate calyx lobes distinctly imbricate in bud; staminate receptacle glabrous; seeds tetragonal; annual herb .... 19. *C. lobatus*

8b. Leaves unlobed or shallowly lobed (less than halfway); staminate calyx lobes mostly valvate in bud; staminate receptacle sparsely to densely villose (glabrous in *S. santaritensis*); seeds not tetragonal.

9a. Stamens over 50; styles more than 5 mm long, twice bifid; stipules tomentose, dentate, 3–6 mm long; seeds ventrally ribbed .... 7. *C. speciosus*

9b. Stamens fewer than 50; styles less than 5 mm long.

10a. Lower cymules of inflorescence with both staminate and pistillate flowers at the same nodes; seeds coarsely ribbed.

11a. Styles bifid; pistillate calyx lobes not reduplicate-valvate; stamens 13 or more; filaments glabrous or nearly so; leaves unlobed, without scattered laminar glands.

12a. Pistillate flowers distinctly pedicellate, the pedicels mostly 3–6 mm long; inflorescences mostly 2–4 dm long; stamens 13–20; styles glabrous or nearly so; seeds less than 5 mm long .... 8. *C. draco*

12b. Pistillate flowers subsessile, the pedicels in fruit not over 2 mm long; inflorescences mostly 1–2 dm long; stamens 25–45; styles distinctly stellate-pubescent; seeds at least 5 mm long .... 9. *C. pungens*

11b. Styles multifid, stellate-pubescent; pistillate calyx lobes reduplicate-valvate; stamens 11 or 12; filaments hirsutulous; leaves more or less 3-lobed, with scattered peltate laminar glands above .... 10. *C. smithianus*

10b. Lower nodes of bisexual inflorescences with solitary pistillate flowers (not with staminate flowers at the same nodes), or inflorescences unisexual.

13a. Styles twice bifid to multifid.

14a. Shrubs or trees; pistillate calyx lobes not strongly unequal, the abaxial ones not deeply lacerate.

15a. Pistillate bracts not deeply lacerate; staminate receptacle villose.

16a. Stamens 14–16; seeds costate or verrucose.

17a. Pistillate calyx lobes elliptic to oblong, valvate, neither reduplicate nor accrescent, glabrous within, less than 5 mm broad; staminate petals not over 4 mm long; leaves mostly 7–9-veined at base, entire; petioles mostly 5–20 cm long .... 11. *C. billbergianus*

17b. Pistillate calyx lobes ovate, reduplicate-valvate, accrescent, stellate-tomentose within, becoming 7–8 mm long and broad; staminate petals 4.5–5 mm long; leaves mostly 5-veined at base, entire to denticulate; petioles 1–4 cm long .... 12. *C. fragrans*

16b. Stamens 10–12; seeds smooth; staminate receptacle sparsely villose.

18a. Leaves mostly alternate (occasionally opposite at 1 or 2 distal nodes), 7–9-veined at base, the margins distinctly dentate (teeth 15–40 on a side), the basal laminar glands small or absent; stipules, bracts, and pistillate calyx lobes coarsely glandular-dentate; inflorescence with 3–12 pistillate flowers; filaments densely hirsutulous below; ovary usually densely stellate-tomentose .... 13. *C. hircinus*

18b. Leaves alternate below, opposite or ternate distally, pinnately veined or obscurely triplinerved, the basal laminar glands long-stipitate; stipules and bracts entire; pistillate calyx lobes entire or obscurely dentate; inflorescence with 1 or 2 (rarely 3) pistillate flowers; filaments glabrous; ovary sparsely stellate-pubescent apically ... 15. *C. brevipes*

15b. Pistillate bracts deeply lacerate; staminate receptacle glabrous; stamens 12–15 ... 14. *C. santaritensis*

14b. Annual herbs; pistillate calyx lobes very unequal, the adaxial ones greatly reduced or obsolete, the abaxial ones lacerate, accrescent (6–8 mm long in fruit); seeds smooth ... 16. *C. argenteus*

13b. Styles once bifid; annual herbs.

19a. Leaves coarsely and sharply serrate (major teeth usually not over 10 per side); stamens 8–10; styles less than 1.5 mm long, spreading ... 17. *C. trinitatis*

19b. Leaves more finely and/or bluntly toothed; stamens mostly 11 or 12; styles 1.5 mm long or more, ascending or erect; seeds minutely beaked.

20a. Stems coarsely hispid; leaves mostly ovate, pointed at the tip, petiolar glands stipitate; bracts with long gland-tipped processes ... 18. *C. hirtus*

20b. Stems not coarsely hispid; leaves mostly elliptic or oblong, blunt at tip, the petiolar glands sessile; bracts eglandular ... [C. *glandulosus*]

32.3. Croton tenuicaudatus Lundell, Phytologia 1: 451. 1940. TYPE: Costa Rica. San José: vicinity of El General, *Skutch 2575* (holotype, MICH).

Additional specimen examined. PANAMA. BOCAS DEL TORO: along road to Chiriquí Grande, 10 road mi. from Continental Divide and 2 mi. along pipeline access road E of highway, ca. 8°55′N, 82°08′W, 350–500 m, *McPherson 8767* (F).

32.5. Croton lanjouwensis Jabl., Mem. New York Bot. Gard. 12: 158. 1965. *C. matourensis* Aublet var. *benthamianus* Muell. Arg., Linnaea 34: 95. 1865. *C. benthamianus* (Muell. Arg.) Lanjouw, Euphorb. Surinam 17. 1931, non *C. benthamianus* Muell. Arg., Fl. Bras. 11(2): 106. 1874. TYPE: Brazil: Río Negro, *Spruce Croton 2* (isotype, NY).

Tree to ca. 12 m high; monoecious; twigs densely lepidote. *Leaves* with petioles lepidote, 1.5–3.5 cm long, distally with 2 large yellowish, subsessile, patelliform glands ca. 1.5–2 mm across; stipules linear-lanceolate, entire, densely lepidote, 8–10 mm long, early deciduous; blades chartaceous, elliptic to elliptic-oblong, acute to short-acuminate at tip, cuneate at base, mostly 8–15 cm long, 3.5–6.5 cm broad, smooth and glabrous above, densely lepidote beneath (scales denticulate-margined, ca. 0.25–0.4 mm across and nearly or quite contiguous); venation distinctly pinnate, the major lateral veins (ca. 11–15 on a side) straight; margins entire and lepidote-marginate. *Inflorescences* terminal, racemose, 13–15 cm long, bisexual; pistillate flowers solitary at 3–6 proximal axils; staminate flowers in cymules of 2 or 3 at distal axils; bracts entire, lepidote, up to 3 mm long. *Staminate flowers* with lepidote pedicels 2–5 mm long; calyx lobes 5, valvate, ovate-triangular, lepidote, 2–2.5 mm long; receptacle villose; petals obovate or narrowly elliptic, ca. 2 mm long, glandular-punctate, densely villose on margins, glabrous on back; stamens 12 or 13; filaments glabrous or sparsely hirsutulous; anthers elliptic, 0.6–0.7 mm long. *Pistillate flowers* with stout lepidote pedicels becoming 8–15 mm long; calyx lobes 5, equal, triangular, ± reduplicate-valvate, lepidote without, ± stellate-lepidote within on the recurved margins, 4.5–5 mm long; disk 5-lobed, adnate to calyx; petals rudimentary (shorter than 1 mm long); ovary densely lepidote (scales ca. 0.6–0.8 mm across); styles twice-bifid, ca. 4 mm long, stellate proximally (branches glabrous). *Capsules* not seen entire; cocci lepidote, ca. 5 mm long; columella slender, ca. 4 mm long; seeds plump, scarcely compressed, brownish, smooth, ca. 3.5 mm long.

The Panamanian plants appear to agree in most respects with *C. lanjouwensis* as defined by Lanjouw (1931: 12–17; as *C. benthamianus*); the broad pistillate calyx with adaxially stellate lobes is apparently diagnostic in separating the species from *C. matourensis* Aublet. However, the Panamanian plants occurring in cloud forest at 800–1,000 m would appear to differ ecologically from the Amazonian plants, which have been collected in lowland rainforests. Jablonski (1965: 157–158) cited *C. matourensis* from comparable altitudes in Venezuela; further comparisons of plants from Panama with the South American plants evidently are needed. The specimens from Panamá Province differ rather strikingly in their duplex petiolar glands, sparsely lepidote upper leaf surfaces, and shorter pistillate pedicels.

Specimens examined. PANAMA. BOCAS DEL TORO: along road to Chiriquí Grande, ca. 1.5 mi. along road E of highway, ca. 8°55′N, 82°10′W, 250–350 m, *McPherson & Allen 9640* (F). COCLÉ: Cerro Pilón, near El

Valle, ca. 900 m, *Duke & Correa 14718* (DAV, MO); cloud forest, hills N of El Valle de Antón, *Dressler 4083* (DAV, MO); cloud forest, El Valle, 800–1,000 m, *Duke 13166* (DAV, MO), *Dwyer & Correa 7951* (DAV, MO), *Correa 311* (MO). PANAMÁ: primary forest, road from El Llano to Cartí-Tupile, 200–500 m, *Croat 22905* (DAV, MO).

32.6. Croton pachypodus Webster, sp. nov. TYPE: Panama. San Blas: km 18 of El Llano–Cartí road, 9°19′N, 78°55′W, 350 m, 1 Oct. 1984, *de Nevers & Herrera 3980* (holotype, MO; isotypes, DAV, F).

Species haec ab *C. pyritico* differt foliis supra glabris petiolo glandulato, ab *C. lanjouwense* differt seminibus majores, ab aliis speciebus Centroamericanis differt pedicellis valde incrassatis.

Tree 7–25 m high; twigs obtusely angular, glabrate. *Leaves* with petioles lepidote, 0.8–1.5 cm long, distally (near base of blade) with 2 subsessile or short-stipitate (to 0.7 mm) blackish patelliform glands 0.5–1 mm across; stipules linear-lanceolate, entire, densely lepidote, 4–10 mm long, 0.9–1.2 mm broad, ± persistent; blades chartaceous, elliptic-oblong to somewhat obovate, subacute or acute to abruptly short-acuminate at tip, cuneate to rounded at base, 8–22 cm long, 3.5–7 cm broad, smooth and glabrate above (with sparse scales on major veins when young), evenly and sparsely lepidote beneath (scales 0.25–0.4 mm across, denticulate, with ca. 50 radii), the scales widely separated; venation distinctly pinnate, the major lateral veins (9–13 on a side) straight or slightly curving, the veinlet reticulum prominulous beneath; margins entire, smooth, without lepidote rim. *Inflorescences* terminal and axillary, racemose, (5–)10–15 cm long, bisexual or staminate; pistillate flowers solitary at lowermost (1–)2–4(–5) nodes of bisexual inflorescences, staminate flowers solitary or paired at distal axils; bracts triangular, blackish, sparsely lepidote, 0.5–1 mm long. *Staminate flowers* (buds only observed) with lepidote pedicels 1.5–2.5 mm long; calyx lobes 5, valvate, triangular, lepidote, ca. 3 mm long; receptacle villose; petals narrowly elliptic, ca. 2.5 mm long, densely villose on margins, sparsely lepidote (often a single scale) on the back, densely hirsutulous adaxially; stamens 14–16, the filaments glabrous, the anthers 0.8–0.9 mm long. *Pistillate flowers* with stout lepidote pedicels ca. 2.5–3.5 mm long, becoming in fruit 4.2–6.5 mm long, 3.2–4 mm broad; calyx lobes 5, equal, triangular-ovate, reduplicate-valvate, densely lepidote without, densely tomentose-villose within, 3–3.5 mm long, 2.5–3 mm broad; disk shallowly 5-lobed, nearly 4 mm across, smooth and glabrous; petals obsolete, represented by whitish tufts of hairs; ovary densely lepidote (scales 0.5–0.8 mm across, denticulate, 50–70-radiate, with 20–30 darkened radii); styles blackish, twice-bifid, 3.5–4 mm long, nearly glabrous. *Capsules* not seen entire; valves of cocci ca. 23–25 mm long; columella slender, ca. 20 mm long; seeds elliptic, somewhat compressed, flattened and obscurely carinate on the back, distinctly keeled on inner face, grayish brown, smooth and shining, 16.2–17.2 mm long, 10.3–11.3 mm broad; caruncle hippocrepiform, obscure, tenuous, ca. 2.5 mm long, 1.5 mm broad.

Collections of this species have been determined as *C. lanjouwensis*, to which indeed it is related and superficially very similar. However, it is distinguished by leaves very sparsely lepidote beneath and with margins free of scales, shorter petioles with smaller darker glands, and especially by the much larger fruits borne on greatly thickened pedicels. Among species earlier reported from Panama, the new species resembles *C. tenuicaudatus*; however, that species has eglandular leaves lepidote on both faces, strongly lepidote staminate petals, and more slender pistillate pedicels. *Croton pyriticus* appears to be even less similar because of its ovate palmately veined eglandular leaves, longer and more slender (1.5 mm or thinner) pistillate pedicels, and verruculose capsules; however, the seeds, although larger, are similar in shape to those of *C. pachypodus*.

Additional specimens examined. PANAMA. SAN BLAS: 12 mi. above Pan-American Hwy., 200–500 m, *Croat 22905* (MO); 20.7 km from Pan-American Hwy., 350 m, *Mori & Kallunki 5116* (MO).

32.7. Croton speciosus Muell. Arg. [Linnaea 34: 83. 1865] subsp. **tacarcunensis** Webster, subsp. nov. TYPE: Panama. Darién: Cerro Tacarcuna, S slope, premontane wet forest on ridge below summit, 1,250–1,450 m, *Gentry & Mori 13925* (holotype, MO; isotype, DAV).

Haec a subsp. *specioso* differt stipulis minoribus, glandulis petioli brevioribus, carunculo seminis ca. 2 mm lato.

Monoecious *tree* 5 m high; twigs subterete, densely tawny-villose with dendritic hairs. *Leaves* with petioles (2–)3–11 cm long, tomentose, apically with 4–6 stalked glands on ventral side, the glands ca. 0.8–1.5 mm long, 0.3–0.4 mm across; stipules lanceolate, densely tomentose, toothed, 3–6 mm long; blades membranous, mostly ovate, long-acuminate at tip, rounded to subcordate at base, the larger ones shallowly 3-lobed, 12–21 cm long, 7–12 cm broad; lamina above copiously pubescent with stellate-tufted hairs, beneath copiously tomentose with whitish dendritic hairs ca. 0.5–1 mm across, 3–5-nerved at base, with 7–10 major lateral veins on each side, connected by a scalariform reticulum of straightish veinlets; margins subentire (obscurely denticulate). *Inflorescences* terminal (or pseudolateral), bisexual, racemose, 2.5–6 cm long, with 1 or 3 proximal flowers and 3–7 distal flowers; flowers solitary at each node; bracts 5–7 mm long, attenuate-acuminate, tomentose, with subulate stipules ca. 3–5 mm long. *Staminate flowers* with stellate-tomentose pedicels 5–8 mm long; receptacle densely tomentose; calyx lobes 5, fulvous-tomentose, obtuse, entire, 3.5–5 mm long; petals obovate, 4.5–5 mm long, densely appressed-pubescent without, glabrous within, woolly-villose along margins; stamens ca. 60–70; filaments slender, glabrous, ca. 4–5 mm long; anthers oblong, apiculate, 1.2–1.6 mm long, 0.5–0.7 mm broad. *Pistillate flowers* with stout tomentose pedicels ca. 2–4 mm long at anthesis (becoming up to 1 cm long in fruit); calyx segments 5, valvate, oblong, densely whitish- to fulvous-tomentose without, sparsely tomentose in distal third within, ca. 10 mm long, 3–5 mm broad; disk inconspicuous, adnate to base of calyx, crenulate, stellate-pubescent, ca. 5 mm across; petals rudimentary, densely hirsute, ca. 1–1.5 mm long; ovary densely fulvous-tomentose; styles twice-bifid near the base, densely stellate-pubescent below (and with scattered stellate hairs distally nearly to tips), ca. 7–9 mm long, the branches dark reddish, dilated and crenulate at tips. *Capsules* subglobose, fulvous-hispidulous, ca. 1 cm long and broad; seeds plump, plumbeous brown, distinctly costate ventrally, obscurely costate on back, ca. 7 mm long, 5 mm broad; caruncle roundish, low, ca. 2 mm across.

This striking *Croton* from the cloud forests at the crest of Cerro Tacarcuna appears to be conspecific with *C. speciosus*, which was described from specimens collected near Caracas, Venezuela. I have examined *Moritz 1329* (A, GH) from Galipán, near Caracas, one of the syntypes cited by Mueller (incorrectly located by him as in Colombia rather than Venezuela), as well as three other collections from near Galipán (*Allart s.n.*, *Pittier 221*, *9577*, A, GH). These plants in general rather closely resemble the Cerro Tacarcuna specimens in leaf shape and pubescence, flower configuration, and seeds; there can be little doubt that we are dealing with a single species. The stamen number in the Venezuelan plants varies from 40 to 80 and hence includes the number for the Cerro Tacarcuna plants. Mueller gave the stamen number of *C. speciosus* as ca. 150, which certainly does not agree with *Moritz 1329*, in which two buds yielded ca. 70 and ca. 80 stamens. Possibly the number may become higher in some Venezuelan plants, as Mueller (1866: 529) also cited two other collections from near Caracas, *Fendler 34* and *231* (cited as *Linden 34* and *201*), which we have not seen.

The publication of a separate subspecies for the Tacarcuna population is made diffidently, as intervening collections may close the gap. However, the Panamanian plants differ strikingly in their much smaller and less lacerate stipules, as well as in having distinctly shorter stalked glands at the apex of the petiole. Furthermore, the caruncle in seeds from Panama is roundish and ca. 2 mm broad, whereas it is distinctly laterally expanded and ca. 3 mm broad in seeds from Venezuela. Provisionally, therefore, it seems best to designate the Cerro Tacarcuna plants as a distinct subspecies.

Additional specimens examined. PANAMA. DARIÉN: S slope of westernmost peak of Cerro Tacarcuna, 1,100–1,300 m, *Gentry et al. 16877* (MO); ridgetop below Alto de Nique base camp, *Gentry et al. 28727* (MO).

32.8. Croton draco Cham. & Schldl. [Linnaea 6: 360. 1831] subsp. **panamensis** (Klotzsch) Webster, stat. nov. *Cyclostigma panamense* Klotzsch in Seem., Bot. Voy. Herald 105. 1853. *Croton panamensis* (Klotzsch) Muell. Arg. in DC., Prodr. 15(2): 546. 1866. TYPE: Panama. Chiriquí: Volcán Chiriquí, *Seemann* (K, not seen). (see Webster & Burch, 1968: 254 for additional synonymy.)

Further examination of Mexican and Central American specimens of *Croton draco* indicates that the Panamanian plants cannot reasonably be maintained as a separate species. Except for the larger, broader stipules (mostly 2 mm or more across), the Mexican populations here assigned to subsp. *draco* show no essential differences from plants with narrow stipules that occur from Guatemala (and sporadically in southern Mexico) to Panama and Colombia.

32.10. Croton smithianus Croizat, J. Arnold Arbor. 21: 93. 1940. TYPE: Colombia. Santander: Mesa de los Santos, *Killip & Smith 15283* (holotype, A; isotype, US).

Tree to 18 m high; twigs angled or sulcate, yellowish-scurfy with pedicellate stellate hairs. *Leaves* with petioles mostly 5–15 cm long; patelliform glands at apex of petiole sessile, 0.9–1.2 mm across; stipules linear-lanceolate to spathulate, 5–9 mm long, 1–2 mm broad; blades mostly ovate, sometimes 3-lobed, blunt to acuminate at the tip, cordate to subcordate at base, the larger ones 15–35 cm long, 10–30 cm broad; venation palmate, with 5(–7) major veins at base, 5–8 laterals on each side above the base, the laterals sometimes dichotomizing towards the margin; veins and veinlets prominulous on both sides, the veinlets scalariform; trichomes on upper surface pedicellate-stellate, 0.2–1 mm across, with stalks 0.1–0.5 mm high, beneath denser and ± floccose; small patelliform glands (0.4–1 mm across) occasional on upper surface; margins denticulate, with occasional small stalked glands. *Inflorescences* terminal, mostly 20–50 cm long; 5–15 proximal cymules bisexual, distal ones staminate; staminate bracts subulate, entire, deciduous, ca. 1–2.5 mm long, subtending several flowers. *Staminate flowers* with stellate-tomentose pedicels 1.5–5 mm long; calyx distinctly gamophyllous, 3.5–4 mm long; calyx lobes ovate, acute, valvate, 2.2–3.7 mm long, 2–2.8 mm broad; petals narrowly spathulate, 3.2–4.5 mm long, 0.5–1 mm broad, densely villose ventrally, strigose-hirsutulous dorsally; receptacle densely villose; stamens 11 or 12; filaments flattened, densely hirsutulous in lower ¾, 3–4.5 mm long; anthers elliptic, the connective glandular-pustulate, 1.1–1.5 mm long. *Pistillate flowers* with stellate-lepidote pedicels becoming 9–14 mm long; calyx lobes 5, valvate (not distinctly reduplicate), elliptic to ovate, entire, stellate-lepidote (trichomes 0.1–0.4 mm across) outside, stellate inside near tip and along margins, 5–7.5 mm long, 3.5–6.5 mm broad; disk entire, thickish, ca. 1.7 mm across; ovary yellowish-stellate or stellate-hispid, trichomes 0.5–1.5 mm across in fruit; styles free, multifid, sparsely to copiously stellate-hispid, ca. 5 mm long. *Capsules* subglobose, yellowish with appressed scales; columella ca. 4 mm long; seeds plump, lenticular, brownish, finely costate-rugulose, bluntly pointed at both ends, 3.9–4.1 mm long, 3.3–3.5 mm broad; caruncle flat, bilobed, 1.7–2.1 mm broad.

Croton smithianus is found in lowland and lower montane forests, up to ca. 1,500 m elevation, Nicaragua to Colombia, flowering July to September.

The Panamanian representative of the widespread and variable South American species complex centering on *Croton palanostigma* Klotzsch is here referred to *C. smithianus* Croizat because of its characteristic indumentum of pedicellate stellate trichomes. The populations in Colombia are rather variable and poorly understood; the isotype at US, which is a fruiting specimen, has the characteristic indumentum, and a specimen from Chocó (*Archer 2062*, US) has the characteristic leaf form and margin, but the trichomes are not distinctly pedicellate as in the Panamanian plants. The Panamanian and Colombian plants somewhat resemble *Croton killipianus* Croizat, described from Boyacá; however, the type collection of that species (*Lawrance 588*; isotype, US) has subentire leaf margins and an appressed, rather sparse indumentum more characteristic of *C. benthamianus* Muell. Arg. *Croton nuntians* Croizat from Guyana is somewhat similar but differs in its smaller fruiting calyx and shorter fruiting pedicel. Until this species complex is revised, it seems best to refer our plants to *C. smithianus*. Several collections from Nicaragua and Costa Rica are also referred to that species.

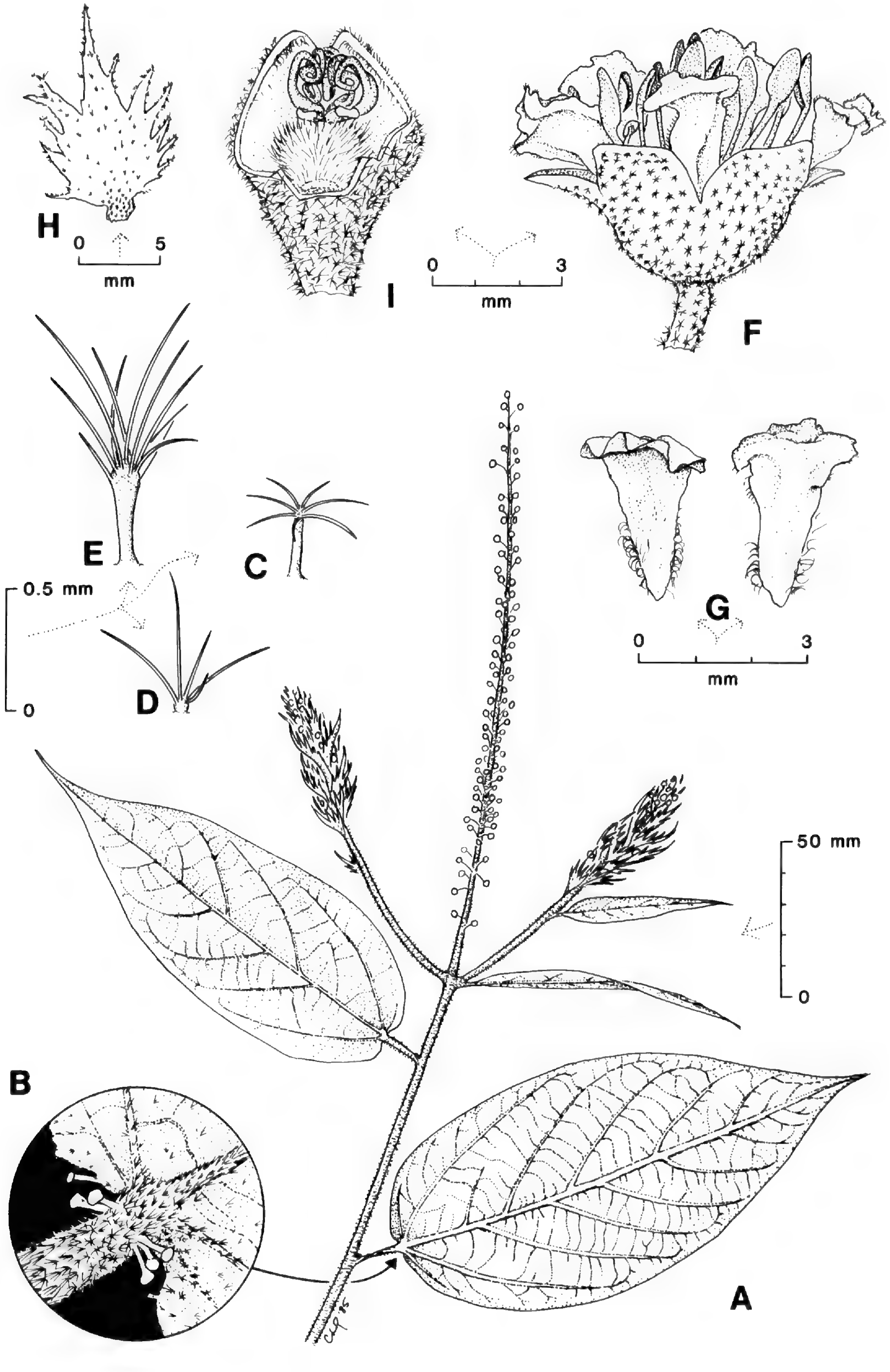
Specimens examined. COSTA RICA. HEREDIA: Finca La Selva, *Hammel & Trainer 12849, 13044* (DAV, DUKE). PUNTARENAS: forest remnants along highway 4 mi. SE of turnoff to Buenos Aires, 9°07′N, 83°17′W, 400 m, *Webster 21883* (DAV, MO); rainforest 17 mi. SE of San Isidro General, 700 m, *Webster & Miller 12394* (DAV). NICARAGUA. RÍO SAN JUAN: Sábalo, *Araquistain 3223* (DAV, MO). ZELAYA: Bluefields, *Neill 2598* (DAV, MO). PANAMA. COLÓN: Río Salud, *Howell 128*, *Lao & Holdridge 224* (MO). DARIÉN: between Manené and Tusijuanda, *Duke 13576* (DAV). PANAMÁ: SE slopes of Cerro Trinidad, *Kirkbride & Duke 1665* (MO).

32.11. Croton billbergianus Muell. Arg., Linnaea 34: 98. 1865; subsp. billbergianus. TYPE: Panama. Colón: Portobelo, *Billberg 316* (not seen).

This species has been collected in three additional provinces.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Súrsuba, Río Changuinola, *Dwyer s.n.* (MO). SAN BLAS: Puerto Obaldía to La Bonga, *Knapp & Mallet 4667* (MO). VERAGUAS: Coquyito mine to Río Barrera, *Hammel 5221* (MO); Santa Fe, *Folsom & Edwards 3392* (MO).

The description in the original treatment (Webster & Burch, 1968: 257–258) applies only to subsp. *billbergianus*. As suggested at that time, *C. pyramidalis* J. D. Smith, extending from Veracruz, Mexico, to Honduras, does not appear to be a distinct species. It may be retained at the subspecific level because of its apparently larger seeds (5.7–6.2 mm in the Veracruz population vs. 4.3–5.5 mm in the Panamanian plants) and longer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stipules (7–15 mm long vs. 5–7 mm in the Panamanian plants). A new combination for the Mexican plant is therefore necessary.[5]

32.13. Croton hircinus Vent., Jard. Malmaison 1: 50, pl. 50. 1804. TYPE: cultivated specimen, *Ventenat* (presumably at G, not seen).

An additional provincial record is cited.

Additional specimen examined. PANAMA. CHIRIQUÍ: Río Cobre bridge, 25 mi. W of Tole, *Dwyer & Hayden 7542* (MO).

32.14. Croton santaritensis Huft, sp. nov. TYPE: Panama. Colón: Santa Rita Ridge Road, 21–26 km from Transisthmian Highway, tropical wet forest, 500–550 m, 9°25′N, 79°37′W, 4 July 1982, *Knapp 5882* (holotype, MO; isotypes, DAV, F, F neg. 62353, PMA). Figure 3.

Frutex monoecus dense villosus, pilis castaneus stellatis. Folia ovata-oblonga vel lanceolata, basi subcordata vel rotundata, apice longicaudata; glandulae petiolares aliquot tubaeformes, stipulae ovatae-deltatae margine fimbriatae. Inflorescentiae unisexuales racemosae, masculinae terminales, femineae axillares; bracteae femineae flabellatae profunde laciniatae flores includentes.

Shrub ca. 1.5 m high; monoecious; twigs subterete, densely villous with brownish stellate hairs. *Leaves* with petioles densely villous as the twigs, 5–20 mm long; petiolar glands several at apex of petiole, stipitate, trumpet-shaped, 0.5–1.5 mm long, 0.3–0.5 mm across; stipules ovate-deltate, membranous, eglandular, appressed, 8–11 mm long, 4–6 mm broad, the margins fimbriate; blades chartaceous, ovate, ovate-oblong, or lanceolate, long-caudate at apex, rounded to subcordate at base, 10–15 cm long, 4–8 cm broad, 1.7–3 times as long as broad, sparsely to moderately stellate pubescent above, sparsely tomentose below, 3–7-nerved at base, the secondary veins 5–8 per side; margin entire to remotely denticulate. *Inflorescences* unisexual, racemose, the staminate ones terminal, the pistillate ones axillary, occurring only at the two subopposite nodes immediately below the terminal staminate raceme; staminate inflorescences 17–22 cm long, densely brown stellate-villous; nodes 15–30; flowers 1–3 at each node on stellately pubescent pedicels 6–9 mm long, the bracts subulate, 2–3 mm long, stellate below, glabrous above; pistillate inflorescences 5–11 cm long, densely brown-villous; bracts flabellate, deeply laciniate, 10–12(–14) mm long, at least the lower ones loosely enclosing the flower buds. *Staminate flowers*: sepals 5, deltate, joined at base, valvate, stellately pubescent, the lobes 2.5–3 mm long, ca. 2 mm broad; petals 5, only slightly exceeding the calyx lobes, ca. 6 mm long, ca. 2 mm broad below the tip, the tip abruptly expanded, ca. 2.5 mm broad, coarsely erose; stamens 12–15; disk consisting of 5 nearly separate glands; receptacle glabrous. *Pistillate flowers* (immature): sepals 5, deltate, fleshy; ovary densely stellate-hispidulous; styles twice-divided. Mature fruits and seeds not seen.

This species may easily be distinguished from all other Central American species of *Croton* by the peculiar arrangement of the inflorescences, the conspicuous fimbriate stipules, and the oblong, laciniate bracts that loosely enclose the young pistillate flowers.

No close relative of *C. santaritensis* is known. Because of its combination of pentamerous calyces in both pistillate and staminate flowers, five petals and glabrous receptacles in the staminate flowers, and the large fimbriate stipules and bracts, it is not easily accommodated in any of the sections recognized by Mueller (1866: 511–700) in the most recent worldwide account of *Croton*. No species closely resembling *Croton santaritensis* has been found among the large holdings of South American *Croton* at the Field Museum or the Missouri Botanical Garden.

32.15. Croton brevipes Pax, Bot. Jahrb. Syst. 33: 290. 1903. TYPE: Costa Rica. Río del Convento, *Pittier 12117* (isotype, US, photo, F).

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[5] **Croton billbergianus** subsp. **pyramidalis** (J. D. Smith) Webster, stat. nov. *Croton pyramidalis* J. D. Smith, Bot Gaz. 35: 7. 1903. TYPE: Guatemala. Alta Verapaz: Río Dolores near Cubilgüitz, *Tuerckheim 7974* (holotype, US; not seen).

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FIGURE 3. Croton santaritensis.—*A. Habit, with staminate and pistillate inflorescences.—B. Detail of leaf base, showing glands.—C. Trichome from upper leaf surface.—D. Trichome from lower leaf surface.—E. Trichome from stem.—F. Staminate flower.—G. Staminate petals, abaxial view on left, adaxial on right.—H. Pistillate bract, abaxial view.—I. Pistillate flower in bud, cut-away view. Based on* Knapp 5882. *Illustration by Clara Richardson.*

Shrub 1–3 m high; monoecious; twigs pale, appressed-stellate. *Leaves* alternate below, mostly opposite or ternate above; petioles densely appressed-stellate, 3–20(–30) mm long (less than ¼ length of blade); petiolar glands (at base of blade) conspicuous, cylindrical, apically truncate and dilated, 1–2.5 mm long, 0.3–0.5 mm across; stipules subulate to narrowly lanceolate, dark, entire, eglandular, stellate-pubescent, 1.4–2.8 mm long; blades thinly chartaceous, elliptic to ovate-elliptic or obovate, acute to acuminate at tip, cuneate to obtuse at base, 4–13 cm long, (1–)2–5 cm broad, sparsely stellate or appressed-hispid above with few-rayed trichomes, sparsely appressed-stellate and inconspicuously glandular-punctate beneath, pinnately veined (or inconspicuously triplinerved) with mostly 5–7 veins on each side; margins subentire to rather coarsely and irregularly dentate (teeth ca. 8–15 on a side), with stalked glands between some of the teeth. *Inflorescences* mostly terminal and bisexual (some also lateral and staminate), racemose, 1.5–3(–4.5) cm long, with 1 or 2 (rarely 3) basal solitary pistillate flowers, the staminate flowers 1 or 2 per bract at distal axils; bracts narrow, entire, eglandular, stellate-pubescent, mostly 1.5 mm long or shorter. *Staminate flowers* with sparsely stellate or nearly glabrous pedicels 1–2 mm long; calyx lobes 5, elliptic-lanceolate, acute, stellate-pubescent, glandular-punctate, 1.2–1.7 mm long, 0.9–1.1 mm broad; receptacle moderately villose; petals obovate-spathulate, 1.4–1.8 mm long, glandular-punctate, barbate-hirsute on lower margins; stamens 10–12; filaments glabrous, 1.8–2.5 mm long; anthers ovate, 0.5–0.7 mm long. *Pistillate flowers* with stout appressed-stellate pedicels becoming 1.3–3.5 mm long; calyx lobes 5, subequal, narrowly oblong-lanceolate or spathulate, subentire (with 1 or 3 obscure teeth), sparsely stellate outside, glabrous inside, 3.5–6.5 mm long, 1–1.5 mm broad; petals rudimentary, subulate; disk entire, glabrous; ovary sparsely stellate-pubescent apically, glabrous below; styles free, ca. 2 mm long, twice bifid, glabrous to hispidulous. *Capsules* subglobose, sparsely stellate-pubescent or glabrescent, ca. 5 mm diam.; columella slender, 3.2–4 mm long; seeds broadly ellipsoid, compressed, apically beaked, brownish, nearly smooth (minutely striolate), 3.8–4.1 mm long, 2.8–3.4 mm broad, the caruncle small, ca. 0.5–0.8 mm across.

Rainforest below 1,000 m, Costa Rica and Panama.

This plant bears a considerable resemblance in habit to *C. hircinus* but differs in having (distally) opposite or ternate pinnately veined leaves with larger laminar glands; the stipules, bracts, and calyx lobes lack the glandular serrations of *C. hircinus.* Examination of material of *Croton macrodontus* Muell. Arg. from Mexico shows that it is extremely close to *C. brevipes.* Although specimens from Costa Rica and Panama may be easily recognized by their distally opposite, less coarsely toothed leaves with more rounded bases and shorter petioles, they are very similar to the Mexican plants in most details, including pubescence, floral details, and fruits. The seeds of the Mexican plants are somewhat larger, but this difference may disappear upon further sampling. Provisionally, the two species may be kept distinct on the basis of the foliar characters, and because no intermediate populations have yet been discovered in Central America between Costa Rica and Mexico.

Specimens examined. PANAMA. COLÓN: Santa Rita Ridge, ca. 300 m, *Antonio 3739* (DAV, F, MO), *Correa & Dressler 912* (F, MO), *Croat 13898* (MO), *Duke 15291* (MO), *Dwyer 8543* (MO), *Dwyer & Gentry 9395* (F, MO), *Foster 1751* (DAV, DUKE, F), *Gentry 1874* (DAV, F, MO), *Kennedy 2756* (MO), *Knapp 5845* (DAV, F, MO), *Sytsma* 2047 (MO), *2054* (F, MO), *Webster & Dressler 16727* (DAV, MO, US); East Ridge, *Duke 15291* (DAV). PANAMÁ: Cerro Jefe, 700–750 m, *Dressler 3844* (DAV, MO, US), *Webster & Dressler 16477* (DAV, DUKE, MO, US); Tortí Arriba, *Folsom et al. 6644* (DAV, MO).

32.16. Croton argenteus L., Sp. Pl. 1004. 1753. *Julocroton argenteus* (L.) Didr., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1857(8–10): 134. 1857; Muell. Arg. in DC., Prodr. 15(2): 703. 1866; Croizat, Revista Argent. Agron. 10: 125. 1943; Correll & Johnston, Man. Vasc. Plants Texas 939. 1970. TYPE: America (not seen; presumably in Hortus Cliffortianus Herbarium, BM; 1140.8 in LINN).

Annual herb 2–10 dm high; stems pseudodichotomizing, with long internodes and pseudoverticels of leaves, appressed stellate-puberulent. *Leaves* with petioles 1–5 cm long, these without paired apical glands; stipules subulate, (2.5–)5–10 mm long; blades chartaceous, ovate or the upper ones oblong-ovate, obtuse or rounded to subacute at tip, cuneate to rounded at base, mostly 3–7(–15) cm long, 2.5–5 cm broad, 5-veined at base; lateral veins above base 3 or 4 on each side, not prominent; above green and finely appressed-stellate, beneath grayish and more densely stellate; margins finely serrulate. *Inflorescences* terminal, bisexual, ca. 1–4 cm long; bracts subtending solitary flowers, the pistillate flowers 4–6 at base of spike; staminate bracts subulate, entire, ca. 3 mm long. *Staminate flowers* with pedicels ca. 1.5–2.5 mm long; calyx lobes lanceolate, acute, valvate, ca. 1.5–2 mm long; petals linear, 2.1–2.3 mm long, 0.3–0.4 mm broad, glabrous except for the ciliate margins; receptacle copiously villose; stamens usually 11; filaments sparsely to rather copiously appressed-hirsutulous, ca. 2–2.5 mm long; anthers elliptic-oblong, 0.6–0.8 mm long. *Pistillate flowers* with short pedicels ca. 1–1.5 mm long, becoming 3–5 mm long in fruit; calyx lobes 5, imbricate, very unequal, the 3 abaxial lobes much larger, in fruit 6–8 mm long, 2.5–6 mm broad, oblong, laciniate, provided on each side with 5–10 teeth ca. 0.5–3 mm long, the 2 abaxial lobes much smaller, nearly or quite obsolete; petals absent; disk strongly asymmetrical, with larger adaxial lobes 0.9–1.2 mm long, 0.5–0.7 mm broad, the 2 adaxial lobes very small; ovary stellate-tomentellous; styles erect, distally quadrifid, hispid-stellate, ca. 2–4 mm long. *Capsules* ca. 5 mm long; columella 3–4.5 mm long; seeds ellipsoid, smooth, mottled gray and brown, apically beaked, 3.1–4 mm long, 2.4–2.9 mm broad; caruncle ca. 1.5 mm broad.

Scattered in weedy habitats from extreme southern Texas to Panama, reappearing in Venezuela, Paraguay, and Argentina, but not reported from most of tropical South America. The two Panamanian collections may represent recent introductions.

Specimens examined. PANAMA. PANAMÁ: marsh area 2 mi. S of Tocumen Airport, *Tyson & Clewell 5899* (MO); Río Tapia, *Bartlett & Lasser 16629* (MO).

Subfamily IV. EUPHORBIOIDEAE

33. *Mabea*

Mabea Aublet, Hist. Pl. Guiane 867. 1775. TYPE: *Mabea piriri* Aublet.

RECENT LITERATURE

HUFT, M. J. 1987. Notes on *Mabea* (Euphorbiaceae) in Central America, together with comments on sect. *Apodae* in Brazil. Phytologia 62: 339–343.

STEINER, K. E. 1983. Pollination of *Mabea occidentalis* (Euphorbiaceae) in Panama. Syst. Bot. 8: 105–117.

The discovery of a distinctive new species of *Mabea* in Panama makes it necessary to provide a new key to the three species now known from the country.

KEY TO THE SPECIES OF *MABEA* IN PANAMA

1a. Leaves acute or subacuminate at apex, usually 3–5 times as long as broad; bracteal glands of the staminate cymules not elevated above the rachis; stamens 15–20 per staminate flower .... 1. *M. montana*

1b. Leaves cuspidate to long-acuminate at apex, usually less than 3 times as long as broad.
  2a. Bracteal glands of the staminate cymules not elevated above the rachis; stamens more than 30 per staminate flower; undivided portion of the style at maturity 12–20 mm long .... 2. *M. occidentalis*
  2b. Bracteal glands of the staminate cymules elevated above the rachis; stamens 10–15 per staminate flower; undivided portion of the style at maturity 4–9 mm long .... 3. *M. jefensis*

33.1. Mabea montana Muell. Arg. in DC., Prodr. 15(2): 1151. 1866. TYPE: Colombia: *Schlim 1132.* Venezuela: *Fendler 24.* Panama: *Sutton Hayes 715* (syntypes, not seen).

Additional collections examined. PANAMA. VERAGUAS: roadside between Santa Fe and San José, *D'Arcy 10314* (MO); 5 km S of Santa Fe, below 500 m, *Folsom & Collins 1644* (MO); a 1 km del puente sobre el desvío del Río San Juan, *Luna 47* (MO).

33.3. Mabea jefensis Huft, Phytologia 62: 341. 1987. TYPE: Panama. Panamá: newly bulldozed trail off Cerro Jefe Road, 0.4 km beyond turnoff to Alto de Pacora, 29 Sep. 1975, *J. T. & F. Witherspoon 8570* (holotype, MO, F neg. 62352). Figure 4.

Montane and premontane rainforests of Central Panama, 350–1,000 m.

Mabea jefensis is known from abundant collections from both the Cerro Jefe area and from the Continental Divide north of El Llano in eastern Panamá Province, as well as from a single collection from the Cañazas mountain range in the western part of the province. It seems likely that this species will prove to be common in the mountainous region along the border of Panamá and San Blas provinces as this area becomes more thoroughly explored.

Additional specimens examined. PANAMA. PANAMÁ: Cerro Jefe area, *Antonio et al. 3399* (F), *Correa et al. 1601, 1610* (MO), *Croat 13031, 14438* (MO), *D'Arcy & D'Arcy 6253* (MO, 2 sheets), *D'Arcy 12185* (MO), *12201* (F), *D'Arcy & Sytsma 14733* (F, MO), *Duke 9474* (MO), *Dwyer et al. 7296* (MO, 2 sheets), *7364* (MO), *Folsom et al. 6709, 7105* (MO), *Hammel 3735* (MO), *Knapp 867* (F), *Liesner 531* (MO), *Porter et al. 5072* (MO), *Sytsma 1475, 4112* (F), *Sytsma et al. 2849* (F), *Sytsma & D'Arcy 3660* (F), *Tyson et al. 3204* (MO), *4355* (MO, 2 sheets), *Tyson 3399* (MO, SCZ), *Wilbur & Weaver 11360* (MO); La Eneida, *Correa & Dressler 824* (MO), *Maas et al. 1567* (MO); El Llano–Cartí road, 6–22 km N of Inter-American Highway, 300–500 m, *Croat 25127, 33805* (MO), *Hammel 867* (MO), *Huft & Knapp 1594, 1613* (MO), *Huft et al. 1868*

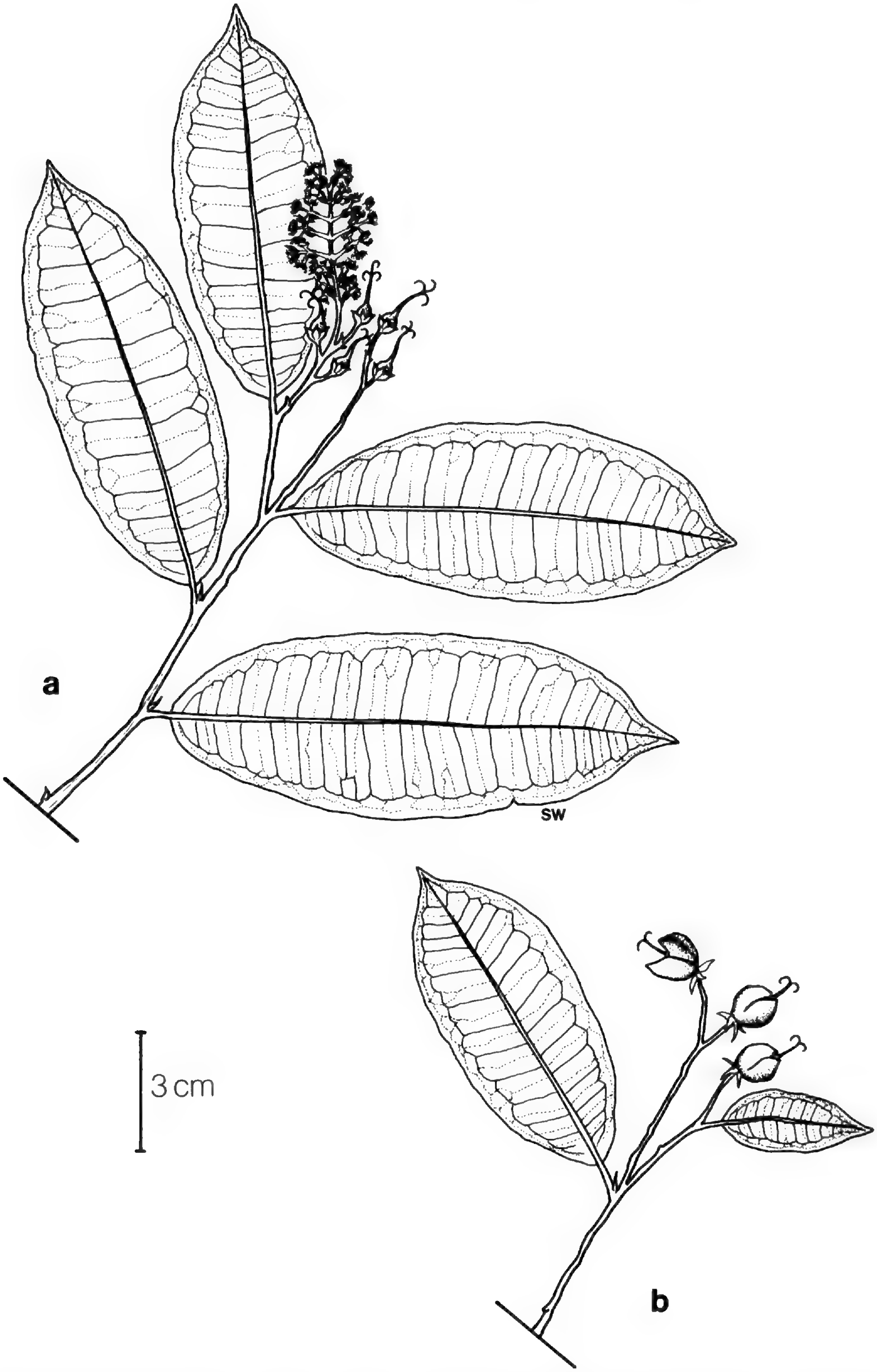

FIGURE 4. Mabea jefensis.—*a. Branch with inflorescence at anthesis and with young fruits.—b. Branch with mature fruits. Based on* Correa et al. 1601 *(a)*, D'Arcy & Sytsma 14733 *(a & b). Illustration by Steve Wilson.*

(MO), *Knapp 1396* (F), *Knapp et al. 4728* (F), *Liesner 1303* (MO), *Maas et al. 1758* (MO), *Mori & Kallunki 1864* (MO), *Nee et al. 8752* (MO), *Sytsma 960* (F, MO); Cañazas mountain chain, near Rancho Chorro, above Tortí Arriba, 400–700 m, *Folsom et al. 6709* (MO).

34. *Senefeldera*

Senefeldera C. Martius, Flora 24 (Beibl.): 29. 1841. TYPE: *Senefeldera multiflora* C. Martius.

Monoecious *shrubs* or trees without evident milky latex; glabrous throughout. *Leaves* alternate (or pseudoverticillate at ends of branches), simple, petiolate; stipules deciduous; blades ± entire, pinnately veined, usually glandular on midrib at base; margins entire. *Inflorescences* terminal, paniculate (of compound spikes or racemes), bisexual. *Staminate flowers* solitary or in glomerules at distal axils of inflorescence axes, subtended by biglandular bracts; calyx 3–5-lobed, sometimes asymmetrical, not covering anthers in bud; petals and disk absent; stamens 5–12; anthers subsessile on an elevated receptacle, extrorse, dehiscing longitudinally; pollen grains subglobose, tectate, 3-colporate; pistillode absent. *Pistillate flowers* solitary at proximal nodes of inflorescence, sessile; calyx 3-parted, segments distinctly imbricate; petals and disk absent; carpels 3, unappendaged, each with a single ovule; styles unbranched, free, or basally connate. *Fruits* capsular, thin-walled; columella slender, usually not persistent; seeds solitary in each locule, plump, carunculate; endosperm copious.

As treated by Jablonski (1965: 171–174), *Senefeldera* is a genus of nine rather poorly understood South American species. It is here recorded from North America for the first time.

34.1. Senefeldera testiculata Pittier, Contr. Fl. Venez. 2: 31. 1923. TYPE: Venezuela. Zulia: Perijá, *Pittier 10910* (US).

Shrub or small tree to ca. 4 m high; twigs subterete, channeled, smooth. *Leaves* with petioles variable in length, 0.5–4 cm long, adaxially channeled; stipules triangular, ca. 2 mm long, deciduous (leaving conspicuous scars); blades chartaceous, elliptic-lanceolate, acuminate at apex, cuneate at base, 12–24 cm long, 4–10 cm broad, usually with a ventral median swollen gland ca. 0.5–1 mm long; major lateral veins ca. 10–15 on a side, slightly curving to margins, the veinlets prominulous on both sides; margins plane to slightly reflexed, entire. *Inflorescences* usually bisexual, mostly 7–20 cm long; lateral axes 5–8, the peduncles 5–11 mm long. *Staminate flowers* 2 or 3 per node; bracts ca. 1–1.5 mm long, acute, the glands infolded on adaxial side; pedicels 0.5 mm long or shorter, subtended by 1 or more bractlets within the bract; calyx segments 3, unequal, acute, as broad as or broader than long, ca. 0.5–0.7 mm long; stamens 5; anthers apiculate, ca. 0.4–0.5 mm long (much longer than the very short filaments). *Pistillate flowers* solitary at the 2 or 3 lowermost nodes of each lateral axis, sessile; bracts apiculate, 1–1.3 mm long, with glands 0.8–1 mm across; calyx segments 3, slightly imbricate, broadly ovate, apiculate, ca. 1.2–1.3 mm long; ovary smooth and unappendaged, 3-locular, carinate; styles nearly free, ca. 1.5 mm long, falcate, thickened below and tapering to an acute tip, ventrally papillate. *Capsules* oblate, ca. 11.5–12 mm diam., 3-lobed, inconspicuously reticulate and ribbed, cocci ca. 7 mm long; columella ca. 5 mm high, unthickened, not persistent; seed plump, ovoid, ca. 5–6 mm long, brownish, streaked or mottled, smooth, ± notched at base; caruncle small; hilum subapical, raphe conspicuous.

Lowland evergreen rainforest, Panama to Venezuela; here reported from Panama for the first time.

The Panamanian specimens are a rather good match for collections of *S. testiculata* from Zulia, Venezuela (*Steyermark 99576, 99917*, VEN). Although they differ from the South American plants in having more acute leaf bases and shorter inflorescences, there seems little doubt that they are conspecific.

Specimens examined. PANAMA. DARIÉN: Río Canglón, *Duke & Bristan 363* (DAV, MO); Río Perrecénico off Río Pirre, *Duke & Bristan 8236* (DAV, MO); ridge 2 hours by piragua upstream above Tucutí, *Duke 5261* (DAV, MO; incorrectly cited as *Caryodendron angustifolium* in the original treatment); Estero Grande off Río Marea, *Duke 10962* (F, MO); Río Ucurgantí, *Bristan 1148* (F, MO); Manené to Río Coasí, *Hartman 12213* (F, MO).

35. *Sebastiania*

Sebastiania Sprengel, Neue Entd. Pflanzenk. 2: 118, pl. 3. 1821. TYPE: *Sebastiania brasiliensis* Spreng.

The discovery of an additional species of *Sebastiania* makes it necessary to provide a key to the two Panamanian species. A third Panamanian species, too fragmentary for identification, is discussed but not included in the key.

KEY TO THE SPECIES OF *SEBASTIANIA* IN PANAMA

1a. Annual herb; leaves linear-lanceolate; staminate flowers borne distichously on the rachis; seeds not over 2.5 mm long .... 1. *S. corniculata*
1b. Shrub 2–3 m high; leaves elliptic-lanceolate; staminate flowers borne spirally on the rachis; seeds ca. 4 mm long .... 2. *S. panamensis*

35.2. Sebastiania panamensis Webster, sp. nov. TYPE: Panama. Chiriquí: N of San Félix at Chiriquí–Bocas del Toro border, on Cerro Colorado copper mine road, 5,000–5,500 ft., 3 May 1975, *Mori & Kallunki 5786* (holotype, DAV; isotype, MO).

A speciebus sect. *Microstachydi* recedit floribus masculinibus spiralibus, seminibus longioribus; a speciebus sect. *Elachocrotoni* differt habitu; a speciebus sect. *Sebastiania* differt ovario armato.

Shrub ca. 2–3 m high, the trunk ± unbranched; twigs slender, subterete, antrorsely ± appressed pubescent. *Leaves* with petioles 3–7 mm long, appressed-pubescent; stipules triangular-lanceolate, dark, 0.8–1.2 mm long; blades thinly chartaceous or membranous, elliptic-lanceolate, ± caudate-acuminate at tip, cuneate at base, (2.5–)5–12 cm long, (1–)2–4 cm broad, concolorous, without laminar glands, glabrous to distinctly hirsutulous on both faces; midrib plane above, distinctly raised beneath; major lateral veins ca. 8–20 on a side, straightish, slightly prominulous beneath, distally anastamosing into intramarginal loops; veinlets forming a delicate inconspicuous reticulum; margins finely crenulate with ca. 8–25 appressed teeth on a side. *Inflorescences* opposite leaves (sometimes pseudoterminal), spiciform, usually bisexual, 2–3 cm long, rachis ± hirtellous; pistillate flowers solitary at base, staminate flowers 1 or 2 per distal bract; bracts spirally arranged, lanceolate, dark, ca. 1 mm long, on each side with a short-stipitate (ca. 0.5 mm) cyathiform gland 0.5–0.8 mm across. *Staminate flowers:* pedicel less than 0.5 mm long; calyx 3-lobed, the lobes obovate, ca. 0.6–0.8 mm long, the anthers ca. 0.3 mm long. *Pistillate flowers:* subsessile or the pedicel up to 1.5 mm long at anthesis, becoming up to 4 mm long in fruit; calyx lobes 3, imbricate (covering ovary in bud), 0.7–1 mm long, eglandular within; ovary glabrous, 3-carpellate, each carpel with a pair of subapical horns; styles nearly free, spreading, tapering, ca. 1.5–2.5 mm long. *Capsules* ca. 6 mm high, ca. 7 mm broad, with 6 subapical lower triangular processes; columella ca. 4.5 mm high; seeds ovoid-ellipsoid, reddish brown and mottled, smooth, ca. 4 mm long; caruncle nearly 1 mm broad.

Montane rainforests or cloud forests, western Panama.

This shrubby species, now represented by several collections from montane rainforests in Chiriquí and Veraguas, does not appear to have been previously described. In overall appearance and floral characteristics it resembles the weedy *S. corniculata* of section *Microstachys* (Adr. Juss.) Muell. Arg. but differs in its woody habit. Its spirally arranged staminate flowers separate it from the woody species of that section. In the treatment of Pax (Pflanzenreich 85: 89ff. 1912) it would key to section *Elachocroton* (F. Muell.) Pax, but it does not resemble any of the species in that section except possibly *S. stipulacea* (Muell. Arg.) Muell. Arg.; that species, however, is entirely glabrous, with broader leaves and multicornute ovaries. The Panamanian plants do not fit into section *Adenogyne* (Klotzsch) Benth. because the staminate calyx is not asymmetric, the fruit is echinate, and the branches are not spiny. Nor do the Panamanian plants agree with species in section *Sebastiania*, because of their leaf-opposed spikes, broader staminate calyx lobes, and echinate fruits.

The sectional divisions used by Pax do not seem to be very well founded, so that a satisfactory systematic placement of *S. panamensis* does not seem to be feasible until the genus is monographed. At present, it appears that *S. panamensis* may represent a possible connecting link between the species of section *Microstachys*, with leaf-opposed spikes and echinate fruits, and the sections with terminal or axillary spikes and usually unarmed fruits.

Additional specimens examined. PANAMA. CHIRIQUÍ: Cerro Colorado, 1,200–1,500 m, *Mori & Dressler 7827* (MO, dupl. at SCZ seen by M. Huft), *Sullivan 391* (MO), *Antonio 1409* (MO, dupl. at PMA seen by M. Huft); above San Félix along mining road, above Chame, 1,200–1,500 m, *Croat 33044* (DAV, MO); near San Félix, 800–1,200 m, *Croat 33437* (MO); Chiriquí Trail, premontane rainforest between Pinola and Quebrada Honda, *Kirkbride & Duke 898* (DAV, MO), *Churchill & Churchill 6083* (F, MO); La Fortune hydroelectric project, 1,100–1,200 m, *Hammel 2165* (DAV, MO), *Knapp 4980* (MO), *Mendoza et al. 110* (MO); E of Fortuna campsite, *Folsom & Dressler 5299* (DAV, MO). VERAGUAS: Cerro Tute, 750–1,400 m, *Antonio 1817* (MO), *Knapp & Kress 4359* (F, MO), *Knapp & Sytsma 2562* (F, MO), *Mori & Kallunki 5232* (DAV, MO), *Mori et al. 7609* (DAV, MO).

35.3. Sebastiania sp. A.

Several fruiting collections from the dry Pacific coast of Panama and Costa Rica and from thorn scrub on the Caribbean coast of Colombia represent a species otherwise unknown in Central America. In its membranous, venose, broadly ovate to rhombiform leaves with crenate to crenulate margins, it closely resembles such species of sect. *Sebastiania* from southern Brazil and Argentina as *S. brasiliensis* Sprengel, *S. anisandra* (Griseb.) Lillo, and *S. warmingii* (Muell. Arg.) Pax. Even closer is *S. macrocarpa* Muell. Arg. of Ceara in northeastern Brazil, with which it shares a large capsule (to 15 mm in diameter).

Until flowering material becomes available, it will remain uncertain whether the Panamanian plant represents an undescribed species or belongs to one of the Brazilian species.

The Costa Rican specimen cited below is the basis for the record of *Ophellantha spinosa* Standley cited by Standley from Costa Rica (Standley, 1938: 1557). That species is definitely known only from northwestern Mexico to Honduras. One of the Colombian collections (*Gentry & Cuadros 47466A*, MO) has an immature inflorescence with a single pistillate flower and the multiparted bracteal glands that are characteristic of several species of section *Sebastiania*.

Specimens examined. COSTA RICA. ALAJUELA: vic. of San Ramón, Los Loros, *Brenes 22679* (CR, NY). PANAMA. LOS SANTOS: 1–2 mi. W of Candelaria, *Duke 12443* (MO, US); Las Tablas, *Dwyer 1100* (MO); Los Santos, 30 m, *Lao 320* (MO). COLOMBIA. ATLÁNTICO: Puerto Colombia, 50–100 m, *Dugand 626* (F, distributed as *S. granatensis* Muell. Arg.). BOLÍVAR: Galerazamba, N tip of Bolívar, thorn scrub forest, 10°48′N, 75°15′W, *Gentry & Cuadros 47456, 47466A, 47474* (F, MO).

36. *Gymnanthes*

Gymnanthes Sw., Prodr. 95. 1788. LECTOTYPE: *Gymnanthes lucida* Sw. (chosen by Grisebach, Fl. Br. W. Ind. 50. 1859).

Actinostemon Klotzsch, Arch. Naturgesch. 7: 184. 1841. TYPE: *A. concolor* (Sprengel) Muell. Arg. (*Gussonia concolor* Sprengel).

Dactylostemon Klotzsch, Arch. Naturgesch. 7: 181. 1841. TYPE: not designated.

Monoecious (rarely dioecious) *shrubs* or trees; latex scanty and scarcely milky; indumentum absent or of simple hairs. *Leaves* alternate, simple, petiolate; stipules small, mostly persistent; blades pinnately veined, entire or crenulate, glandular or eglandular. *Inflorescences* terminal or axillary, bisexual (or less commonly unisexual), spiciform, of 1–several basal solitary pistillate flowers and many distal staminate cymules; bracts mostly biglandular, subtending solitary pistillate flowers and 1–several staminate flowers. *Staminate flowers* mostly pedicellate; calyx of 1 lobe or rudimentary or absent; petals and disk absent; stamens mostly 2–5; filaments free or basally connate; anthers extrorse, dehiscing longitudinally; pollen grains subglobose, tectate, 3-colporate; pistillode absent. *Pistillate flowers* sessile or pedicellate; calyx mostly 3-lobed, the lobes sometimes reduced or obsolete, eglandular within; petals and disk absent; carpels 3, each with a single ovule; styles free or basally connate, unbranched. *Fruits* capsular; columella ± persistent; seeds solitary in each locule, caruncullate; testa smooth; endosperm copious.

As here circumscribed, *Gymnanthes* includes *Actinostemon* Klotzsch and *Dactylostemon* Klotzsch. Although most authors have upheld at least *Actinostemon* as a distinct genus, this seems to have been due more to inertia rather than to critical assessment of diagnostic characters. Pax & Hoffmann (1912: 13) did not provide any convincing distinctions in their key, nor did Jablonski (1967: 164, 178), who candidly stated that "the distinction between *Actinostemon* and *Gymnanthes* is very vague." Even when *Actinostemon* is merged with *Gymnanthes*, the enlarged genus is difficult to distinguish from *Sebastiania*. Mueller (1866: 1164–1165), in fact, combined the two, but called the composite genus *Sebastiania* because the name *Gymnanthes* (which has priority) seemed inappropriate to him. The distinctly reduced staminate calyx of *Gymnanthes* furnishes only a tenuous difference from *Sebastiania*, in which the staminate calyx is presumably usually well developed. As Pax & Hoffmann (1912: 89–90) pointed out, *Sebastiania* may be an unnatural genus, part of which should be combined with *Gymnanthes*. Clarification of these difficulties will have to await the efforts of a very intrepid monographer.

Rothmaler (1944), following a suggestion by Hallier (1918), adopted the name *Ateramnus* P. Browne (1756: 338) in place of *Gymnanthes*. However, this is not justifiable, as has been shown recently (Webster, 1983); *Ateramnus* is best disposed of by lectotypifying it so that it becomes a synonym of *Sapium*.

As here construed, *Gymnanthes* is then a neotropical genus of about 40 species; the two Panamanian species are reported here for the first time.

LITERATURE

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JABLONSKI, E. 1969. Notes on neotropical Euphorbiaceae. 4. Monograph of the genus *Actinostemon*. Phytologia 18: 213–240.

PAX, F. & K. HOFFMANN. 1912. Euphorbiaceae—Hippomaneae. *In:* A. Engler, Das Pflanzenreich IV. 147. V(Heft 52): 1–319 (*Gymnanthes*, pp. 81–88).

ROTHMALER, W. 1944. Nomina generica neglecta 1753–1763. Repert. Spec. Nov. Regni Veg. 53: 1–37.

WEBSTER, G. L. 1983. A botanical gordian knot: the case of *Ateramnus* and *Gymnanthes* (Euphorbiaceae). Taxon 32: 304–305.

KEY TO THE SPECIES OF *GYMNANTHES* IN PANAMA

1a. Staminate bracts each with 1 gland on each side, subtending 3 flowers; leaves glandular on margins; staminate calyx of 1 segment; fruiting pedicels 13–21 mm long; seeds 6.3–6.6 mm long .... 1. *G. actinostemoides*

1b. Staminate bracts (at least in part) with paired glands on each side, each bract subtending 1 flower; leaves eglandular on margins; staminate calyx absent; fruiting pedicels 40–50 mm long; seeds ca. 5.5 mm long .... 2. *G. dressleri*

36.1. **Gymnanthes actinostemoides** Muell. Arg., Linnaea 32: 103. 1863; Pax & Hoffmann, Pflanzenreich IV. 147. V(Heft 52): 85. 1912 (as *G. actinostemonoides*). *Sebastiania actinostemoides* Muell. Arg. in DC., Prodr. 15(2): 1184. 1866. TYPE: Mexico. Veracruz: Zacuapan, *Linden 1357* (holotype, G, microfiche seen).

Tree to 10–12 m high; twigs of current year obtusely angled, short-puberulent (glabrate in age). *Leaves* with petioles 3–10 mm long, ± puberulent; stipules lanceolate, ca. 1–2 mm long; blades chartaceous, elliptic-oblong, mostly caudate-acuminate at tip (the acumen acute, ca. 0.5–1.5 cm long), acutely cuneate at base, ca. 6–16 cm long, 2–6 cm broad, without laminar glands but with 1–3 depressed cyathiform glands at proximal marginal crenulations; midrib raised on both sides and puberulent proximally; major lateral veins ca. 10–15 on a side, arcuate; veinlets distinctly prominulous beneath (slightly so above), forming irregular areoles; margins plane, remotely crenulate (teeth mostly 12–17 on a side), the distal teeth with a minute deciduous glandular tip, the proximal teeth with depressed cyathiform glands. *Inflorescences* axillary, racemiform, unisexual or bisexual, 2–7 cm long, the rachis puberulent. *Staminate flowers* in cymules of 3, subtended by umbonate bracts ca. 1 mm long, each bract with a pair of cyathiform glands 0.6–0.8 mm across attached above the base (subapical); pedicels 0.5–1.5 mm long (longer in central flower); calyx usually of 1 triangular segment ca. 0.5–0.7 mm long; stamens 2 or 3; filaments free, ca. 0.8–1.2 mm long; anthers ca. 0.4 mm long. *Pistillate flowers* solitary, 1 or 2 per raceme; bract eglandular; pedicel puberulent, ca. 2–4 mm long at anthesis, increasing to 13–21 mm long in fruit; calyx segments 3, pointed, not imbricate, 0.6–0.7 mm long; ovary unappendaged, smooth, puberulent; styles 3, basally connate for ca. ¼–½ their length, 2.5–5 mm long. *Capsules* not seen entire; cocci 11–13 mm long, smooth; seeds plump, ovoid, ca. 6.3–6.6 mm long, 5.8–6 mm broad, brownish, smooth, obscurely beaked; caruncle 0.8–1.3 mm broad.

Montane and perhaps also lowland rainforests, eastern Mexico (Veracruz) to Panama.

The single Panamanian collection of this species bears only fruits, so the identification of Bristan's plant with a Mexican species must be provisional. However, the characteristic leaf venation and especially the distinctive marginal foliar glands suggest that our plant is conspecific with specimens from Veracruz, Mexico (such as *Purpus 3795, 8060* from Zacuapan, *4410* from Fortín, all at UC, from which the floral characters have been taken).

Specimen examined. PANAMA. DARIÉN.: Río Pirre, *Bristan 1466* (DAV, MO).

36.2. **Gymnanthes dressleri** Webster, sp. nov. TYPE: Panama. Panamá: La Eneida, region of Cerro Jefe, 3 Jan. 1968, *Dressler 3323* (holotype, MO; isotype, DAV).

Species haec aff. *G. granatensi*, differt foliis integris late ellipticis, cuspidato-acuminatis, glandulis bractearum masculinis duplicatis, calyce nullo.

Tree 2 m or more, glabrous; twigs slender, subterete, smooth, brownish. *Leaves* with petioles 3–5 mm long; stipules ovate, rounded, scarious, ca. 1 mm long; blades chartaceous, broadly elliptic, rather abruptly cuspidate-acuminate at tip (the acumen obtuse, 0.5–1 cm long), cuneate at base, 3–8 cm long, 1.5–4 cm broad, appearing eglandular but sometimes with a few scattered minute (diam. ca. 0.2 mm) embedded laminar glands, distinctly paler and glaucous beneath; major lateral veins ca. 6–8 on a side, straightish or distally arcuate; veinlets distinctly prominulous beneath, often as prominent as the laterals, forming areoles partly parallel to the laterals; margins entire, with a plane or slightly reflexed subcartilaginous rim. *Inflorescences* axillary, mostly at the base or lower axils of annual increments, racemiform, unisexual or bisexual, where bisexual with 1 or 2 basal pistillate flowers and ca. 8–13 distal staminate flowers; bracts all subtending solitary flowers, ovate, scarious, ca. 0.5–0.7 mm long, mostly with paired subsessile cyathiform glands on each side at base, the larger gland of each pair ca. 0.3 mm across. *Staminate flowers* with pedicels ca. 0.4–1.2 mm long, articulated at the top; calyx, petals, and disk absent; stamens 2–4; filaments free or basally united, 0.4–0.7 mm long; anthers 0.4–0.5 mm long. *Pistillate flowers* with pedicels ca. 3–5 mm long at anthesis, increasing to 40–50 mm long in fruit; calyx lobes 3, ovate, not overlapping, ca. 0.5–0.7 mm long, eglandular within, the margins minutely crenulate; ovary smooth and unappendaged; styles 3, ca. 1.5–2 mm long, thickish, recurved, slightly connate at base. *Capsules* not seen entire; columella 5.5–6 mm long, subpersistent; seeds ovoid-oblong, ca. 5.5 mm long, ca. 4–4.5 mm broad, essentially smooth, dark brown, shiny, apically beaked; caruncle ca. 1 mm across.

This new species from Cerro Jefe appears to be closely related to *G. granatensis* Muell. Arg., which was described (Linnaea 32: 107. 1863) from the vicinity of Ocaña in northern Colombia. Although the type collection of *G. granatensis (Schlim 586)* has not been examined, study of a photograph of the type and Mueller's description (in DC., Prodr. 15(2): 1189–1190. 1866) suggests that the Panamanian plant differs in some important particulars: the leaves are broader, more abruptly cuspidate, distinctly glaucous beneath, and entire at the margins. The staminate flowers completely lack a calyx, whereas there are two subulate calyx lobes in *G. granatensis*, and the staminate bracts have duplex glands on each side, while in the Colombian species (judging from Mueller's description), the bracteal glands are single on each side.

In the system of Pax & Hoffmann, *G. granatensis* would probably fit best into the "genus" *Actinostemon*, although they listed it under *Sebastiania* (Pax & Hoffmann, 1912: 150). However, because of its glabrous inflorescence and well-developed pistillate calyx, it would not readily fit into either of the sections of *Actinostemon*. Within *Gymnanthes* (sensu Pax), perhaps the species most similar to *G. dressleri* and *G. granatensis* is *G. farinosa* (Griseb.) Webster[6]. That West Indian species has somewhat similar leaves but differs in its three-flowered staminate bracts with a single gland on each side, and in its well-developed staminate calyx. Among the species with bracts subtending solitary flowers, the closest to *G. dressleri* appears to be the Cuban species *G. albicans* (Griseb.) Urban; however, in that species the leaves are more elongated and lack cuspidate tips, the bracts are eglandular, and the staminate flowers have 5–12 stamens.

37. *Maprounea*

Maprounea Aublet, Hist. Pl. Guiane 2: 895. 1775. TYPE: *Maprounea guianensis* Aublet.

Shrubs or trees, glabrous throughout; latex neither copious nor milky; monoecious. *Leaves* alternate, simple, petiolate; stipules small, persistent; blades pinnately veined, entire, glandular or eglandular. *Inflorescences* terminal, usually bisexual, of 1–4 solitary, pedicellate, pistillate flowers at basal nodes, the staminate flowers densely aggregated in a strobiliform mass at the end of the fleshy enlarged rachis, separated from the pistillate portion by an elongated internode (pseudopeduncle); bracts biglandular. *Staminate flowers* mostly 3 per bract; pedicel very short; calyx ± 3-lobed, distinctly gamophyllous, the lobes imbricate, ± covering the stamens in bud; petals and disk absent; stamens usually 2; filaments completely connate into a slender tube that is exserted from the calyx at anthesis; anthers bluntly apiculate, dehiscing extrorsely and longitudinally; pollen grains subglobose, tectate-perforate, 3-colporate, colpi marginate; pistillode absent. *Pistillate flowers* solitary to each bract, distinctly pedicellate; calyx 3-parted, segments imbricate, eglandular within; petals and disk absent; carpels 3, each with a single ovule; ovary unappendaged; styles connate into a column, the tips unbranched, spreading. *Fruits* capsular; columella not persistent; seeds solitary in each locule, the testa distinctly foveolate; caruncle large and partly occluding top of seed; endosperm copious.

A well-marked genus of three or four species, one or two in tropical America and two in tropical Africa, easily distinguished from the genera in the *Gymnanthes–Sebastiania* complex by its characteristic headlike staminate inflorescence, elongated staminal column, and hypertrophied caruncles on the seeds. *Maprounea* is here reported from North America for the first time.

RECENT LITERATURE

ALLEM, A. C. 1976. Uma especie unica de *Maprounea* (Euphorbiaceae) na America do Sul. Acta Amazonica 6: 417–422.

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[6] **Gymnanthes farinosa** (Griseb.) Webster, comb nov. *Excoecaria farinosa* Griseb., Abh. Ges. Wiss. Goettingen 7: 169. 1857. TYPE: Guadeloupe: *Duchassaing* (presumably GOET, not seen).

37.1. Maprounea guianensis Aublet, Hist. Pl. Guiane 2: 895, tab. 342. 1775. TYPE: French Guiana, *Aublet* (not seen).

Trees to ca. 12 m high, glabrous; twigs subterete, smooth, brownish. *Leaves* with petioles ca. 0.5–1.5 mm long, slender; stipules triangular to lanceolate, scarious, ca. 0.5–1 mm long, persistent; blades thinly chartaceous, ovate to elliptic, rather abruptly short-acuminate at tip, cuneate at base (and minutely auriculate at junction with petiole), ca. (2–)3–7 cm long, 1.5–4 cm broad, usually with 1 or 2 elliptic laminar glands on the underside near midrib (occasionally with a few small circular glands towards the tip, or sometimes entirely eglandular); midrib plane above, distinctly raised beneath; major lateral veins ca. 10–15 on a side, straightish; veinlets prominulous on both sides, forming areoles ± parallel to lateral veins; margins plane or recurved, entire. *Inflorescences* terminal mostly on short lateral branches, 1–2 cm long; pistillate flowers solitary at 1–4 basal nodes; staminate flowers in heads ca. 3–9 mm long; staminate bracts rather fleshy, the tip acute, less than 0.5 mm long, the cyathiform glands subsessile, ca. 0.3–0.4 mm across. *Staminate flowers* articulate above very short pedicels; calyx gamophyllous, basally contracted into a stipe ca. 0.3–0.8 mm long; staminal column slender, mostly 0.7–1 mm long; anthers 0.3–0.4 mm long. *Pistillate flowers* on ascending or recurved pedicels (1–)2–5 mm long at anthesis, these becoming 6–13 mm long in fruit; calyx lobes 3, ovate, pointed, ca. 0.7–1 mm long; ovary smooth; styles 3, 2–3 mm long, united nearly or quite halfway into a stout column. *Capsules* ± oblate, not lobed, 6–6.5 mm diam.; seeds ovoid, somewhat compressed, grayish brown, shiny, distinctly beaked, deeply and coarsely foveolate on both sides, 2.9–3.6 mm long, 2.8–3.5 mm broad (including caruncle); caruncle large, covering nearly half the face of the seed ventrally, appearing 2-armed dorsally.

Rainforests at low elevations, Panama and Trinidad south to Peru and Brazil (localities in South America summarized by Jablonski, 1967: 180).

It is curious that this distinctive plant has been collected only a single time in a well-known area in the center of the Canal Zone. Presumably it will eventually turn up in various lowland areas toward the Colombian border.

Specimen examined. PANAMA. CANAL ZONE: 1 mi. N of summit on road to FAA radar tower, *Tyson et al. 2761* (MO, US).

38. *Stillingia*

Stillingia Garden ex L., Syst. Nat. ed. 12. 2: 637. 1767; Mant. Pl. 19. 1767. TYPE: *Stillingia sylvatica* L.

39. *Sapium*

Sapium P. Browne, Civ. Nat. Hist. Jamaica 338. 1756. TYPE: *Sapium jamaicense* Sw.

In the original treatment, the account of *Sapium* was avowedly tentative, pending the appearance of Jablonski's study of the Caribbean and Central American species. Jablonski's work, as well as a study of more recently collected specimens, necessitates an entirely new treatment of the Panamanian species. Of the four species recognized in the original treatment, only *S. eglandulosum* remains unchanged. We have followed Jablonski in referring the species called *S. aucuparium* by Burch to *S. jamaicense* and in uniting *S. caudatum* and *S. biglandulosum* under the name *S. aucuparium*. Jablonski's action in restoring the name *S. jamaicense* seems straightforward and is adopted here. The nomenclatural subtleties connected with *S. aucuparium* are still unresolved, however, and Jablonski's choice is followed as a tentative conclusion only.

Three additional species of *Sapium* are now known from Panama, bringing the total to six. Recent sterile collections of a seventh, possibly undescribed, species have been made on Barro Colorado Island.

RECENT LITERATURE

CROIZAT, L. 1943. Novelties in American Euphorbiaceae. J. Arnold Arbor. 24: 165–189.

HUFT, M. J. 1987. Four new species of *Sapium* (Euphorbiaceae) from Central and South America. Phytologia 63: 441–448.

JABLONSKI, E. 1968. Notes on neotropical Euphorbiaceae. 3. Synopsis of Caribbean *Sapium*. Phytologia 16: 393–434.

KEY TO THE SPECIES OF *SAPIUM* IN PANAMA

1a. Petioles eglandular .... 2. *S. eglandulosum*
1b. Petioles with two apical glands.
  2a. Leaf tips plane, not inflexed or cucullate.
    3a. Style base persistent on mature capsule; capsule pedicellate; secondary foliar veins straight ...... 6. *S. rigidifolium*
    3b. Style base not persistent on mature capsule; capsule subsessile; secondary foliar veins arcuate-ascending .... 5. *S. pachystachys*
  2b. Leaf tips inflexed or cucullate.
    4a. Spikes clustered at tips of branchlets;

secondary foliar veins straight, slightly arcuate near margin ...... 3. *S. jamaicense*
- 4b. Spikes solitary at tips of branchlets; secondary foliar veins strongly arcuate-ascending.
    - 5a. Leaves oblong or oblong-elliptic, less than 2.5 times as long as broad; the secondary veins usually 10–15 per side .... 3. *S. oligoneurum*
    - 5a. Leaves usually elliptic-lanceolate, more than 3 times as long as broad, usually longer than 10 cm, the secondary veins usually more than 20 per side .... 1. *S. aucuparium*

39.1. Sapium aucuparium Jacq., Select. Stirp. Amer. Hist. 249. 1763. LECTOTYPE: Jacquin, Select. Stirp. Amer. Hist., pl. 158 (chosen here).

?*Sapium biglandulosum* (L.) Muell. Arg. (Linnaea 32: 116. 1863) sensu auctt. *Hippomane biglandulosa* L., Sp. Pl. ed. 2, 1431. 1762, correction of *H. glandulosa* L., Sp. Pl. ed. 1, 1191. 1753. *Excoecaria biglandulosa* (L.) Muell. Arg. in DC., Prodr. 15(2): 1204. 1866.

Sapium salicifolium Kunth, Nov. Gen. Sp. Pl. 2: 65. 1817. TYPE: Colombia: *Humboldt & Bonpland* (P, not seen).

Sapium moritzianum Klotzsch in Seem., Bot. Voy. Herald 100. 1853. *Sapium biglandulosum* (L.) Muell. Arg. var. *moritzianum* (Klotzsch) Muell. Arg., Linnaea 32: 119. 1863. *Excoecaria biglandulosa* (L.) Muell. Arg. var. *moritziana* (Klotzsch) Muell. Arg. in DC., Prodr. 15(2): 1206. 1866. *Sapium aucuparium* Jacq. subsp. *moritzianum* (Klotzsch) Pittier, Contr. U.S. Natl. Herb. 20: 127. 1918. TYPE: presumably Colombia: *Moritz 236*. Panama: *Seemann 1243* (syntypes, not seen); no specimens cited in protologue.

Sapium caudatum Pittier, Contr. U.S. Natl. Herb. 20: 127. 1918. LECTOTYPE: Panama. Canal Zone: hill near Gamboa, 25 June 1911, *Pittier 3713* (US) (chosen by Jablonski, 1968).

Sapium giganteum Pittier, Contr. U.S. Natl. Herb. 20: 128. 1918. TYPE: Panama. Colón: Fato, sea level, 10 Aug. 1911, *Pittier 4141* (holotype, US).

Stillingia haematantha Standley, Ann. Missouri Bot. Gard. 27: 314. 1940. TYPE: Panama. Coclé: N rim of El Valle, 9 July 1939, *Allen 1915* (holotype, F; isotype, MO, F neg. 62368).

Monoecious *tree* to 10 m. *Leaves* membranous to chartaceous, rarely coriaceous; petiole 1–5 cm long, the 2 apical glands prominent, cylindrical, ca. 1 mm long; stipules ovate-deltate, 1–1.5 mm long, 1.5–2 mm broad, persistent; blades elliptic-lanceolate to oblong-obovate, 5–40 cm long, 1.5–8 cm broad, 3–5 times as long as broad, the base rounded to acute, the margins entire, obscurely toothed or coarsely serrate, the apex short-acuminate or cuspidate, strongly cucullate. *Spikes* solitary, terminal, to 22 cm long, bisexual or staminate. *Staminate flowers* in groups of 7–10, the subtending bract flabellate, ca. 0.5 mm long, biglandular, the glands circular to oblong, 0.5–3 mm long, 0.5–1 mm broad; calyx ca. 1 mm long, cupular, 2-lipped; stamens 2. *Pistillate flowers* to 10, solitary at basal nodes, the bracts and glands as those of the staminate flowers; calyx cupular, 2-lobed; ovary orbicular, the style simple, the style-branches strongly reflexed, the tips expanded. *Capsules* ovoid, to 1 cm long, smooth; seeds ovoid, flattened laterally, the surface warty.

There has been considerable controversy concerning the proper name of this species. The name *S. aucuparium* Jacq. had long been applied to it, but Croizat (1943: 175), whom Burch followed in the original treatment, referred that name to the species usually known as *S. jamaicense* Sw. and resurrected *S. biglandulosum* for this species. Jablonski correctly restored Jacquin's name to the present species, but rejected the name *S. biglandulosum* as a *nomen confusum*, leaving *S. aucuparium* as the earliest available name. It would seem, however, that the application of *S. biglandulosum* can be fixed by a proper lectotypification. More study is needed before that can reasonably be done, and, in any case, it is not clear to the present author whether any of the elements originally cited under *S. biglandulosum* actually belong to this species. The best course, then, seems to be the tentative acceptance of *S. aucuparium* Jacq. for this species until the matter can be satisfactorily resolved.

We are following Jablonski (1968) in uniting *Sapium caudatum* and *S. biglandulosum* (sensu Croizat and Burch) under *S. aucuparium*. Examination of a wide range of collections from Panama and from northern South America shows that the leaf characters used by Burch to distinguish these species are continuously variable and do not correlate with other characters. This is a commonly collected, highly variable species of lowland tropical forests.

39.2. Sapium eglandulosum Ule, Bot. Jahrb. Syst. 35: 673. 1905. TYPE: Brazil. Amazonas: Bom Fin on the Rio Juruá, Nov. 1900, *Ule 5356* (holotype, B, F neg. 5522).

The following collection records a considerable westward range extension for this species, which was previously known in North America only from eastern Darién.

Additional specimen examined. PANAMA. PANAMÁ: Cerro Jefe region, 2 km N of turnoff to radio tower on roadside of Alto de Pacora, 2,600 ft., *Hammel 4868* (F, MO).

39.3. Sapium jamaicense Sw., Adnot. Bot. 62. 1829. TYPE: Jamaica: *Swartz s.n.* (BM, not seen).

Sapium aucuparium sensu Croizat, J. Arnold Arbor. 24: 174. 1943, sensu Burch, Ann. Missouri Bot. Gard. 54: 325. 1967, *non* Jacq. 1763.

Sapium pleiostachys Schumann & Pittier, Contr. U.S. Natl. Herb. 12: 164. 1908. TYPE: Costa Rica. Puntarenas: Golfito de Osa, near seashore, Mar. 1896, *Pittier s.n., Inst. Fis. Geog. Costa Rica no. 9906* (holotype, US-578902; isotypes, F, F neg. 62366, GH, F neg. 62360).

Sapium anadenum Pittier, Contr. U.S. Natl. Herb. 12: 164. 1908. TYPE: Costa Rica. Cartago: Hacienda Valverde at Orosi, 1,200 m, Mar. 1902, *Pittier s.n., Inst. Fis. Geog. Costa Rica no. 16366* (holotype, US-578045; isotype, F, F neg. 62364).

Rainforests, West Indies, Mexico to Panama, and recently discovered in Colombia.

The correct name of this species has also been a matter of some confusion. *Sapium jamaicense* had been used universally until Croizat (1943: 174) asserted that *S. aucuparium* sensu Jacq., *Enum. Pl. Carib.* 31, 1760, properly refers to this plant, in contradistinction to Jacquin's intention stated in his *Selectarum Stirpium Americanum Historia* (1763), which had been followed by most other authors, who had applied the name *S. aucuparium* as in this paper. Jablonski (1968), however, correctly pointed out that Jacquin's publication of *S. aucuparium* in 1760 is invalid, since a description is lacking, and that the traditional application of *S. aucuparium* as published by Jacquin in 1763 is correct.

Jablonski (1968) recognized *Sapium pleiostachys* as distinct from *S. jamaicense,* referring all collections from Panama and Costa Rica, as well as a few from Guatemala and Chiapas, to the former species, and restricting the latter to the West Indies and northern Central America. The only difference he adduced was the presence of petiolar glands on *S. pleiostachys* and their absence on *S. jamaicense.* Even granting this difference, recognition of *S. pleiostachys* would be tenuous indeed, given the inadvisability of maintaining a species on the basis of a single morphological feature and the assertion that both variants occur in northern Central America (indeed, specimens collected by Matuda at Escuintla, Chiapas, are cited under each species by Jablonski). A thorough examination of collections from throughout the range, however, shows that even these meager grounds are untenable. Plants with petiolar glands occur commonly in the West Indies (cf. *Ekman 5512* from Hispaniola, *Harris 9156* from Jamaica, and *Pringle 104* from Cuba, all F), and thus there is no morphological discontinuity. *Sapium jamaicense* is simply a variable species in regard to the presence or absence of petiolar glands, and there is no justification for recognition of *S. pleiostachys.*

A few new provincial records are recorded below.

Additional specimens examined. PANAMA. DARIÉN: Río Pirre, *Bristan 1475* (MO). PANAMÁ: N of highway ca. 2 mi. E of El Llano, 200 m, *Foster & Kennedy 1971* (F, NY). VERAGUAS: Isla de Coiba (Penal Colony), *Dwyer 1566* (MO). COLOMBIA. ANTIOQUIA: Municipio de San Luis, Cañon del Río Claro, 330–425 m, *Cogollo 965, 1232* (MO).

39.4. Sapium oligoneurum Schumann & Pittier, Contr. U.S. Natl. Herb. 12: 168. 1908. *Sapium biglandulosum* (L.) Muell. Arg. var. *oligoneurum* (Schumann & Pittier) Monach., Bull. Torrey Bot. Club 67: 772. 1940. TYPE: Costa Rica: near San Rafael on road from Cartago to Cot, 1,500 m, July 1899, *Pittier s.n., Inst. Fis. Geog. Costa Rica no. 13403* (holotype, US-578903).

Sapium sulciferum Pittier, Contr. U.S. Natl. Herb. 12: 169. 1908. *Sapium biglandulosum* (L.) Muell. Arg. var. *sulciferum* (Pittier) Monach., Bull. Torrey Bot. Club 67: 772. 1940. TYPE: Costa Rica. La Palma, 1,500 m, 15 Aug. 1898, *Tonduz s.n., Inst. Fis. Geog. Costa Rica no. 12428* (holotype, US-577588; isotype, NY).

Sapium schippii Croizat, Amer. Midl. Nat. 29: 477. 1943. TYPE: Belize. Toledo District: Forest Home, Punta Gorda, *Schipp 1049* (holotype, A, F neg. 62361; isotypes, F, F neg. 62365, MO, F neg. 62363).

Monoecious *tree* to 20 m. *Leaves* membranous or chartaceous; petiole 1–3(–6) cm long, the two glands near the apex opposite or subopposite, cylindrical, 1–2 mm long; stipules ovate-deltate, oblique, 2–3 mm long, 1.5–2 mm broad, appressed, persistent; blade oblong or elliptic-oblong, 4–10(–18) cm long, 2.5–4.5(–8) cm broad, 1.2–2.4 times as long as broad; midvein prominent, the secondary veins 10–15(–20) per side, somewhat inconspicuous; base rounded to obtuse; margin appearing entire, remotely denticulate with minute glandular teeth; apex acute or more often abruptly short-cuspidate, conspicuously and tightly cucullate. *Spikes* solitary, terminal, to 22 cm long, bisexual or staminate. *Staminate flowers* in groups of 5–7, the subtending bract short, broad, 1–1.2

mm long, 1.8–2.1 mm broad, rounded, hyaline, slightly erose, biglandular, the glands suborbicular to oblong, 1.8–3 mm long, 1.8–2.5 mm broad, flattened; calyx cupular, 1.7–2 mm long, 2-lipped; stamens 2, the filaments free. *Pistillate flowers* 10–22, borne singly at basal nodes of bisexual spikes; bracts and calyces as in the staminate flowers; ovary globose; styles simple. *Capsules* subglobose to slightly obovoid, subsessile, 5–9 mm long, 5–12 mm diam., smooth; seeds subglobose, slightly compressed, yellowish, the surface warty.

Montane and cloud forests, forest edges, and clearings, Chiapas, Mexico, to Panama.

Specimens examined. PANAMA. BOCAS DEL TORO: region of Cerro Colorado, 3.3 mi. above Camp Chamí, 8°35′N, 81°45′W, ca. 1,350 m, *McPherson 9587* (F). CHIRIQUÍ: E of Boquete on Cerro Azul near Quebrada Jaramillo, 1,500–1,620 m, *Croat 26820* (MO, NY); along road between Gualaca and Fortuna Dam site, 10.1 mi. NW of Los Planes de Nornito, 8°45′N, 82°17′W, 1,250 m, *Croat 50032* (MO); Boquete, 4,000 ft., *Davidson 852* (MO, US; cited in the original treatment as *S. aucuparium* sensu Burch); near Cerro Colorado, ca. 3.5 mi. along road from Chamí Camp, ca. 8°35′N, 81°45′W, ca. 1,350 m, *McPherson 8997* (F); pastures around El Boquete, 1,000–1,300 m, *Pittier 2880* (F, US); valley of the upper Río Chiriquí Viejo, *G. & P. White 95* (MO).

These specimens have been distributed under the names *S. caudatum*, *S. aucuparium*, *S. oligoneurum*, or *S. sulciferum*.

39.5. Sapium pachystachys Schumann & Pittier, Contr. U.S. Natl. Herb. 12: 168, tab. 16. 1908. TYPE: Costa Rica. San José: Dota Mountains, El Copey, 1,800 m, Feb. 1898, *Tonduz s.n.*, *Inst. Fis. Geog. Costa Rica no. 11875* (holotype, US-333961; isotype, F, F neg. 62367).

Monoecious *tree* to 25 m; older twigs covered with crowded persistent stipules. *Leaves* membranous or chartaceous; petiole 2–5 cm long, the 2 glands near the apex subopposite, cylindrical, 1–3 mm long; stipules deltate, 4–6 mm long, 2–3 mm broad, appressed, persistent; blade elliptic, elliptic-obovate, or elliptic-lanceolate, 5–20 cm long, 2.5–7.5 cm broad, 1.6–2.4(–4.5) times as long as broad; base rounded or obtuse, rarely acute; margins entire or obscurely crenate; apex obtuse or acute, occasionally short-acuminate, plane. *Spikes* solitary at the apex of smooth lateral shoots, to 20 cm long, bisexual. *Staminate flowers* in groups of 7–10(–12), the subtending bract short, broad, to 2 mm long, hyaline, erose, biglandular, the glands oblong, 2.5–3 mm long, 1–1.5 mm broad, flattened, calyx 1–1.5 mm long, cupular, 2-lipped; stamens 2, the filaments free. *Pistillate flowers* 14–22, solitary at basal nodes; bracts as in the staminate flowers; calyx 1–1.5 mm long, cupular, 2-lipped; ovary globose; styles simple, fused for ⅓–½ their length, the free portion strongly coiled. *Capsules* globose, subsessile, 7–10 mm long, smooth; seeds subglobose, flattened laterally, ca. 4 mm diam., the edges short-winged, the surface somewhat warty.

Montane rainforest and cloud forest, 700–2,000 m, Costa Rica and Panama.

The twigs densely covered with persistent stipules and the large, broad leaves with noncucullate apices are characteristic features of this species. A related species, *S. allenii* Huft, has recently been described from eastern Costa Rica (Huft, 1987) and may eventually be discovered at lower elevations in western Panama. It differs from *S. pachystachys* in having axillary spikes, smaller, stipitate capsules, and a small membranous calyx that does not persist on the mature capsules.

Specimens examined. PANAMA. BOCAS DEL TORO: border with Chiriquí, Cerro Colorado mine area, from Chamí Station to ca. 9 mi. along road, 8°35′N, 81°54′W, 1,100–1,700 m, *Hammel & Trainer 15004* (F). CHIRIQUÍ: Boquete, Finca Collins, *Blum & Dwyer 2558* (MO); SO de campamento Fortuna (8°45′N, 82°15′W), sitio de presa, desde la finca Pitti hasta e filo del Cerro Fortuna, 1,000–1,200 m, *Correa et al. 2797* (MO, 2 sheets); Cerro Colorado, along road to copper mine 24.1 km beyond bridge over Río San Félix (13.1 km beyond turnoff to Escopeta), 1,390 m, *Croat 37305* (MO); Cerro Punta, 2,000 m, *Lao 328* (MO); above Los Llanos, 8°47′N, 82°38′W, ca. 2,100 m, *McPherson 9258* (F, MO); Cerro Colorado, 50 km N of San Félix on the Continental Divide, 1,200–1,500 m, *Mori & Dressler 7819* (MO, NY); between Río Ladrillo and Las Siquas Camp, southern slope of Cerro de la Horqueta, 1,200–1,700 m, *Pittier 3165* (US); slopes of Volcán Barú near town of Cerro Punta, 6,300 ft., *Stern & Chambers 97* (MO, US). COCLÉ: N of El Copé on road past sawmill, 2,400 ft., *Antonio 3264* (F, MO). PANAMÁ: 5–10 km NE of Altos de Pacora, on trail at end of road, 700–800 m, *Mori & Kallunki 6065* (MO, NY, 2 sheets).

39.6. Sapium rigidifolium Huft, Phytologia 63: 444. 1987. TYPE: Costa Rica. Heredia: pastures above San Rafael, 30 km W of Vaca Blanca, 1,750 m, 8 Aug. 1971, *Lent 2041* (holotype, F; isotypes, MO, NY, US), distributed as *Sapium thelocarpum* Schumann & Pittier. Figure 5.

Sapium rigidifolium, which is known only from high altitudes in Costa Rica and Chiriquí Province in Panama, belongs to the otherwise wholly South American subsection *Emmenostylum* (Hemsley)

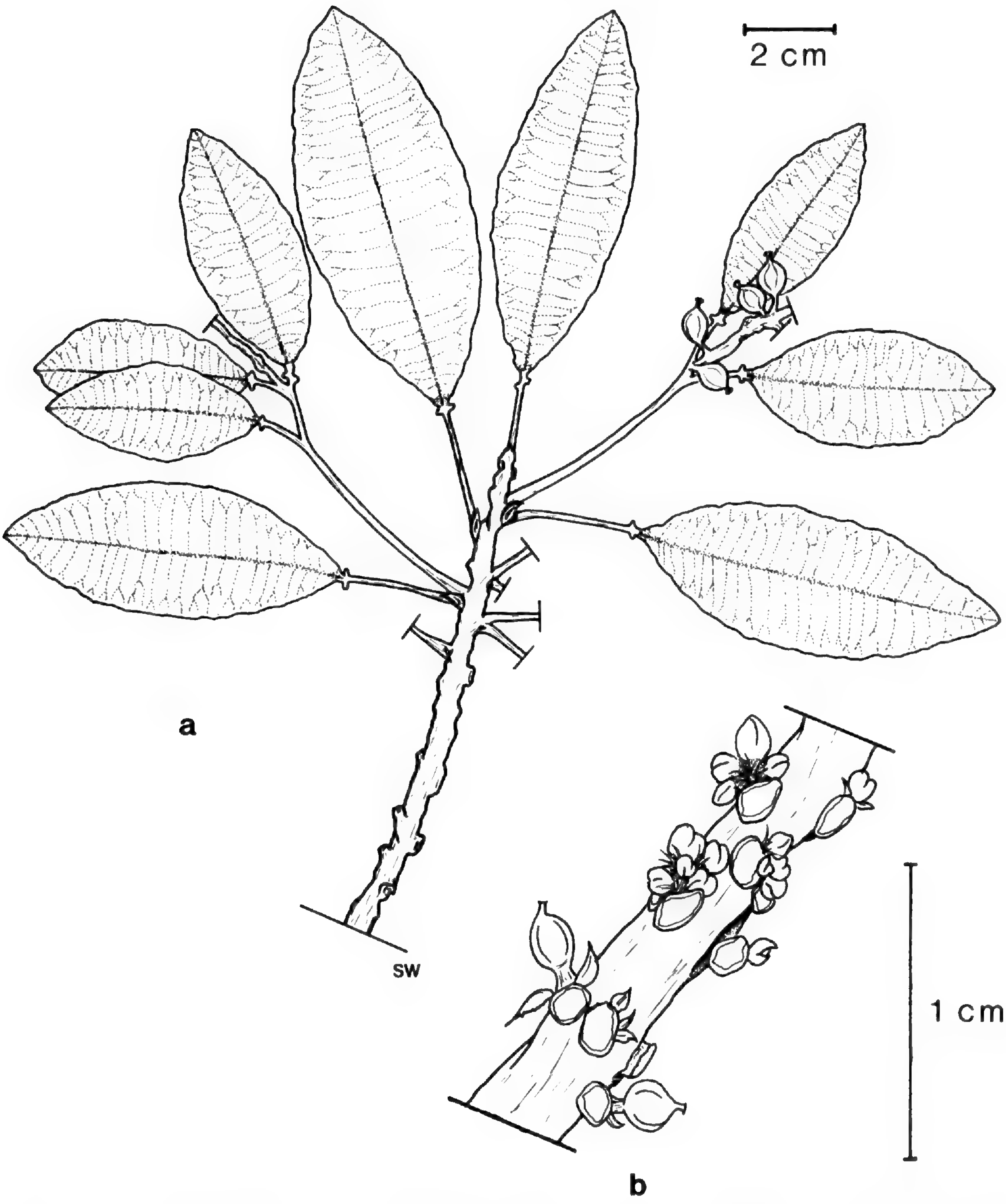

FIGURE 5. Sapium rigidifolium.—*a. Branch with mature capsules.—b. Detail of portion of inflorescence, showing staminate flowers at anthesis and pistillate flowers in young fruit. Based on* Lent 2041. *Illustration by Steve Wilson.*

Pax (Pflanzenr. IV. 147. V(Heft 52): 211. 1912), characterized by styles that are connate for most of their lengths and whose columns persist on the mature capsule, and by leaves with planar apices and nearly horizontal, prominent, closely spaced secondary veins. The South American representatives are restricted to high altitudes in the northern Andes and include such species as *S. verum* Hemsley, *S. stylare* Muell. Arg., and *S. putumayense* Croizat.

Specimens examined. PANAMA. CHIRIQUÍ: Guadalupe Arriba, above Cerro Punta, 8°52′N, 82°33′W, 2,100 m, *de Nevers & Charnley 6057* (F); Boquete, Cerro Horqueta, 5,000–6,000 ft., *Dwyer & Hayden 7685* (MO); Cerro Punta, 2,000 m, *Lao 391* (MO, PMA); slopes of Volcán Barú, near town of Cerro Punta, 6,000 ft., *Stern & Chambers 85* (A, MO, US).

40. *Hippomane*

Hippomane L., Sp. Pl. 1191. 1753. TYPE: *Hippomane mancinella* L.

41. *Hura*

Hura L., Sp. Pl. 1008. 1753. TYPE: *Hura crepitans* L.

42. *Euphorbia*

Euphorbia L., Sp. Pl. 450. 1753. LECTOTYPE: *Euphorbia antiquorum* L. (chosen by Millspaugh, Publ. Field Columbian Mus., Bot. Ser. 2: 306. 1909).

Poinsettia Graham, Edinburgh New Philos. J. 20: 412. 1836. *Euphorbia* sect. *Poinsettia* (Graham) Baillon, Etud. 284. 1858. *Euphorbia* subg. *Poinsettia* (Graham) House, New York State Mus. Bull. 254: 472. 1924. TYPE: *Poinsettia pulcherrima* (Willd. ex Klotzsch) Graham.

Four species new to Panama are reported here. In addition, the Panamanian endemic, *Euphorbia apocynoides*, which was merely mentioned in passing in the original treatment, is here treated in full. These changes make it necessary to provide a new key. Both of the present authors are agreed that *Poinsettia*, treated as a separate genus in the original treatment, is best regarded as a subgenus of *Euphorbia*; thus *Poinsettia* is suppressed in the generic key, and the two Panamanian species are included in the key to *Euphorbia*.

LITERATURE

DRESSLER, R. L. 1961. A synopsis of *Poinsettia* (Euphorbiaceae). Ann. Missouri Bot. Gard. 48: 329–341.

KEY TO THE SPECIES OF *EUPHORBIA* IN PANAMA

- 1a. Leaves more than 15 cm long, leathery; cyathia 4–6 mm long .... 3. *E. elata*
- 1b. Leaves less than 8 cm long, membranous; cyathia less than 3 mm long.
  - 2a. Gland of cyathium 1; floral bracts usually with pale or colored spots; seeds coarsely tuberculate.
    - 3a. Involucral gland cup-shaped; floral leaves green, white, or purple-spotted at base, never red; seeds angulate, coarsely tuberculate .... 1. *E. heterophylla*
    - 3b. Involucral gland bilabiate; floral leaves red, at least at base; seeds ovoid-cylindrical, finely and sharply tuberculate .... 2. *E. cyathophora*
  - 2b. Glands of cyathium 4 or 5 (rarely 2).
    - 4a. Leaves all whorled; stems articulate; trees or large shrubs.
      - 5a. Floral leaves white .... 4. *E. leucocephala*
      - 5b. Floral leaves green (unknown in *E. apocynoides*).
        - 6a. Leaf blades ovate, 3–5 cm broad; petioles 2–6 cm long .... 5. *E. cotinifolia*
        - 6b. Leaf blades oblong or narrowly obovate, 1.5–2 cm broad; petioles to 1 cm long .... 6. *E. apocynoides*
    - 4b. Leaves alternate; herbs.
      - 7a. Involucres and capsules pubescent.
        - 8a. Inflorescence glandular-pilose; leaf blades mostly 1 cm long or shorter .... 7. *E. ocymoidea*
        - 8b. Inflorescences nonglandular; leaf blades mostly longer than 2 cm.
          - 9a. Cyathial glands 4 or 5, plane .... 8. *E. xalapensis*
          - 9b. Cyathial glands 2, bilabiate .... 9. *E. oerstediana*
      - 7b. Involucres and capsules glabrous.
        - 10a. Cyathial appendages obsolete; glands with 2 conspicuous lateral horns .... 10. *E. peplus*
        - 10b. Cyathial appendages present; glands elliptic.
          - 11a. Seeds terete, the surface smooth; cyathia ca. 2 mm in diameter; glands 4, dark; appendages equaling glands, ciliate-pubescent above .... 11. *E. dwyeri*
          - 11b. Seeds strongly angled, the surface deeply punctate with pits in regular longitudinal rows; cyathia ca. 1 mm in diameter; glands 4 or 2, green; appendages obsolete (Panamanian specimens) to prominent and white, several times size of gland, glabrous .... 12. *E. graminea*

42.3. Euphorbia elata Brandegee, Univ. Calif. Publ. Bot. 6: 55. 1914. TYPE: Mexico. Chiapas: Finca Irlanda, *Purpus 7026* (holotype, UC; isotypes, A, BM, F, GH, MO, F neg. 62362, UC, US).

Euphorbia valerii Standley, J. Wash. Acad. Sci. 17: 11. 1927. TYPE: Costa Rica. Guanacaste: Los Ayotes, near Tilarán, 600–700 m, *Standley & Valerio 45338* (holotype, US; isotype, US).

Shrub or small tree to 3.5 m high, glabrous; branches few or none. *Leaves* alternate, clustered at apex of stem; petioles 2–4(–6) cm long, ca. 2 mm thick; stipules fleshy, light-colored, deltate to rounded, 3–4 mm long, 3–4 mm broad; blades coriaceous, glabrous, oblanceolate or narrowly elliptic, the apex rounded to bluntly short-acuminate at tip, acute to cuneate at base, 15–35 cm long, 4–10(–12) cm broad, 3–5(–7) times as long as broad; midrib prominent below, to 2 mm thick; lateral veins 17–30 pairs on a side, obscure, nearly at right angles to midrib; margin entire. *Inflorescences* single, terminal or rarely axillary, long-pedunculate, cymose; peduncle 10–30 cm long, glabrous, minutely brown-puberulent, or covered with a waxy brown reticulum; cyme up to 5 times divided, the cyathia ultimately in 2–4 compact groups; bracts opposite, scalelike, attached to the stem along a broad base, deltate, ca. 4 mm long, 2.5–3 mm broad; margin entire, sometimes ciliate, hyaline; apex blunt, somewhat cucullate. *Involucres* campanulate, glabrous, minutely brown-puberulent or covered with a waxy brown reticulum, green, drying to brown, 4–6 mm high, (3–)4–5.5 mm diam.; pedicels 1.5–3 mm long, 1–1.5 mm thick; lobes 5, 1.5–2 mm long, ca. 2 mm broad, erose to fimbriate, rarely entire, erect, concolorous or dark red; glands 5, round, 1.7–2 mm diam., placed vertically on rim of involucre, looking outwards, but positions of lobes making glands appear below rim; gland sometimes erect and thick-stalked so that surface is flat with respect to orifice, the margin then crisped; appendages none. *Capsules* exserted from the cyathium no more than 1 mm (the gynophore erect), green, glabrous, 8–9 mm high, 10–11 mm diam.; styles ca. 1.5 mm long, united at base for ca. ⅓ of their length, strongly recurved, bifurcate; seeds subglobose, truncate at apex, 4.7–5 mm diam., ca. 4.5 mm long, ecarunculate, dark brown, with lighter, low, broken, irregular longitudinal ridges.

Euphorbia elata, which occurs in moist evergreen forests of low to middle elevations, is definitely known to range from southern Veracruz, Mexico, to Colombia, and may occur as far south as Bolivia. It is the most widespread species of sect. *Adenorima* (Raf.) Webster, a group of several highly divergent species of trees and shrubs from the West Indies, western and southern Mexico, and the northern Andes. The species closest to *E. elata* are all highly restricted in range and are poorly understood. *Euphorbia sinclairiana* Benth. (in Seemann, Bot. Voy. Sulphur 163. 1844), known only from the island of Gorgona off the Pacific coast of Colombia, is characterized by a deeply bifurcate and much-branched inflorescence with conspicuous foliaceous bracts, but is otherwise similar to *E. elata*. The Peruvian *E. tessmannii* Mansf. (Ber. Deutsch Bot. Ges. 46: 674. 1929; Notizbl. Bot. Gart. Berlin-Dahlem 11: 137. 1931) is known only from the type collection, and no original material is definitely known to be extant. Until either new or original material is available, the status of that species cannot be determined. *Euphorbia capansa* Ducke (Arq. Inst. Pesq. Agron. 1: 21. 1938), described from western Amazonian Brazil, appears to be synonymous with *E. elata*. Another collection from Bolivia (*Bang 619*, MO, NY, US) was given an unpublished name but will probably also prove to be *E. elata*.

Specimens examined. PANAMA. BOCAS DEL TORO: road to Chiriquí Grande, 300 m, *McPherson 10085* (MO). COLÓN: trail from end of Santa Rita Ridge Rd. to Río Pedros, 600 m, *Antonio 3750* (F, MO); Distr. Portobelo, stream off N slope of Río Gatún, 2,200 ft., *Antonio 3804* (MO); Santa Rita, E of mountainous zone, *Correa & Dressler 973* (PMA); Santa Rita Ridge, E of Colón, *Dressler 3338* (PMA), *3348* (F, PMA); Santa Rita lumber road, ca. 15 km E of Colón, *Dressler & Lewis 3728* (MO, PMA); Santa Rita Ridge, 4 hour walk from end of road, *Hammel 6318* (MO); ca. 2–3 mi. up the Río Guanche, 10–20 m, *Kennedy & Foster 2170* (MO); Santa Rita Ridge Rd., ca. 6 km from Boyd-Roosevelt Hwy., *Mori & Kallunki 2151* (MO, NY); Santa Rita Ridge, on fork in road on main Santa Rita Ridge Road, *Mori & Kallunki 3053* (MO, NY). DARIÉN: Cerro Pirre, valley between Pirre and next most southerly peak, sloping hillside, *Folsom 4385* (MO). PANAMÁ: on road near slopes of Cerro Jefe, 2,400 ft., *Antonio et al. 3426* (F, MO); just before La Eneida along new trail beside Lopez House, *Correa & Dressler 724* (DUKE, 2 sheets), *Correa et al. 816* (MO); El Llano–Cartí road, 14–18 km from road to Chepo, 400 m, *Correa et al. 1867* (PMA); El Llano–Cartí road, 12 mi. above Pan-Am Hwy., *Liesner 1244* (MO); El Llano–Cartí road, 11 km from Pan-Am Hwy., *Mori & Kallunki 3057* (MO, NY). VERAGUAS: Escuela Agricultura, Alto Piedra near Santa Fe, 0.3 mi. beyond fork in road near school, toward Atlantic slope along trail to top of Cerro Tute, 3,400–3,800 ft., *Antonio 3498* (MO); 6.4 km outside of Santa Fe on road past agricultural school, toward the cordillera, *Folsom 2970* (F, MO).

42.4. Euphorbia leucocephala Lotsy, Bot. Gaz. (Crawfordsville) 20: 350, pl. 24. 1895. LECTOTYPE: Guatemala. Huehuetenango: Cuilco, Dec. 1891, *Shannon 305* (presumably US, not seen; chosen by Standley & Steyermark, Fieldiana, Bot. 24(6): 107. 1949).

Shrub to 3 m high; branches terete, glabrous, swollen at the nodes. *Leaves* verticillate; petioles (1–)2–6 cm long, slender, glabrous; stipules glanduliform, 0.3–0.5 mm long; blades glabrous, elliptic to linear-elliptic, mucronate and rounded or bluntly acute at tip, acute at base, (2–)3–7 cm long, (0.7–)1.5–2.7 cm broad, 2–3(–4) times as long as broad; margin entire. *Inflorescences* terminal, cymose; bracts white, narrowly spatulate; petioles 3–7 mm long, thinly pilose; blades 5–10 mm long, 1.2–2 mm broad; base narrowly acute; margin entire; apex rounded, mucronate. *Cyathia* on peduncles 1–2.5 mm long; involucre campanulate, 1–1.8 mm high, 1.1–1.7 mm diam., densely tomentose just below the glands, otherwise sparsely pilose; glands 5, green, 0.8–1 mm long parallel to the rim of the cyathium, 0.4–0.5 mm broad, the center of the inner margin strongly inflexed forming a deep convex trough; appendages white, linear-lanceolate, exceeding glands by 2–3(–3.5) mm, 0.5–1 mm broad, the apex narrowly rounded. Gynophore erect, exserted from cyathium 1–1.5 mm. *Capsules* glabrous, smooth, 5–6 mm high, 4.5–5.5 mm diam., shallowly 3-lobed, the cocci distinctly 3-angled; styles 0.6–0.7 mm long, united at base, deeply trifid, the style branches strongly recurved; seeds (immature) ca. 3.5 long, trigonous, ca. 1.8 mm wide, caruncuIate.

The reports of this species from central Panama represent a considerable range extension; the previously known range is from western and southern Mexico to Honduras. *Euphorbia leucocephala* is a commonly cultivated ornamental in Central America, and the Panamanian collections may be from cultivated trees, but the label data are not clear on this point.

Capsules are unknown in Panamanian collections and are scarce in the numerous collections from northern Central America. Our description of the capsules is taken from a specimen collected in Depto. Huehuetenango, Guatemala (*Molina 21389*, F).

Specimens examined. PANAMA. COCLÉ: El Valle de Antón, 1,000–2,000 ft., *Lewis et al. 2570* (MO); El Valle, *Ramos 19* (MO, PMA). PANAMÁ: Panama Viejo, *Girón 1* (MO); near Cerro Azul, *Cambra 49* (MO, PMA).

42.6. Euphorbia apocynoides Klotzsch in Seemann, Bot. Voy. Herald 99. 1853. TYPE: Panama. Darién: Punta Garachiné, *Seemann 1096* (holotype, BM; isotype, K; photo of isotype, K, MO).

Shrub to 2 m high; stems glabrous, terete, swollen at nodes; internodes 2–4 cm long. *Leaves* ternate; petioles slender, 7–10 mm long, very sparsely pilose; blades membranous or chartaceous, dark green above, lighter or even somewhat glaucous below, oblong to narrowly obovate, rounded at tip, acute at base, 4.5–6 cm long, 1.5–2 cm broad, 3–3.5 times as long as broad, glabrous or with very few hairs below; margin entire. *Inflorescences* unknown. *Cyathia* turbinate, ca. 2.5 mm high, ca. 2.5 mm diam. below the appendages, sparingly to evenly appressed-pubescent, the hairs short, straight, nonoverlapping; peduncles 3–4 mm long, subglabrous; appendages 5, narrowly flabellate, white, pubescent as the involucre below toward the base, ciliate on the margins near the juncture with the involucre, otherwise glabrous, entire in the lower half, deeply and coarsely crenellate along the distal margin. *Flowers* and *fruits* not seen.

This poorly known species is apparently endemic to Panama and is still known only from the fragmentary type collection and an equally fragmentary recent collection from the type locality. The type is sufficiently complete, however, to enable the species to be placed with reasonable certainty in section *Alectoroctonum* (Schldl.) Boissier, a group characterized by verticillate branching and swollen nodes, and to say that it is unlike any other species in the section. Contrary to the statement in the original treatment (Webster & Burch, 1968: 335), the cyathium is quite unlike that of sect. *Dichilium* Boissier, which is characterized by a reduced number (usually 2) of bilabiate glands and small, erect, or often obsolete, appendages. The species of sect. *Dichilium* are also characterized by alternate leaves and stems that are pinched just above the nodes.

A plant vegetatively very similar to *Euphorbia apocynoides*, collected near Puerto Colombia on the Caribbean coast of Colombia (*Elias 1197*, F), has been identified as *E. nudiflora* Jacq., a West Indian species. The cyathium, however, differs from that of *E. apocynoides* in that it is campanulate, the pubescence is crisped with overlapping hairs, and the appendages are completely glabrous, obovate, and with smaller and more numerous crenellations on the distal margin. In all of these characters it matches *E. nudiflora*, which differs vegetatively in its more highly branched habit and shorter, broader leaves. An elucidation of the relationship of the Colombian plant to the Panamanian one, and of both to *E. nudiflora*, must await fuller collections from Panama and Colombia.

We are indebted to Mr. A. Radcliffe-Smith of Kew for providing a description and a sketch of the cyathium from the isotype of *E. apocynoides* at K, from which our description has been taken.

Additional collection examined. PANAMA. DARIÉN: thorn forest near Punta Garachiné, *Duke 10485* (MO, 2 sheets).

42.7. Euphorbia ocymoidea L., Sp. Pl. 453. 1753. TYPE: Mexico. Campeche: *Houston s.n.* (BM, not seen).

E. astroites Fisch. & Mey., Index Sem. Hort. Petrop.

10: 44. 1845. TYPE: Mexico: Tampacoala, *Karwinsky* (LE, not seen).

A thorough examination of collections from throughout the range of this species (western Mexico to Panama) makes it clear that *Euphorbia astroites* cannot be separated from *E. ocymoidea.* The only consistent character separating the two is the glandular-pilose stems of the former, as opposed to the glabrous or short-pilose, eglandular stems of the latter. The two forms occupy roughly the same geographical range (the glandular form is not yet known from western Mexico, and the eglandular form has not been collected south of Nicaragua) and the same habitats, and they exhibit similar variation patterns, particularly in the shape of the leaves, which range from broadly ovate or deltate to somewhat reniform. As suggested by McVaugh (1961: 177), several names based on collections from western Mexico, particularly *E. subreniformis* S. Watson, undoubtedly belong here.

The only known Panamanian collections are glandular-pilose, a fact that was omitted from the original treatment, and thus would have been placed under *E. astroites.* The species has apparently not been collected in Panama since the appearance of the original treatment.

42.8. Euphorbia xalapensis Kunth, Nov. Gen. Sp. Pl. 2: 61. 1817. *Poinsettia xalapensis* (Kunth) Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 253. 1859. TYPE: Mexico. Veracruz: near Xalapa, *Humboldt & Bonpland s.n.* (P, not seen).

Euphorbia enalla Brandegee, Univ. Calif. Publ. Bot. 6: 54. 1914. TYPE: Mexico. Chiapas: Cerro del Boquerón, *Purpus 7035* (holotype, UC; isotypes, F, F neg. 60269, GH, MO, NY; distributed under an unpublished name).

Euphorbia amphimalaca Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 313. 1929. TYPE: Honduras. Comayagua: near Siguatepec, Feb. 1928, *Standley 56341* (holotype, F; isotypes, F, F neg. 60244, US).

Perennial rhizomatous *herb* to 50 cm high, the stems shaggy brown-pilose. *Leaves* opposite or verticillate above, alternate below; petioles 1.5–2.5 cm long, brown curly-pubescent; stipules glanduliform, brown or black, minute, 0.1–0.2 mm long; blades ovate, acute at tip, rounded to obtuse at base, dark green, 1.5–3.5 cm long, 1–2 cm broad, 1.5–1.8 times as long as broad, densely shaggy-pilose below, more sparsely so above, base rounded to obtuse; margins entire, ciliate, acute. *Inflorescences* terminal, cymose, often appearing one-sided by the abortion of one branch at a node, shaggy-pubescent; bracts similar to the leaves but greatly reduced, often aborting. *Cyathia* on pedicels 1–3 mm long; involucre campanulate, 0.7–1.3 mm high, 0.5–1.3 mm diam., crisp-pubescent; glands 5, green, elliptic to reniform; appendages whitish or greenish, broadly ovate, exceeding the gland by 1–2 mm, 1.5–2 mm broad, the margin entire or crenate; gynophore glabrous, erect or somewhat recurved, exserted from the cyathium 1.5–2 mm. *Capsules* sparsely to densely pilose, 1.5–1.9 mm high, 1–1.5 mm diam.; styles 0.7–0.8 mm long, free to the base, deeply bifid, thinly pilose; seeds ca. 1.5 mm long, 0.9–1 mm diam., ovoid, grayish, coarsely pitted, tuberculate, ecarunculate.

Euphorbia xalapensis is a common species of forest borders and thickets that ranges from western Mexico to Honduras, and thus the new reports cited here from Panama and Costa Rica represent a considerable range extension. This species was erroneously treated in the *Flora of Guatemala* (Fieldiana, Bot. 24(part 6): 108. 1949) as *E. oerstediana* (Klotzsch & Garcke) Boissier, a very different species that has mostly glabrous stems, articulated nodes, two cyathial glands that are more or less bilabiate and that have inconspicuous or obsolete appendages, and densely white-pubescent capsules. The latter species, which belongs to section *Dichilium* Boissier, is very rare in Central America and is somewhat better known from the West Indies and northern South America. It is still unknown from Guatemala, and nearly all of the putative collections from there are referable to *E. xalapensis.* It has not been re-collected in Panama since the collection cited in the original treatment.

Euphorbia xalapensis is also frequently confused with *E. graminea,* a highly variable and widespread species of the same section, *Cyttarospermum* Boissier, and the two are indeed very similar in aspect. *Euphorbia xalapensis,* however, can be distinguished by the distinctly perennial and often strongly rhizomatous habit; the shaggy brown pubescence of the stems, leaves, and inflorescence; the one-sided appearance of the inflorescence, which is due to the frequent abortion of one branch at a node; and the five glands that have ample, usually greenish appendages.

Additional specimens examined. COSTA RICA. SAN JOSÉ: along Quebrada Tablazo and on forested slope above creek, NE part of Altos Tablazo, 9°50′N, 84°03′W, 1,700–1,800 m, *Grayum & Schatz 5157* (MO). PANAMA. CHIRIQUÍ: Volcán Chiriquí above Boquete, roadside, *D'Arcy 9805* (DAV, MO), distributed as "*Euphorbia graminea* Jacq. (s. lat.)."

42.10. Euphorbia peplus L., Sp. Pl. 456. 1753. TYPE: Europe (presumably in Hortus

Cliffortianus Herbarium, BM, not seen; 630.24 in LINN).

Annual glabrous *herb* 18–35 cm high. *Leaves* alternate below, opposite or ternate above, sessile or short-petiolate, numerous, early deciduous below; stipules obsolete; blades bright green, membranous, spatulate, rounded at tip, acute or cuneate at base, 10–14 mm long, 8–12 mm broad; margins entire; floral leaves slightly smaller, somewhat reflexed, congested. *Cyathia* solitary in forks of upper branches, on peduncles 0.6–1 mm long; involucre campanulate, light green, ca. 1 mm high, 0.5–0.7 mm diam.; glands 4, green, crescent-shaped, exappendiculate, ca. 0.5 mm long parallel to the rim of the involucre, with prolonged narrow horns 0.5–0.7 mm long; gynophore exserted, ca. 1.3 mm long, recurved. *Capsules* green, 1.8–2 mm high, 2–2.2 mm diam., broadest below the middle, shallowly 3-lobed, the cocci each with 2 narrow longitudinal ridges; styles ca. 0.1 mm long, bifurcate, the style branches bifurcate; seeds ovoid-oblong, weakly 6-angled, gray, ca. 1.5 mm long, ca. 0.8 mm diam., caruunculate, deeply pitted, minutely white-tuberculate.

This is apparently the first report from southern Central America of this cosmopolitan weed of temperate Eurasian origin.

Specimens examined. PANAMA. CHIRIQUÍ: trail from Paso Respingo to Bajo, Chorro Cerro Punta to Boquete, along stream near Guadalupe, *Hammel et al. 7077* (MO); forest remnant beside Las Cumbres, 1 mi. from road near Cerro Punta dairy, 8,000 ft., *D'Arcy et al. 13193* (F, MO); Cerro Punta, *Tyson 7058* (MO, PMA).

42.11. Euphorbia dwyeri Burch, Ann. Missouri Bot. Gard. 54: 182. 1967. TYPE: Panama. Chiriquí: Cerro Horqueta, NW of Boquete, *Dwyer et al. 434* (holotype, MO; isotypes, GH, K, US).

A second collection of this species has been found, misidentified as *E. caracasana* Boissier.

Additional specimen examined. PANAMA. CHIRIQUÍ: humid forest of Cuesta de Las Palmas, southern slope of Cerro de la Horqueta, 1,700–2,100 m, *Pittier 3216* (US).

43. *Chamaesyce*

Chamaesyce Gray, Nat. Arr. Brit. Pl. 2: 260. 1821. TYPE: *Chamaesyce maritima* Gray = *C. peplis* (L.) Prokh. (*Euphorbia peplis* L.) (See Wheeler, 1943: 461, for a discussion of the type.)

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Index to Latin Names

Numbers in boldface type refer to descriptions or principal entries; numbers with ! refer to illustrations; names in boldface type refer to new taxa or combinations; names in italic refer to synonyms.

NOTES

A NEW SPECIES OF *HYMENOLOBIUM* (LEGUMINOSAE—PAPILIONOIDEAE) FROM CENTRAL AMERICA

Among the numerous trees of the Amazonian Hylea, the genus *Hymenolobium* is considered to be one of the main suppliers of excellent timber. It is closely related to the genus *Andira* (tribe Dalbergieae) but is distinguished by having a flat, reticulately veined fruit with one or two prominent submarginal nerves. Although delimitation of the species still presents various difficulties due to insufficient collections in herbaria, the 15–17 taxa previously recognized (Mattos, 1979; Lima, 1982) are restricted to South America from Venezuela and Surinam to southeastern Brazil.

During examination of material in the herbarium of the Missouri Botanical Garden (MO), some new collections from Central America were encountered. These represent a new species:

Hymenolobium mesoamericanum Lima, sp. nov. TYPE: Costa Rica. Heredia: alt. 220 m, Río Tirimbina, Istarú Farm, Tiribina, Sarapaquí, 16 July 1971 (fl), *Roy W. Lent 2003* (holotype, MO; isotypes, NY, US). Figure 1.

A omnibus specibus fructibus alatis adhuc cognitis floribus majoribus (18–20 mm) et calycibus tenue-coriaceis pubescentis differt.

Large tree to 40 m, dbh to 90 cm. Trunk with smooth, grayish bark; wood yellow. Terminal branches grayish, with numerous scars of caducous leaves, pubescent on the newest growth. Stipules caducous, ovate-lanceolate, 1–1.4 × 0.5–0.9 cm, stipels filiform, 0.1–0.2 cm long. Leaves imparipinnate, aggregated at the branch apices, 8–17-jugate (up to 25-jugate on regrowth branches or young plants); petiole pubescent, 2.5–4 cm long (to 6 cm long on regrowth branches or young plants); rachis pubescent, 12–28 cm long (to 56 cm long on regrowth branches or young plants); leaflets oblong, oblong-elliptic or ovate-oblong, the terminal one elliptic, 2.5–7 × 1.5–3 cm, the base rounded, subcordate or obtuse, the apex retuse or obtuse, mucronate, the lower face pubescent, the upper face sparsely pubescent to subglabrous; petiolules 1.5–2.5 mm long. Panicles 10–15 × 15–22 cm, the branches pubescent; bracts and bracteoles caducous, the bracteoles ovate-lanceolate, pubescent, 1–1.5 × 0.5–0.7 mm. Flowers 18–20 mm long; pedicels 5–8 mm long; calyx campanulate, slightly coriaceous, pubescent, 5-toothed, 8–10 mm long; corolla rose, the petals papery; vexillum 16–18 × 14–15 mm, wings 15–17 × 5–6 mm; keel 14–16 × 5–6 mm; stamens 10, monadelphous, 15–16 mm long; anthers 0.8–1 × 0.3–0.4 mm; ovary long-stipitate, pilose along the margins; ovules 2–3; style sparsely pilose, the stigma punctiform. Immature fruit flat, with wide lateral wings.

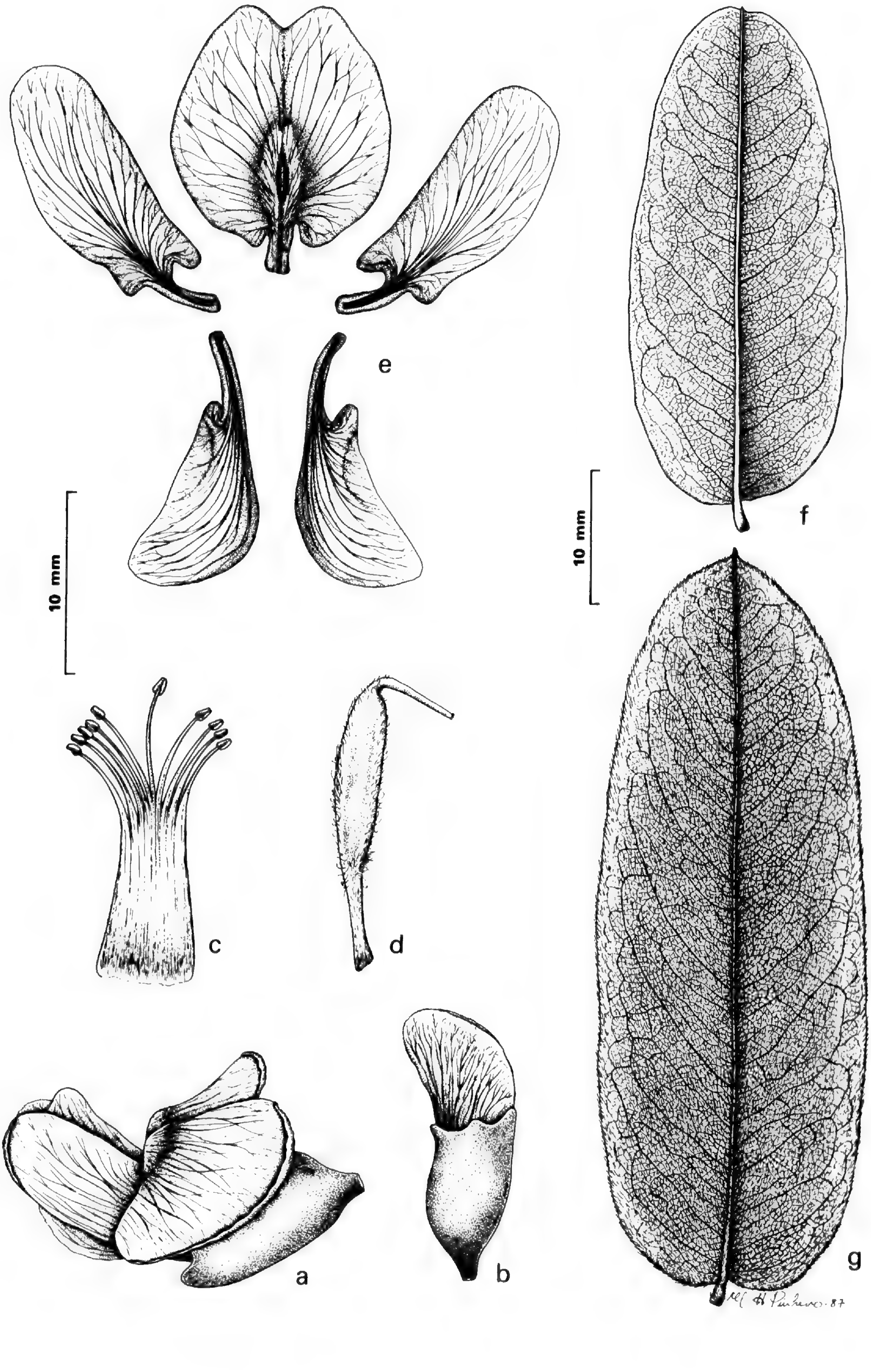
Habitat and distribution. Emergent tree of gallery forests of low altitude (50–300 m), or left uncut in pasture land, in Costa Rica, Nicaragua, and Panama.

Additional material examined. COSTA RICA. HEREDIA: along Río Frio Road, after entrance to Starke's hacienda, 25 Apr. 1976 (fl, lvs), *G. S. Hartshorn 1843* (MO, NY). NICARAGUA. ZELAYA: Kurinwacito, 18–22 Mar. 1984 (lvs), *P. P. Moreno 23688* (MO, RB); 23 Mar. 1984 (lvs), *P. P. Moreno 23862* (MO, RB); ca. 1.5 km W of Cara de Mono, 6 June 1980 (lvs), *W. D. Stevens 17500* (MO); Awas Tingni, 40 km S de Waspán, 20 Mar. 1971 (lvs), *E. L. Little, Jr. 25272* (MO, US). PANAMA. CANAL ZONE: hills north of Frijoles, 19 Dec. 1923 (lvs), *P. C. Standley 27584* (US).

Hymenolobium mesoamericanum is distinguished from other species in the genus principally by its large flowers (18–20 mm) with slightly coriaceous, pubescent calyces. It shows affinities with *H. heterocarpum*, which possesses slightly larger flowers (22–23 mm) with coriaceous, tomentose calyces and suborbicular to oblong-reniform fruits with rudimentary lateral wings. The young fruit of *H. mesoamericanum* is provided with wide lateral wings, which suggest a samaroid fruit type as found in the majority of the species in the genus. However, collections of completely mature fruit are necessary to confirm this character.

Size and consistency of leaflets frequently vary in species of *Hymenolobium* (Lima, 1982). The

ANN. MISSOURI BOT. GARD. 75: 1145–1147. 1988.


e
10 mm
f
10 mm
c
d
g
a
b
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variation is related to leaf fall and/or to environmental factors, mainly intensity of solar radiation. The latter element determines the development of smaller, more rigid leaflets on the upper branches of the crown of adult individuals than on lower (regrowth) branches or on young individuals (Fig. 1f, g).

The wood of this species supplies planks for construction and is commonly called "colepáo" (Costa Rica, Prov. Heredia) and "carolillo" or "nogal" (Nicaragua, Dept. Zelaya).

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—*Haroldo C. de Lima, Jardim Botânico do Rio de Janeiro, Rua Pacheco Leao 915, CEP 22460, Rio de Janeiro, Brazil.*

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FIGURE 1. Hymenolobium mesoamericanum.—*a. Flower.*—*b. Bud.*—*c. Androecium.*—*d. Pistil.*—*e. Corolla* (Lent 2003).—*f. Leaflet from the upper branches of adult individual* (Moreno 23688).—*g. Leaflet from young individual* (Standley 27584).

A NEW SPECIES OF *VANTANEA* (HUMIRIACEAE) FROM PANAMA

Recently collected flowering material of the central Panamanian species of *Vantanea* hitherto considered conspecific with the Colombian *V. occidentalis* Cuatr. (Gentry, 1975; Croat, 1978) has forced a reconsideration of the taxonomic status of the Panamanian entity. It is here recognized as a new species, *V. depleta*, differing most importantly in stamen number and ovary pubescence from *V. occidentalis*, which it otherwise strongly resembles.

Of significance to the current generic concept of *Vantanea* is the low number of stamens diagnostic of the new species. Cuatrecasas, in his revision of the family (1961), characterized *Vantanea* (sole member of the Vantaneoideae) as having 50–180 stamens, among other attributes, but *V. depleta* rejoices in no more than 15–18. Nevertheless, since the new species has the bilocular anther thecae, biovulate ovary locules, and the drupe morphology typical of the genus, there can be little doubt that it is correctly placed in *Vantanea*.

Vantanea depleta McPherson, sp. nov. TYPE: Panama. Panamá: Cerro Jefe, 650 m, 2 May 1987, *McPherson & Stockwell 10892* (holotype, PMA; isotypes, F, MO). Figure 1.

Species floribus parvis (6 mm longis), petalis glabris, staminibus paucis (15–18), et ovario puberulo dignoscenda.

Tree 9–40 m; twigs often strongly angled, glabrous, marked by elongate lenticels. Leaf blades elliptic or elliptic-ovate, (5.5–)8.5–16 cm long, (3–)4–8 cm wide, entire, coriaceous; base acute, often somewhat reflexed abaxially, extending down the petiole as a pair of tapering wings; apex obtuse, not or only obscurely acuminate; midrib prominent on upper surface, somewhat raised on the lower surface; secondary veins (6–)7–9(–11), only slightly raised; both surfaces dull, glabrous, 1 or 2 small sunken laminar glands in most cases associated with each of the secondaries. Petiole somewhat poorly delimited from blade, 3–9 mm long, swollen at the base, glabrous. Inflorescences terminal as well as sometimes also from the uppermost axils, broadly paniculate, the branches puberulent. Pedicels 1.5–3 mm, less puberulent than the rachises. Sepals semicircular, 1 mm long, 1.5–2 mm wide, obtuse, puberulent, mostly bearing one centrally placed raised crateriform gland. Petals narrowly triangular-ovate, slightly imbricate in bud, 5 mm long, 2 mm wide, glabrous on both surfaces, white. Stamens 15–18, the filaments 3–5 mm long, fused basally for ca. 1 mm, glabrous, white; anthers ca. 0.7 mm long, the thecae bilocular, about as long as the distal prolongation of the connective. Disk ca. 1 mm high, sharply dentate, glabrous. Ovary 2 mm long, densely puberulent, the hairs much shorter than the width of a filament; style 3 mm long, geniculate. Fruit 2.5–3.5 cm long, 1.5–1.7 cm diam., puberulent, rounded basally, acute distally; endocarp smooth, with 5 broad ribs alternating with 5 oblong valves, 2.4–3.3 cm long, 1.5–1.8 cm in diam.

Additional specimens examined. PANAMA. VERAGUAS: Cerro Tute, 1,200 m, *Lao & Gentry 530* (MO). CANAL AREA: Barro Colorado Island, *Garwood 440* (MO); Pipeline Road, *Gentry 1931*, *7406* (MO). PANAMÁ: Cerro Jefe, 650 m, *McPherson 11008* (MO), *11296* (MO, PMA). SAN BLAS: between Río Irgandí and Río Cartí Senni, *de Nevers & Herrera 6597* (MO).

Vantanea depleta is known from central Panamanian forests from near sea level to 1,200 m.

I thank John K. Myers for the illustration.

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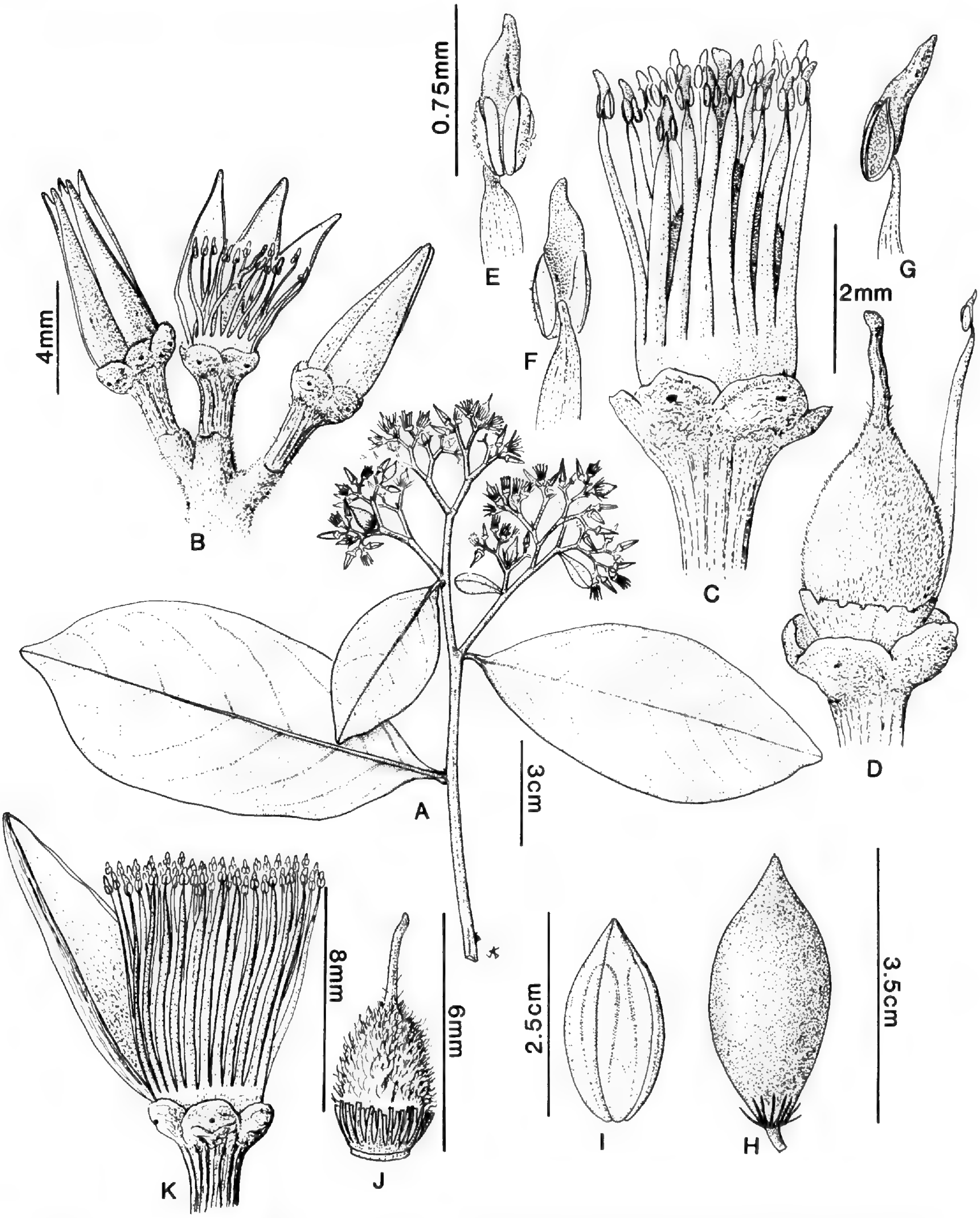

FIGURE 1. *A–I.* Vantanea depleta *McPherson (A–G drawn from the type,* McPherson & Stockwell 10892; *H, I from* McPherson 11296).—*A. Twig.—B. Buds and opened flower.—C. Flower with corolla removed.—D. Gynoecium.—E–G. Stamens.—H. Drupe.—I. Endocarp. J, K.* V. occidentalis *Cuatracasas (drawn from* Gentry 24054*).—J. Gynoecium.—K. Flower with four petals removed.*

NOMENCLATURAL CHANGES IN THE GENUS *FUCHSIA* (ONAGRACEAE)

In Berry (1982), ten new species of *Fuchsia* were described. A typographical error was made in one of these descriptions (the first "i" was omitted) and is corrected as follows:

Fuchsia coriacifolia P. Berry, Ann. Missouri Bot. Gard. 69: 150. 1982.

Examination of specimens from Cambridge University revealed that the type of *F. parviflora* Lindley, treated by Breedlove (1969) as a species of the Mexican and Central American sect. *Encliandra*, does not belong to that group. Instead, it belongs to the monotypic sect. *Kierschlegeria* and is conspecific with the earlier described *F. lycioides*. As a result, the following nomenclatural changes are needed:

Fuchsia lycioides Andrews, Bot. Rep. 2: pl. 120. 1800. TYPE: plate 120 of the Botanists Repository, vol. 2 (lectotype, here designated).

Fuchsia parviflora Lindley, Bot. Reg. 13: 1048. 1827. TYPE: cultivated in the Chiswick Garden, England, from seed presented to the Horticultural Society by George Canning in 1824, *without collector*, July 1826 (holotype, CGE).

The type of *F. parviflora* has alternate leaves and both series of stamens erect, clearly excluding it from sect. *Encliandra*, in which all members have opposite leaves and the antipetalous stamens reflexed back into the floral tube (Breedlove, 1969). Lindley, in fact, noted the close similarity of *F. parviflora* to *F. lycioides*, distinguishing his species mainly by the smaller flower size and the longer petioles. *Fuchsia lycioides* is subdioecious, however, with the pistillate flowers nearly half the size of the hermaphrodite ones (Atsatt & Rundel, 1982). Lindley's type was from a pistillate individual, whereas Andrews's type of *F. lycioides* was from a hermaphrodite plant with larger flowers. Leaf size in *F. lycioides*, on the other hand, is too variable to distinguish it from *F. parviflora*. Quite likely Lindley's report of *F. parviflora* as a native of Mexico was in error, since *F. lycioides* is restricted to a narrow coastal area of central Chile, and his type was from a specimen cultivated in England.

Fuchsia cylindracea Lindley, Bot. Reg. 24: 66. 1838. TYPE: cultivated at the Horticultural Society, London, England, raised from Mexican seeds presented by George Barker, *without collector* (lectotype, CGE).

Fuchsia parviflora Lindley, sensu Breedlove, Univ. Calif. Publ. Bot. 53: 56. 1969.

The type sheet of *F. cylindracea* has two separate branches, one male and the other female. The male portion is here designated as the lectotype, since the species is dioecious (Breedlove, 1969), and an illustration of a male branch accompanies the type description.

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BACTRIS DIVISICUPULA AND *BACTRIS FUSCOSPINA* REEXAMINED

Work on a forthcoming paper on the palms of western San Blas, Panama required the determination of similar-looking specimens labeled *Bactris divisicupula* Bailey (Palmae, Cocoeae) or *B. fuscospina* Bailey. Bailey (1943a) described both species, from one specimen each, from semi-isolated peaks in west-central Panama. The type collections actually intergrade, and collections since then also bridge the distinctions, indicating that the two taxa are synonymous.

Bailey (1943b) used the following couplet to distinguish the types of *B. divisicupula* (*Allen 1817*) and *B. fuscospina* (*Allen 2086*):

e.	Pinnae short-caudate or only acuminate, marked on upper surface with cross-lines between the nerves: cupule of an outer series (calyx) of 3 deep lobes and an inner series (corolla) with nearly entire margin and setose	*B. fuscospina*
ee.	Pinnae long-caudate and [with] no elevated cross-lines: cupule divided into deep lobes in both series	*B. divisicupula*

Collections amassed since 1943 demonstrate that leaf shape and venation in this species are variable and do not provide consistent separation. *Allen 2086* bears an inflorescence just past flowering, while *Allen 1817* has mature fruits. The difference in developmental stages may have been a reason Bailey described two species. He stated (1943a: 230) that the setae of the calyx of *B. fuscospina* (from the less-developed material of *Allen 2086*) are "likely to perish with handling," which does occur, thus rendering the vestiture indistinguishable from that of the more-developed *B. divisicupula*. *Allen 1817* actually retains some setae on the calyx, identical to those of *Allen 2086*. The lobing of the "cupule" (corolla) is also an artifact of development, the corolla being parted into lobes by the expanding fruit.

I here include *B. fuscospina* in synonymy with *B. divisicupula*.

Bactris divisicupula Bailey, Gent. Herb. 6: 230. 1943. TYPE: Panama. Cocle: Él Valle de Antón, 21 May 1939, *Allen 1817* (hololectotype, MO; isolectotypes, BH, GH, here designated).

B. fuscospina Bailey, Gent. Herb. 6: 228. 1943. TYPE: Panama. Panamá: Cerro Campana, 31 Dec. 1939, *Allen 2086* (hololectotype, MO; isolectotype, BH, here designated).

Bailey did not designate a holotype. The BH and GH specimens are fragments. The description appears to be based on the MO sheet, which is the only one containing the information included in the description. For these reasons the MO duplicate is here chosen as lectotype.

When Bailey described the two palms, the flowers were unknown. The collections *de Nevers 6127*, *Moore 6531*, and *Johnston 1552* allow the following description:

Flowers crowded on the rachillae; pistillate flowers in triads with 2 staminate flowers; the triads mixed with numerous solitary staminate flowers in proximal third of rachillae; distal ⅔ of rachillae with exclusively staminate flowers; staminate sepals 3, unequal, linear, connate at base, 1 mm long; staminate petals connate in lower third, free and valvate above, 5 mm long, thick, apically acute, inequilateral; stamens 6, the filaments adnate to the petals basally, free distally, twice folded or bent, ca. 2 mm long; anthers ovate, dorsifixed just below the middle, dehiscing longitudinally; pistillode minute; pistillate sepals connate into a vertically striate tube 3–4 mm long, minutely 3-lobed at apex; pistillate petals connate into a tube 2 mm long, truncate to obscurely 3-lobed apically, minutely spinescent without, striate within; staminodes absent; stigma sessile, truncate, 0.5 mm long; ovary oblong. Ovule basal.

Bailey (1943a) described the rachillae of the two species as "pubescent" (*B. divisicupula*) and "indifferently pubescent" (*B. fuscospina*). The pubescence is strongly eroded in the material he saw: the indument of the rachillae is a dense mat of multicellular hairs, each reminiscent of a string of beads. *Moore 6531* has these hairs well developed and is unique among the flowering specimens seen in having the spinescent indument of the corolla tube continue onto the rim of the tube as a fringe.

Bactris divisicupula ranges from the provinces of Limón and Puntarenas in Costa Rica to the Department of Valle in Colombia. It inhabits tropical moist forest, tropical wet forest, premontane wet forest, and premontane rain forest (sensu Holdridge et al., 1971) between sea level and 1,000 meters. The Colombian material has larger fruits than the Panamanian material and may tie *B. divisicupula* to additional specimens at MO from Amazonian Peru and Venezuela. Comparison with the Amazonian material is deferred to a later date pending collections from Amazonian Colombia and Ecuador.

Additional specimens examined. COSTA RICA. LIMÓN: woodlands S of La Lola on the railroad, 120 m, 15 Apr. 1953, *Moore 6711* (BH). PUNTARENAS: Palmar, 6 Mar. 1956, *Schubert 1184* (A). PANAMA. CANAL AREA: Skunk Hollow, Caribbean side, 22 Oct. 1965, *Blum 1496* (MO); Pavón Road W of Gatún Locks, 4 Aug. 1955, *Johnston 1538* (BH); near Marú Towers W of Gatún Locks, *Johnston 1552* (BH); Pipeline road near Gamboa, 50 m, 7 Nov. 1973, *Nee 7846* (MO, NY); Frijoles, 20 Aug. 1923, *Stevens 1185* (US); Agua Salúd, 13 July 1923, *Cook & Martin 63* (US); Barro Colorado Island, 6 July 1931, *Bailey 505* (BH). COLÓN: Santa Rita Ridge, 8 Apr. 1971, *Croat 14182* (MO). DARIÉN: Urutí River, *Duke & Bristan 220* (MO, US). PANAMÁ: Cerro Campana, 31 Mar. 1969, *Dwyer, Croat & Castillón 4859* (BH, MO); Cerro Azúl, 26 July 1970, *Croat 11551* (MO); 3 mi. NE of Alto Pacora, 500–800 m, 10 Mar. 1973, *Croat 22767* (MO); Cerro Jefe, 23 Apr. 1946, *Allen 3440* (BH, MO); El Llano–Cartí road km 8, 5 Mar. 1974, *Nee & Warmbrodt 10400* (MO). COMARCA DE SAN BLAS: El Llano–Cartí road km 19, 350 m, 9'19"N, 78'55"W, 2 Nov. 1985, *de Nevers, Herrera & Charnley 6127* (MO); Cangandi, 30 m, 9'24"N, 79'24"W, 10 Feb. 1986, *de Nevers & Herrera 7121* (MO); Cangandi, swampy flats, 10 m, 5 Apr. 1986, *de Nevers, Herrera & Charnley 7697* (MO); Aila Tiwar (Río Acla), 25–100 m, 8'48"N, 77'40"W, 12 Feb. 1979, *Sugden 430* (MO). COLOMBIA. CHOCÓ: La Mojarra, near Istmina, up Río San Juan, 30–90 m, 5'12"N, 76'37"W, 6 Nov. 1983, *Juncosa 1319* (MO); Hoya del Río San Juan, Quebrada La Sierpe, 5 m, 4'10"N, 77'10"W, 25 Mar. 1979, *Forero et al. 3966* (MO). VALLE: Río Naya upriver from Puerto Merizalde, 10 m, 3'15"N, 77'25"W, 23 Feb. 1983, *Gentry & Juncosa 40679 (MO)*.

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CHROMOSOMAL OBSERVATIONS ON *FUCHSIA* SPECIES AND ARTIFICIAL HYBRIDS

The two largest sections of *Fuchsia*, sects. *Fuchsia* and *Hemsleyella*, are concentrated in the tropical Andes and together comprise 75 of the nearly 105 species of the genus. Both sections have been recently revised by Berry (1982, 1985), who reported chromosome numbers for 52 species. Species from both sections are primarily diploid ($n = 11$; 43 species), but seven are tetraploid ($n = 22$), and one species has both diploid and tetraploid populations. In an effort to obtain counts for the remaining species and for interesting new collections or interspecific hybrids in these sections, we examined eight specimens cultivated by members of the Dutch Circle of Fuchsia Friends in 1986. Young floral buds were fixed in Carnoy's solution and stained in 1% aceto-orcein, as described in Berry (1982). Photomicrographs were taken with a Nikon Biophoto camera using Kodak Technical Pan film.

Results of the chromosomal observations are presented in Table 1 and Figure 1. The diploid counts for *F. decussata*, *F. furfuracea*, *F. scabriuscula*, and *F. simplicicaulis* are the first reports of chromosome numbers for these species, all belonging to sect. *Fuchsia*. They lend further support to Berry's (1982) finding of predominant diploidy in that section. The collection of *F. cinerea* studied, however, proved to be tetrapoloid, unlike an earlier diploid count for another population of this species (Berry, 1982). *Fuchsia cinerea* occurs in the same high-elevation areas of northern Ecuador as *F. corollata* and *F. vulcanica*, two members of the *F. petiolaris* species group that also have tetraploid populations, as well as problematical species limits. A more extensive cytological sampling of the *Fuchsia* populations in this area would be helpful in resolving the complex variation patterns observed in this group and to determine if tetraploidy has arisen repeatedly in these taxa.

Fuchsia magdalenae (sect. *Fuchsia*) was introduced into cultivation just over ten years ago

TABLE 1. *Additional chromosome counts in* Fuchsia.[1]

Taxon	Meiotic Chromosome Number	Collection Data[2]
F. cinerea P. Berry	$n = 22$	*Berry 004-86*, from seed of *Koenen 153-06-81*, Prov. Carchi, Ecuador, 6 km NE of El Angel
F. decussata R. & P.	$n = 11$	*Berry 014-86*, from seed of *Berry 3049*, Dept. Ayacucho, Peru
F. furfuracea Johnst.	$n = 11$	*Berry 010-86*, from seed of *Solomon 12573*, Dept. La Paz, Bolivia
F. scabriuscula Benth.	$n = 11$	*Berry 012-86*, from seed of *Berry 3574*, Prov. Pichincha, Ecuador
F. simplicicaulis R. & P.	$n = 11$	*Berry 016-86*, from plants long established in cultivation in Europe, originally from Peru
F. magdalenae Munz	$n = 22$	*Berry 017-86*, from progeny of the type collection of *F. lampadaria* J. O. Wright, originally from Santa Marta, Colombia
F. magdalenae × *F. denticulata*	$2n = 33$[3]	*Berry 009-86*, artificial cross made by D. Reiman
F. magdalenae × *F. pilaloensis*	$2n = 33$[3]	*Berry 018-86*, artificial cross made by D. Reiman

[1] All species belong to sect. *Fuchsia* except for *F. pilaloensis*, from sect. *Hemsleyella*.

[2] All collections from plants cultivated by Mrs. Drude Reiman-Dietiker in Hollandsche Rading, the Netherlands, with vouchers at MO.

[3] Many laggard and bridge chromosomes at Anaphase I.

FIGURE 1. *Photomicrographs of meiotic metaphase (A, B), anaphase (C), and telophase (D) chromosomes of* Fuchsia.—*A.* F. magdalenae *(2n = 22II)*.—*B–D.* F. magdalenae × F. denticulata *(2n = 33); note the numerous laggard and bridge chromosomes in C and D. Scale = 10 µm.*

(Wright, 1978) and has since been used to produce a novel series of attractive interspecific crosses in England and the Netherlands. The original, parental stock of *F. magdalenae* was cytologically reexamined, showing it to be tetraploid with normal bivalent formation (Fig. 1A). This agrees with previous counts by Wright (1978) and Berry (1982).

The first *F. magdalenae* hybrid, with the diploid *F. denticulata* (Berry, 1982), yielded triploid progeny with meiotic irregularities such as bridges and laggard chromosomes (Fig. 1B–D). The second *F. magdalenae* hybrid was with *F. pilaloensis*, a member of the apetalous sect. *Hemsleyella*. The chromosome number of this species was not reported in Berry's (1985) revision of the section, but the triploid chromosome number of the F_1 hybrid with *F. magdalenae* indicates that it must be diploid. Unless spontaneous or induced chromosome doubling occurs in the F_1 of these triploids, they are likely to prove infertile and will need to be propagated vegetatively.

We wish to thank Mrs. Drude Reiman-Dietiker for providing buds from her extensive collection of living *Fuchsia* species and hybrids, and Lois Brako for assistance in collecting the bud material.

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UNA NUEVA COMBINACION EN *BAUHINIA* (FABACEAE—CAESALPINIOIDEAE)

La especie *Amaria sessilifolia* fue descrita por De Candolle (1825) con base en material coleccionado por Mutis (*Mutis 2724*) en Colombia. Wunderlin (1976, 1983) sugirió que esta especie debería ser considerada como sinónimo de *Bauhinia petiolata* (Mutis ex DC.) Triana ex Hook. f. Sin embargo, el examen de las iconografías de la Real Expedición Botánica del Nuevo Reino de

FIGURA 1. *Fotografía de* Bauhinia sessilifolia *(*Mutis 2397, *MA)*.

ANN. MISSOURI BOT. GARD. 75: 1155–1156. 1988.

Granada lo mismo que del material tipo y otros ejemplares de las dos especies en cuestión en el Real Jardín Botánico de Madrid me ha convencido de que existen características vegetativas y florales que permiten mantenerlas como entidades taxonómicas independientes en el género *Bauhinia*. Por lo tanto, la siguiente nueva combinación se hace necesaria:

Bauhinia sessilifolia (Mutis ex DC.) L. M. Quiñones, comb. nov. *Amaria sessilifolia* Mutis ex DC., Prodr. 2: 519. 1825. TIPO: Colombia: *Mutis 2724* (holotipo, MA).

Bauhinia sessilifolia se caracteriza por presentar hojas sésiles, de base profundamente cordada; inflorescencias axilares, umbeliformes; pétalos emarginados; estambres insertos, 5 mayores que los otros 5; y fruto más ancho (2 cm de ancho). *Bauhinia petiolata* tiene peciolos 0.5–3 cm de longitud; base truncada o redonda; inflorescencias terminales o axilares en racimos cortos; pétalos agudos; estambres exertos, todos de igual longitud; y fruto delgado 1.5 cm de ancho.

Distribución. Se conoce solamente de Colombia.

Ejemplares adicionales estudiados. COLOMBIA. Sin localidad precisa: *Mutis 2397* est. (MA), *4203 fr* (MA).

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UNA NUEVA ESPECIE DE *GUETTARDA* L. (RUBIACEAE, GUETTARDEAE) PARA COSTA RICA

English Summary

A new species of the genus Guettarda *(*G. turrialbana *Zamora & Poveda) is named and described from Costa Rica. Its distribution, habitat, and affinities are discussed.*

La presente especie se enmarca dentro de la tribu Guettardeae por poseer un ovario con dos o varios lóculos, cada uno con un óvulo anátropo; los estambres insertos en la boca del tubo de la corola; y una inflorescencia por lo general cimosa (Standley, 1934).

En base a la revisión bibliográfica hemos encontrado que las características de diagnóstico entre el género *Guettarda* y *Antirhea* no son convincentes para separar ambos géneros, ya que el traslape de caracteres es muy amplio (ver Cuadro 1), por lo tanto consideramos que la especie aquí tratada corresponde al género *Guettarda.* Esta es una especie muy particular debido a que los frutos son lisos, glabros y sus lóculos estan distribuídos al azar.

Guettarda turrialbana Zamora & Poveda, sp. nov. TIPO: Costa Rica. Cartago: Turrialba, CATIE, Bosque los Espaveles, 625 m, 26 June 1986 (fl, fr), *N. Zamora V., M. M. Chavarría y H. Gómez 1263* (holotipo, CR; isotipos, F, K, MO, NY). Figura 1.

Arbor 30 metralis. Folia petiolata; laminis oblongo-ellipticis, supra glabris, subtus glabris vel minute sericeis, 8–24 cm longis 3–12 cm latis. Inflorescentiae axillares oppositae, cymis dicotomis, pedunculo 3.5–7 cm longo. Flores sessiles, extus glabratis intus pubescentibus; calyce cupuliformi, truncato, 1.5–4 mm longo 2–3 mm lato; corolla alba, tubo 5.2–6.5 cm longo, 5 lobis 5–6 mm longis 3–4 mm latis; staminibus coralinis, antheris 5, 3.5–4 mm longis 0.5 mm latis. Fructus drupaceus glabratus laevis ovoideo-ellipsoideus 3.3–3.8 cm longus 1.4–1.6 cm latus; semine 8–9 cylindrico 1.5–1.8 cm longo 2 mm lato.

Arbol de 30 m de altura y 80 cm DAP, fuste derecho, cilíndrico, pardo-claro o pardo-grisáceo; corteza exfoliándose en pequeñas plaquitas escamosas, dejando a veces cicatrices crateriformes, corteza interna rosado-rojiza, gruesa hasta de 2.5 cm de espesor, muy suave; ramitas glabras, pardo-claras, cilíndricas; entrenudos muy juntos, 3–15 mm de largo; estípulas triangulares, ápice acumi-

CUADRO 1. *Algunas características morfológicas de diagnóstico entre* Guettarda *y* Antirhea.

Característica	*Guettarda*	*Antirhea*
Cáliz	truncado o dentado persistente o decíduo	truncado o dentado persistente o decíduo
Corola	hipocrateriforme o tubular serícea lóbulos 4–9, imbricados, 2 de ellos exteriores	hipocrateriforme glabra o serícea lóbulos 4–5, imbricados, 2 de ellos exteriores
Estambres	4–9, insertos filamento corto o ausente	4–5, insertos o subexsertos filamento corto o raramente elongado
Ovario	lóculos 2–9 estigma capitado, subcapitado o con 2 o 3 lóbulos óvulos solitarios, cilíndricos y péndulos	lóculos 2–10 o más estigma capitado o con 2 o 3 lóbulos óvulos solitarios, cilíndricos y péndulos
Fruto	drupa usualmente velutina, a menudo angulada	drupa usualmente glabra, algunas veces angulada

ANN. MISSOURI BOT. GARD. 75: 1157–1159. 1988.

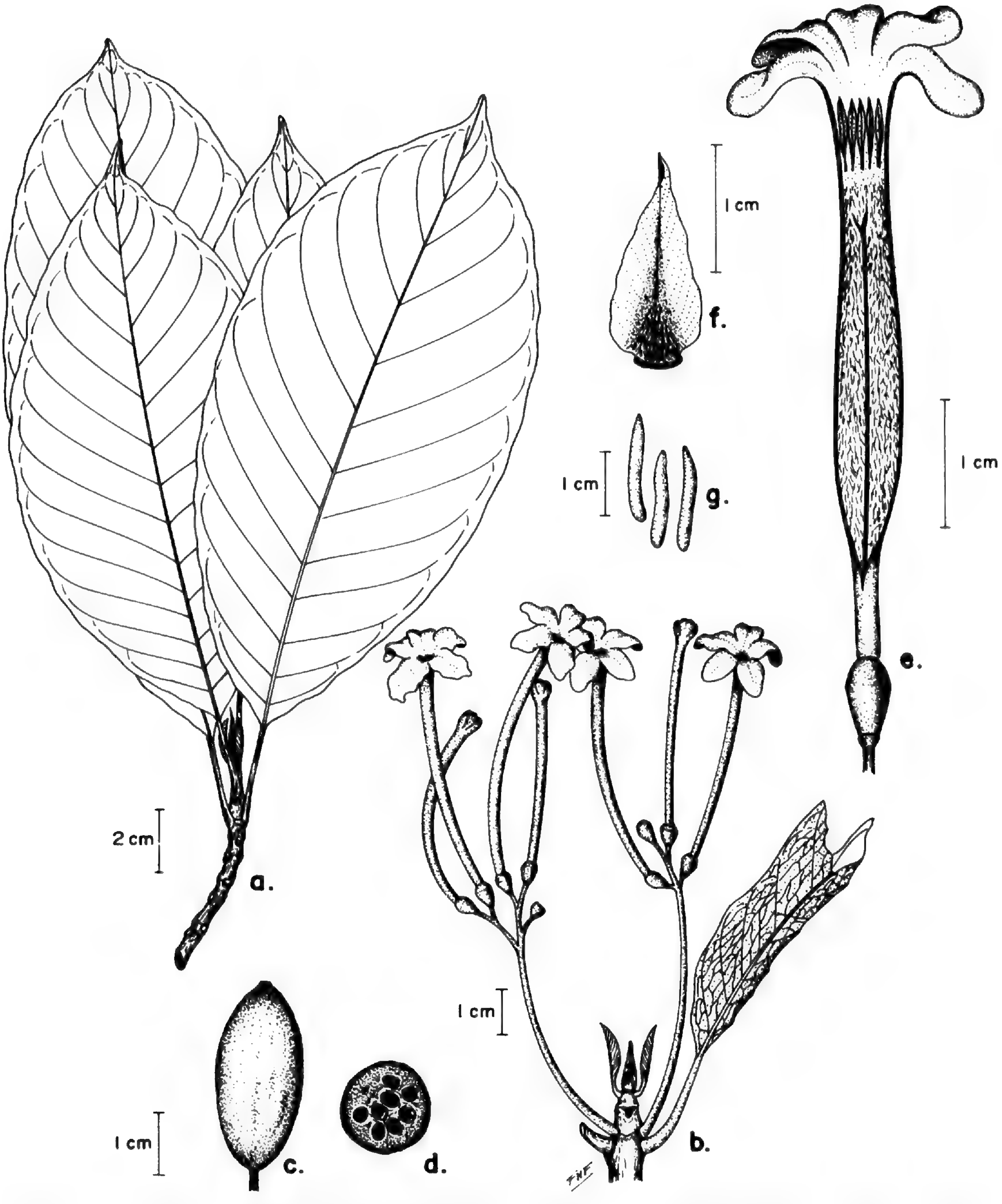

FIGURA 1. Guettarda turrialbana *Zamora & Poveda.—a. Rama.—b. Inflorescencias.—c. Fruto.—d. Corte transversal del fruto.—e. Flor con corte longitudinal de la corola.—f. Superficie interna de la estípula.—g. Semillas.*

nado, 1.2–3.3 cm de largo y hasta 7 mm de ancho en su parte media, glabras en la superficie externa, con un grupo de pelos gruesos en la base de la superficie interna, persistentes sólo en el ápice de las ramitas. Hojas decusadas; pecíolo 1.8–3.8 cm de largo, acanalado adaxialmente; lámina oblongo-elíptica, 8–24 cm de largo y 3–12 cm de ancho, ápice apiculado o corto-acuminado, base cuneada, glabra en la haz y con escasos pelos principalmente en la axila de los nervios o diminutamente seríceo-pubescente por el envés, cartáceo-membranácea, nervaduras secundarias broquidódromas, prominentes en el envés. Inflorescencia una cima dicótoma, axilar y opuesta, con 3–5 flores en cada ramificación, pedúnculo 3.5–7 cm de largo; flores sésiles, sostenidas por una bracteola glabra, cupuliforme, 0.5–0.9 mm de largo, caediza; cáliz truncado, cupuliforme, 1.5–4 mm de largo y 2–3 mm de ancho, glabro en ambas superficies; corola blanca, hipocrateriforme; tubo cilíndrico, 5.2–6.5 cm de largo y hasta 3 mm de diám. en su parte media, glabro en el exterior y con densa pubescencia argenteo-seríceo-reflexa en el interior debajo de los estambres, hasta 7 mm arriba de la base; lóbulos 5, imbricados en los botones, de ovados a elíptocos, hasta de 6 mm de largo 3–4 mm de ancho, reflexos, ápice redondeado u obtuso, algunos planos y otros cocleados en el ápice; estambres 5, coralinos, insertos, interlobulares, sésiles, 7–12 mm abajo de la boca; anteras con dos tecas, lineares, subuladas, 3.5–4 mm de largo y hasta 0.5 mm de ancho en su parte media, ápice agudo por sobresalir el conectivo, base estrechamente sagitada; estilo glabro, 1.6–2.3 cm de largo, estigma bífido, a veces una de las ramas levemente bifurcada, las dos ramificaciones principales con el ápice curvado o algo circinado; ovario glabro, obovoide, ápice truncado, 2 mm de largo, 2.6 mm de ancho, con 8–9 lóculos, óvulos solitarios y péndulos, disco glabro, 1.9 mm de largo y 2.5 mm de diám. Fruto drupáceo, ovoide elípsoide, 3.3–3.8 cm de largo, 1.4–1.6 cm de diám. en su parte media, verde claro, glabro, liso, pericarpo delgado y carnoso; cáliz caduco; semillas 8–9, en cavidades de paredes leñosas, prácticamente cilíndricas, elongadas, 1.5–1.8 cm de largo y 2 mm de diám., péndulas, finamente esponjas, presentando en su base restos del funículo, éstos cilíndricos y cóncavos en los extremos, 5 mm de largo, 3 mm de diám. y de consistencia también finamente esponjosa.

Ejemplares examinados adicionales. COSTA RICA. CARTAGO: Turrialba (IICA), *J. León 2858* (CR); Bajo del Chino (CATIE), *R. Morales y L. J. Poveda s.n.* (CR); Cajón (CATIE), *L. J. Poveda y J. A. Sáenz s.n.* (CR). PUNTARENAS: Bahía de Rincón de Osa, *S. Salas 5718* (CR); Parque Nacional Corcovado cerca de Playa Llorona, *L. J. Poveda et al. s.n.* (CR).

Distribución y habitat. La nueva especie hasta el momento parece endémica para Costa Rica, conocida de Turrialba (Prov. Cartago), y de Península de Osa (Prov. Puntarenas), además de Fila de Cal entre San Vito de Java y Ciudad Neily (Prov. Puntarenas) y de Florencia de San Carlos (Prov. Alajuela) (B. Hammel, com. pers., 1987). Se distribuye principalmente desde el nivel del mar hasta los 625 m, creciendo en Bosque muy Húmedo Premontano y Bosque muy Húmendo Tropical (Tosi, 1969). En Turrialba, se ha observado asociada con *Anacardium excelsum, Oreamunnea pterocarpa, Sideroxylon contrerasii, Spondias radlkoferi, Guarea pterorhachis, Lafoensia punicifolia,* y otras. Se encuentra en lugares planos, de buen drenaje, y en laderas con pendientes medias. Se han observado flores de junio a agosto y frutos de agosto a octubre.

Nuestro sincero agradecimiento a Julian A. Steyermark, David H. Lorence, y J. D. Dwyer por la revisión del manuscrito y sus valiosas sugerencias al mismo, y a Francisco Hodgson F. por la ilustración.

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UNA NUEVA ESPECIE DE *CARYODAPHNOPSIS* AIRY SHAW (LAURACEAE) PARA LA REGION NEOTROPICAL

ENGLISH SUMMARY

Caryodaphnopsis *was previously known only from Yunnan to Indochina, with the exception of* C. tonkinensis, *which extends as far as the Philippines and Borneo (Kostermans, 1974). Recently, van der Werff & Richter (1985) transferred two species of* Persea *from South America (*P. theobromifolia *Gentry and* P. inaequalis *A. C. Smith) to* Caryodaphnopsis. *Dr. R. Foster collected some specimens of this genus in the Parque Nacional Manú, Perú, that turned out to be a new species (*C. fosteri *van der Werff, 1986). We describe in this paper a new species of* Caryodaphnopsis *from Costa Rica. Its distribution, habitat, affinities, specimens studied, and wood anatomy are discussed.*

Caryodaphnopsis Burgeri Zamora & Poveda, sp. nov. TIPO: Costa Rica. Puntarenas: Península de Osa, Estación Biológica Marenco, 50 m, *N. Zamora V., F. Almeda & B. Anderson 1208* (holotipo, CR; isotipos, F, K, MO, NY). Figura 1.

Arbor 30 m alta, 80 cm diam., trunco cylindrico, corona ovata-rotundata, ramulis tetrangulatis vel subteretis, pilis brevibus sericeis vel glabratis. Folia opposita mediocri breviter petiolata, chartacea vel tenue chartacea, trinervata; petiolis 0.5–1.4 cm longis, supra canaliculatis, sparse minute sericeis vel glabratis; lamina oblongo-elliptica, 5–16.3 cm longa, 1.9–7.3 cm lata, apice acuta, acuminata vel cuspidata, basi cuneata, supra glabra, lucida, nervis impressis, subtus glaucae, sparse minute sericeis, nervis elevatis. Inflorescentia paniculata, pedunculis brevibus vel sessilibus, axillaribus, ramis decussatis, sparse minute sericeis, ramis floribusque bracteis minutis, caducis, acutis, minute sericeis; pedicellis ad 2.5–9 mm longis, minute sericeis, gracilibus; tepalis 6, 3 externis ovato-deltoideis, minute puberulis sericeis utrimque, 1.9 mm longis, 0.9 mm latis; 3 internis subulatis, minute sericeis extrinsecus, dense argenteo-sericeis intrinsecus, 7–10 mm longis, 2–2.2 mm latis; staminibus 9, libris, 5 mm longis, dense pilosis, staminum interiorum filamentis 2 glandulis basibus sessilibis conspicuis munitis; antheris rectangularibus vel oblongis, 4-loculatis; staminoidiis 3, sagittatis, 2–2.8 mm longis, filamentis brevibus dense pilosis; ovario obovoido, 1.9 mm longo, 1.5 mm lato, fere glabro; stilo fere 3 mm longo, basi sparse minute sericeo. Fructus globosus, glaber, 18–20 mm longus, usque 17 mm latus, lucidus, viridi-pallidus, sparse rubro-maculatus in siccitate; seminibus sphaericis, 12 mm longis, usque 12 mm latis.

Arbol de 30 m de altura, 80 cm DAP, con pequeñas gambas; tronco cilíndrico, gris-oscuro, exfoliándo en plaquitas, finamente fisurado, corteza muy gruesa, internamente blanquecina, sin olor característico; follaje verde claro, las hojas jóvenes de un tono verde pálido; ramitas tetrangulares, glabras o diminuto y esparcidamente seríceas. Hojas opuestas; pecíolo 0.5–1.4 cm de largo, acanalado adaxialmente, glabro o con diminutos y esparcidos pelos seríceos; lámina oblongo-elíptica, 5–16.3 cm de largo, 1.9–7.3 cm de ancho, ápice agudo, acuminado o cuspidado, base cuneada, brillante, lisa y glabra en la haz, glauca, con diminutos y muy esparcidos pelos seríceos en el envés, trinervada, los nervios principales impresos en la haz y prominentes en el envés, proyectándose hasta el ápice, los terciarios marginales arqueados y los terciarios centrales onduladamente perpendiculares al nervio central, cartáceas a delgadamente cartáceas. Inflorescencia panícula corimbiforme, axilar, decusada, flores terminales en grupos de 3 o más, pedúnculo ausente o hasta 1 mm de largo, ejes de la panícula 8–15 mm de ancho, 10–30 mm de largo o altura y diminutamente seríceos; ramificaciones y flores sostenidas por bracteolas muy pequeñas, agudas, seríceo-pubescentes y caducas en la madurez; algunas veces aparecen de 1–3 flores en la base de la panícula; pedicelos 2.5–9 mm de largo, delgados, diminuto-seríceo-pubescentes; tépalos 6, fuertemente desiguales, los 3 externos 1.9 mm de largo, 0.9 mm de ancho, ovado-deltoides, diminuto-seríceo-pubescentes en ambas superficies, los 3 internos 7–10 mm de largo, 2–2.2 mm de ancho, subulados, externamente diminuto seríceos e internamente con densa pubescencia, de pelos más largos, argenteo-seríceos. Estambres 9, libres, 5 mm de largo, aplanados y densamente pilosas; 3 de los internos con 2

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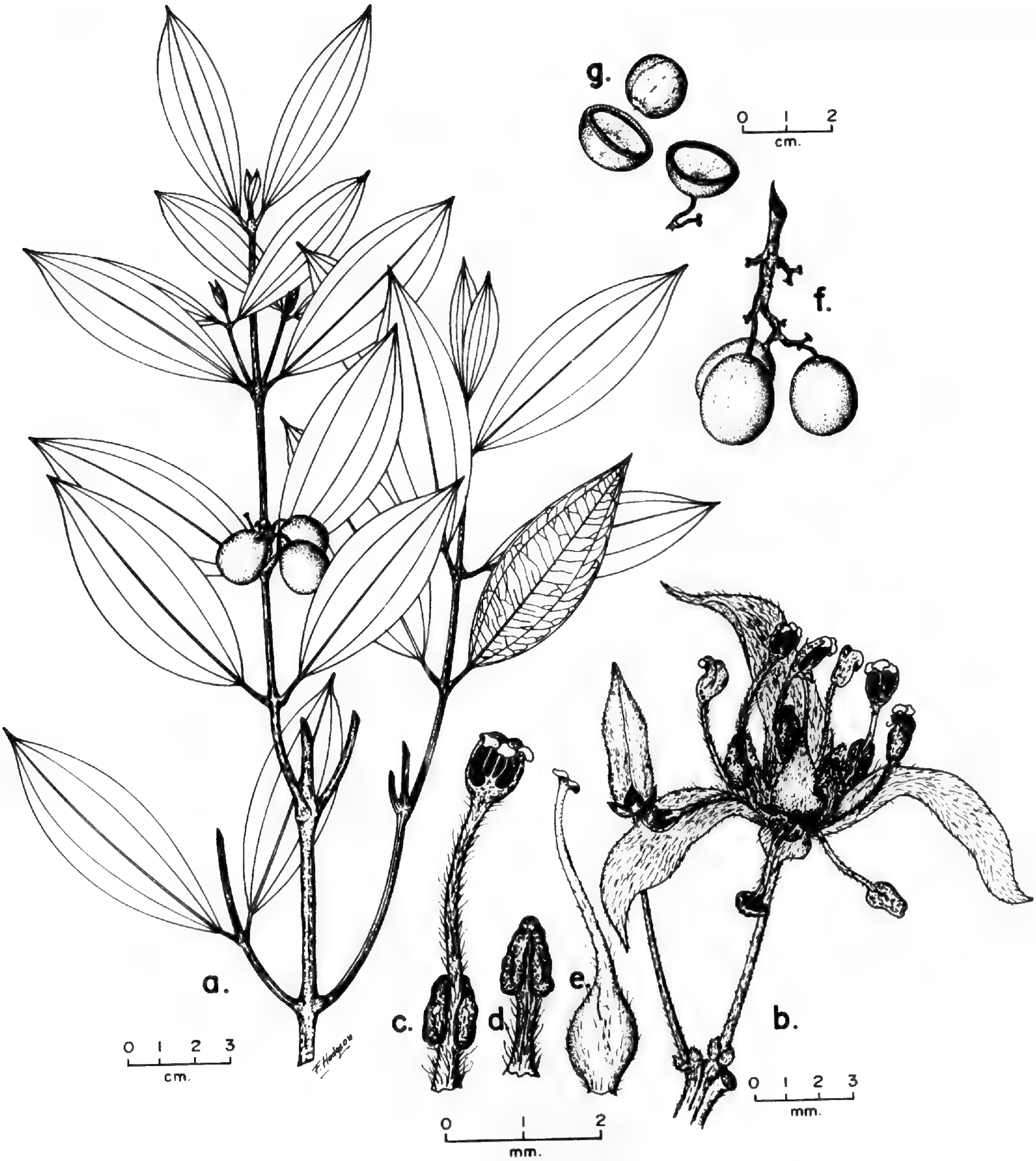

FIGURA 1. Caryodaphnopsis Burgeri.—*a. Rama.—b. Flor y butón.—c. Estambre con glándula.—d. Estaminodio.—e. Pistilo.—f. Frutos.—g. Corte transversal del fruto mostrando la semilla.*

glándulas bien desarrolladas y sésiles a ambos lados cerca de la base del filamento; anteras con 4 cavidadees; estambres arreglados en 4 verticilos, los 2 verticilos externos con anteras introrsas, rectangulares, con las celdas en 2 planos, las bases de las 2 celdas superiores lateralmente tangenciales a los ápices de las 2 celdas inferiores; las anteras en el 3 verticilo interno oblongas y extorsas; el 4 verticilo formado por 3 estaminodios relativamente grandes (2–2.8 mm de largo), sagitados y con corto filamento, densamente pilosos. Ovario 1.9 mm de largo, 1.5 mm de ancho, obovoido, con escasos pelos seríceos; estilo aprox. 3 mm de largo, con pelos seríceos esparcidos en la base. Frutos globosos, 18–20 mm de largo, hasta 17 mm de ancho, glabros, brillantes, verde amarillentos y algo moteado rojizos al madurar; pedicelo 8 mm de largo; mesocarpo delgado y suave; endocarpo delgado y dura. Semilla 1, esférica 12 mm de largo, hasta 12 mm de ancho, cubierto por una delgada testa

CUADRO 1. *Algunas características morfológicas de diagnóstico entre* Caryodaphnopsis Burgeri *y* C. fosteri *de Perú.*

Característica	*C. Burgeri*	*C. fosteri*
Pubescencia del envés de la hojas	diminuta y esparcidamente seríceas	densamente pilosas
Apice de las hojas	agudo, acuminado, o cuspidado	agudo a redondeado
Tamaño de la panícula	1–3 cm	3–6 cm
Pubescencia de la panícula	diminuta y esparcidamente serícea	densamente pilosa
Longitud y pubescencia de los pedicelos	2.5–9 mm, diminuto seríceos	5 mm, pilosos
Longitud de los tépalos externos	1.9 mm	1 mm
Longitud y pubescencia de los tépalos internos	7–10 mm, diminuto-seríceos externamente, con dense pubescencia, de pelos más largos, argenteo-seríceos internamente	5–6 mm, ferrugíneo-pilosos en ambas superficies
Longitud y pubescencia del ovario	1.9 mm, con escasos pelos seríceos	1 mm, glabro
Tamaño del fruto	1.7 cm diám.	± 1 cm diám.

que al madurar queda adherida al endocarpo, quedando un espacio aéreo entre estos y la semilla.

Ejemplares examinados adicionales. COSTA RICA. SAN JOSÉ: Mastatal de Puriscal, 400 m, *L. J. Poveda A., N. Zamora V., P. Sánchez V. y otros 3908* (CR). PUNTARENAS: Refugio de Fauna Silvestre Golfito, Golfito, 150–200 m, *N. Zamora V. 1070* (CR).

Dedicamos esta especie en honor al Dr. William C. Burger, editor de *Flora Costaricensis*, por su gran aporte en las investigaciones botánicas de nuestro país. El actualmente está elaborando la monografía de la familia Lauraceae de Costa Rica.

La identificación a nivel genérico fue posible gracias al análisis anatómico de maderas y hojas realizado por el Dr. Henk van der Werff en 1984.

El descubrimiento de esta nueva especie es de mucha importancia pues amplia la distribución conocida del género en América (ver van der Werff & Richter, 1985; van der Werff, 1986), y abre nuevas posibilidades para entender la distribución geográfica de las especies de esta familia.

Distribución y habitat. Hasta el momento la especie es endémica para Costa Rica, conocido en Santa Rosa y Mastatal de Puriscal (Prov. San José) y la Península de Osa (Prov. Puntarenas), de 50 a 400 m de elevación, ocupando la Zona de Vida Bosque Muy Húmedo Tropical (Tosi, 1969). Se

CUADRO 2. *Algunas características anatómicas comparativas entre* Caryodaphnopsis inaequalis, C. theobromifolia *y* C. Burgeri.

Características del xilema	*C. inaequalis* *C. theobromifolia*	*C. Burgeri*
Vasos		
Frecuencia	9–12 (nr./mm^2)	6–7 (nr./mm^2)
Diámetro tangencial de vasos más grandes	200–250 μm	200–300 μm
Perforaciones	exclusivamente simples	exclusivamente simples
Fibras septadas	septos frecuentes	septos frecuentes
Aliniamiento (sección transversal)	irregular (sección transversal de las fibras poligonal)	radial a irregular (sección transversal de las fibras poligonal)
Distribución de parenquima	paratraqueal escaso	paratraqueal escaso
Radios		
Altura de los más largos	2–3 mm	2–3 mm
Ancho de los radios grandes	5–6(8) células	3–6 células
Punteado radio vascular	grandes y redondeados	grandes y redondeados a ovalados
Contenido inorgánicos	ausentes	ausentes

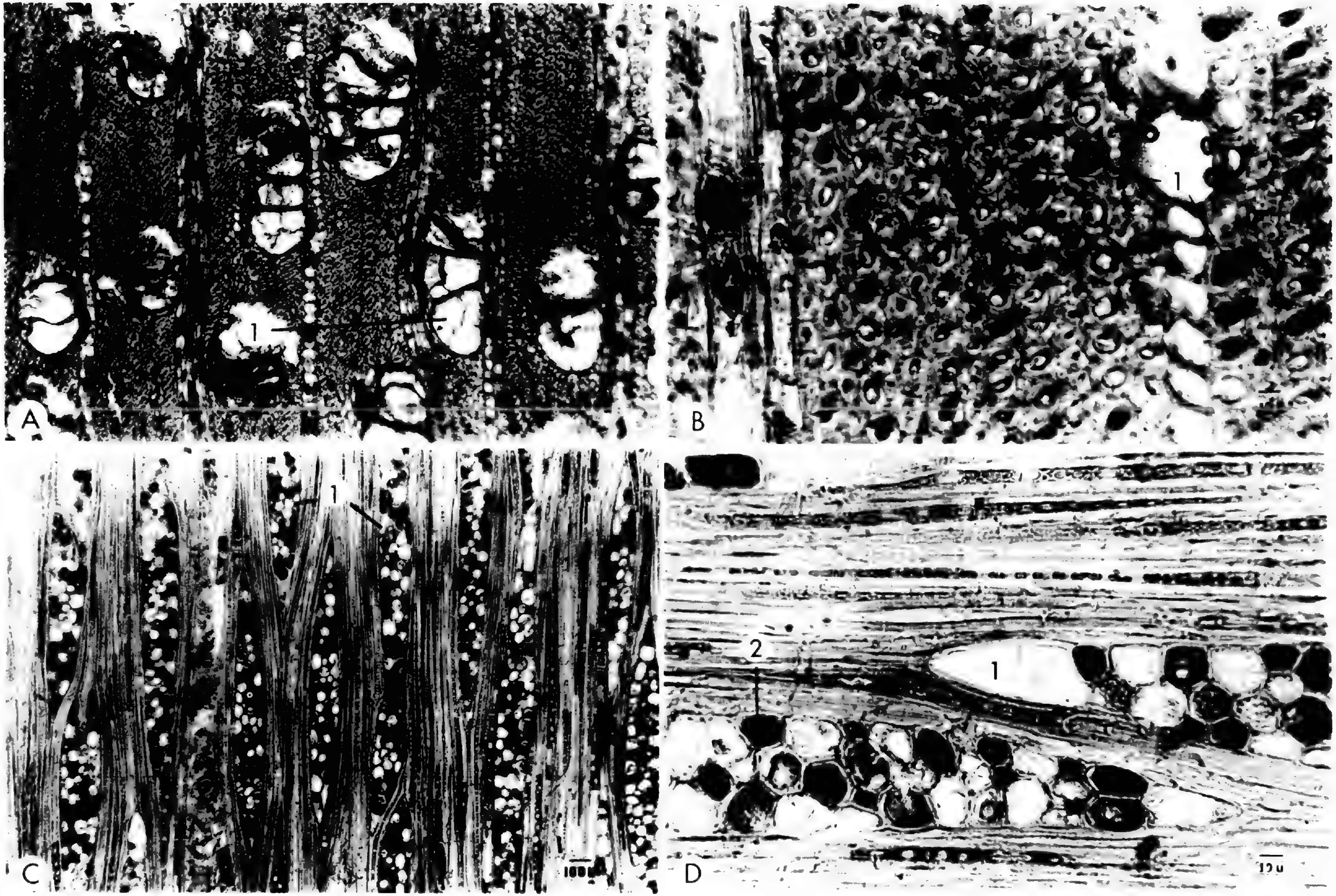

FIGURA 2. *Madera de* Caryodaphnopsis Burgeri, *secciones transversal y tangencial.—A. Sección transversal mostrando poros multiples con tilides (1).—B. Sección transversal en la que se puede ver la gruesa pared de las fibras y las gomas (1) dentro de algunas de ellas.—C. Sección tangencial mostrando radios multiseriados (1).—D. Células oleíferas (1) y gomas (2) en los radios.*

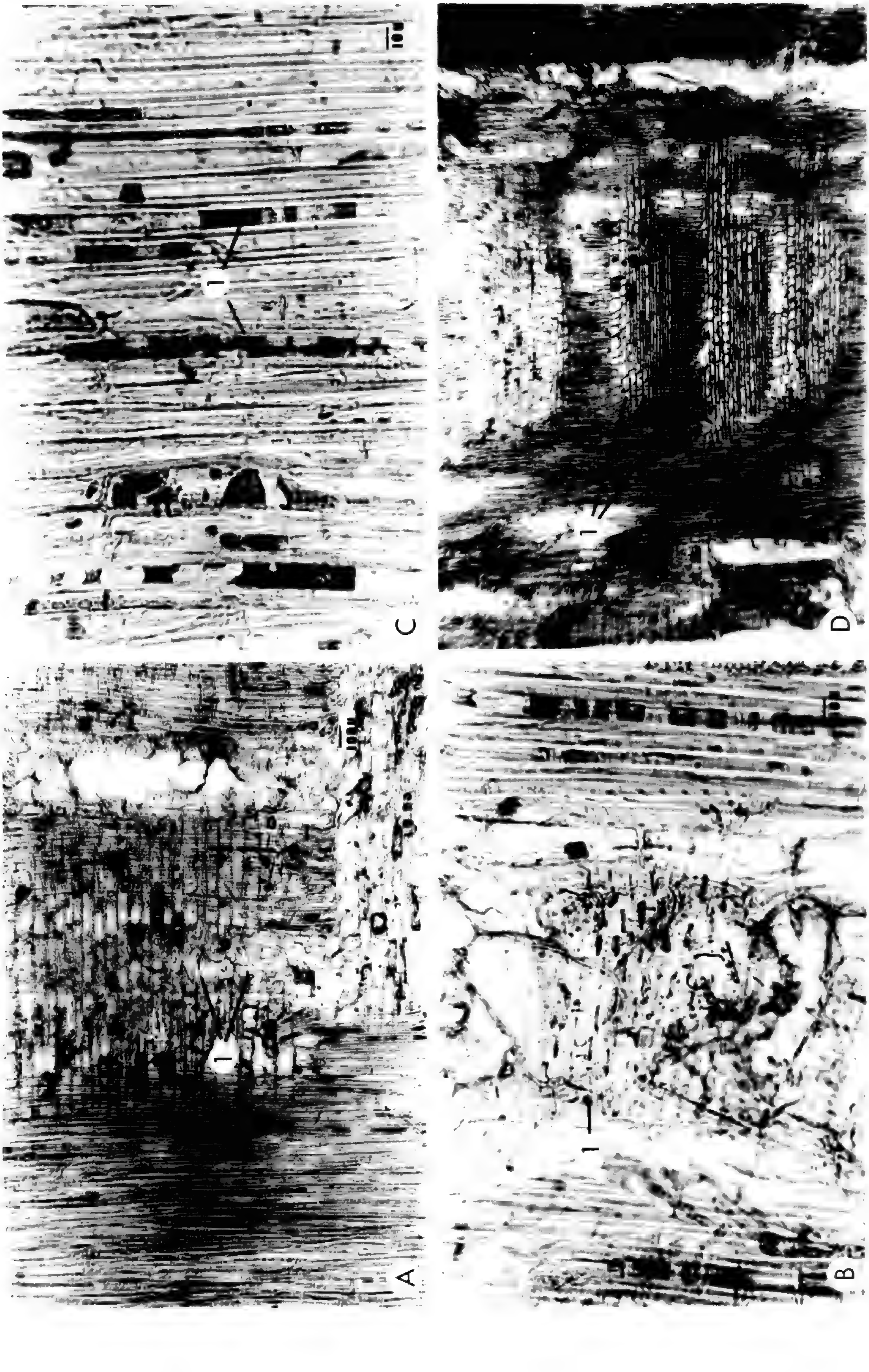

FIGURA 3. *Madera de* Caryodaphnopsis Burgeri, *sección radial.—A. Punteado radio-vascular (1).—B. Punteado intervascular alterno (1).—C. Gomas (1) en las cavidades de las fibras.—D. Radios heterogeneos (1).*

FIGURA 4. *Madera de* Caryodaphnopsis Burgeri, *platinas de perforasion simple (1) y punteaduras del segmento vascular (2).*

encuentra en laderas de pendientes medias y sitios planos. Se ha observado buena regeneracíon natural, principalmente en claros de luz. Produce flores desde finales de enero hasta principios de febrero, y hemos encontrado frutos maduros a mediados de mayo.

En las localidades de Santa Rosa y Mastatal de Puriscal, se le conoce el nombre de "carne" o "cocobola" los habitantes mencionan que la madera tienen excelentes propiedades para la construcción de viviendas.

Se compara *C. Burgeri* con *C. fosteri* en Cuadro 1.

DESCRIPCIÓN ANATÓMICA DE LA MADERA DE *CARYODAPHNOPSIS BURGERI*

Propiedades generales

Madera dura y pesada. Duramen color pardo-claro a pardo-rojizo, con vetas longitudinales oscuras, casi negras. Presenta olor característico, pero ningun sabor en especial; textura media y lustre de mediano a elevado.

Descripción macro- y microscópica

Presenta anillos de crecimiento visibles debido a bandas (zonas) tangenciales oscuras, de espesor irregular con poca concentración de poros.

Poros pequeños, visibles a simple vista, con diámetro tangencial promedio de 225 μm, abundantes (60 o más por 5 mm^2), distribuídos en una porosidad difusa con ligera tendencia a formar hileras oblicuas con respecto a los radios de más de 4 poros (rango de 3 a 7). En su mayoría son solitarios, algunos múltiples radiales de 2 a 4, y ocasionalmente racemiformes. Hay abundancia de tilides.

En las caras longitudinales, los vasos a simple vista como estrias claras sobre un fondo ligeramente más oscuro. Segmentos vasculares cortos con platinas de perforación simples, éstas de poco a medianamente inclinadas. Su punteado intervascular alterno, con punteaduras aeroladas de tamaño mediano (10 μm) y de aperturas angostas.

El parenquima axial invisible a simple vista o con lupa. Paratraqueal muy escaso, con algunas pocas células alrededor de los poros. El parenquima radial (radios), apareciendo a simple vista en sección transversal como líneas finas de color claro sobre un fondo más oscuro, hasta 1 mm de altura. Los radios multiseriados en su mayoría, de 3 a 6 células de ancho. Los uniseriados escasos. Heterogéneos tipo II (según clasificación de Kribs, 1968) con 2 o 3 hileras de células marginales erectas y el cuerpo formado por células procumbentes. Hay presencia de radios agregados. Células oleiferas frecuentes, y con gran cantidad de gomas rojizas en las células del cuerpo. Punteado radio-vascular de alterno a opuesto, con punteaduras semi-aeroladas grandes de redondeadas a oblicuas.

Fibras del tipo fibro-traqueidas con punteaduras areoladas pequeñas, de pared muy gruesa y frecuentemente septadas. Contenidos gomozos rojizos en el lumen de las mismas.

No presenta marcas de estratificación.

Nuestro sincero agradecimiento a Henk van der Werff por la revisión del manuscrito y sus valiosas sugerencias al mismo, a Frank Almeda por facilitarnos literatura reciente, y a Francisco Hodgson F. por su excelente ilustración.

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TOWARDS MOLECULAR GENETICS IN *CLARKIA*: GENE DUPLICATIONS AND MOLECULAR CHARACTERIZATION OF PGI GENES[1,2]

L. D. Gottlieb[3]

ABSTRACT

I review the phylogenetic implications of eight duplications of nuclear genes encoding isozymes in Clarkia *(Onagraceae). These include ADH, cytosolic PGI, and both plastid and cytosolic isozymes of PGM, 6PGD, and TPI. The PGI duplication has been studied intensively from biochemical and genetic standpoints. Recent results have identified two levels of regulation that operate in species with this duplication, one that reduces cytosolic PGI activity to the level characteristic of species without the duplication (dosage compensation), and the second that results in differential accumulation of the products of the duplicate genes. These factors appear to reduce the impact of the duplication on metabolic function. I also describe our recent cloning and sequencing of two genes encoding PGI obtained from a genomic DNA library of* C. unguiculata, *a species with the duplication. The two genes encode proteins of 548 and 543 amino acids, respectively, and their predicted amino acid sequences are 58% homologous. They show 65% homology to a previously published partial amino acid sequence of pig muscle PGI. Both genes lack introns. The two genes are the first nuclear genes sequenced in wild plants. They are being studied as part of a research program on gene evolution and the application of nuclear gene sequences for phylogenetic reconstruction in higher plants.*

Questions about phylogeny have the form, "Is A more closely related to B than to C?" For flowering plants, the best phylogenies are thought to take into account the "maximum number of attributes possible" (Davis & Heywood, 1967: 485), with evidence from morphology, cytology, chemistry, reproductive compatibility, and other fields somehow combined. However, accurate phylogenetic reconstruction is more often a goal than an achievement because of problems brought about

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[1] *This and the following three papers comprise the proceedings of the Missouri Botanical Garden's 34th Annual Systematics Symposium—Macromolecular Approaches to Phylogeny. The symposium took place in St. Louis, Missouri on October 9 and 10, 1987.*

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by character convergence, functional and developmental correlations, and unequal rates of evolution in different lineages. The essential difficulty is that little or nothing is known about how genetic changes that affect developmental processes result in differences in character expression.

The consequence is that no present procedure can translate the extent of morphological divergence into a measure of the closeness of phylogenetic relationship. I believe the way out of this impasse is to utilize a new source of evidence to assess phylogenetic relationships. The data of morphology, the traditional source of information about phylogeny, should be viewed as relevant to studies of plant development.

There is good reason to believe that information derived directly or indirectly from the structure and sequence of protein and DNA can be used to settle many phylogenetic questions. Interestingly, in this context, the molecular data are self-sufficient in that their usefulness does not depend on concordance with other lines of phenotypic evidence. For example, certain types of changes, particularly duplications of nuclear genes encoding enzymes (Gottlieb & Weeden, 1979; Gottlieb, 1983; Odrzykoski & Gottlieb, 1984) and large inversions of the chloroplast genome (Jansen & Palmer, 1987) appear to occur only once within a lineage. Thus taxa that now possess them probably descended from a single common ancestor and can be considered monophyletic without regard to their present morphological and cytological divergence.

In addition to phylogenetic inferences made on the basis of unique genetic and molecular traits, cladograms based on shared derived mutations or the extent of overall similarity can be constructed by comparing nucleotide sequences of genes or the size pattern of fragments cut from homologous DNAs by restriction endonucleases. The increasing availability of molecular data suggests that biosystematics no longer has to be considered an "unending synthesis" (Constance, 1964).

Phylogenetic relationships can now be determined accurately and reliably at many taxonomic levels. When this is done, the phylogeny can be used as a framework to ask important questions in other areas of biology. For example, how the attributes of species reflect both genetic legacy and selected and other changes since their origins, how genetic changes lead to specific modifications of ontogeny that result in new characters, and how and whether these new traits facilitate adaptation to different habitats. From this perspective, phylogeny can begin to inform both developmental and ecological analyses by providing evidence that A indeed derived from B and not from C.

In this paper, I review genetic and biochemical studies from my laboratory on gene duplications in *Clarkia* with emphasis on their phylogenetic implications. In addition, I describe very recent studies in which we have cloned and sequenced several genes encoding the glycolytic enzyme phosphoglucose isomerase from genomic libraries of *Clarkia* DNA. One purpose of these studies is to infer correct phylogenetic relationships in this well-studied plant genus. When the beginning and end points of species' genealogies are identified, we can ask about the steps in between.

BACKGROUND

Previous to our studies and, indeed, making them appropriate, were the intensive investigations by Professor Harlan Lewis and his students and colleagues in the 1950s and 1960s (Lewis, 1953, 1962, 1973; Lewis & Lewis, 1955; Lewis & Raven, 1958). They correlated evidence from field studies, morphology, and a major program of hybridization and cytogenetical analysis. *Clarkia* was found to comprise at least 43 species, 33 being diploid. The diploid species were distinguished by substantial amounts of chromosomal repatterning in addition to aneuploidy. The extent of morphological divergence varied from a difference in a single character between some pairs of species to differences in entire suites of traits that might serve as evidence of generic distinction in other plant groups. The degree of morphological resemblance was frequently not concordant with the amount of chromosomal rearrangement. Nevertheless it was possible to discern meaningful phylogenetic patterns among the diploid species, and they were assigned to seven taxonomic sections (Lewis & Lewis, 1955). Allopolyploid species linked several sections so that as a whole the genus was considered a natural unit.

Lewis formulated an elegant model of speciation to account for these relationships. The critical features of this model included the following: (1) species were regarded as progenitor and derivative and not as siblings; (2) a new species differed from its parent by gross chromosomal rearrangements and sometimes by a change in basic number; (3) the speciation process was rapid and abrupt; (4) speciation was independent of the evolution of new adaptations and therefore was largely fortuitous; (5) speciation, in general, occurred at the xeric margin of the distribution of the parent species.

Lewis's model and his proposed examples of progenitor-derivative species made *Clarkia* appropriate for the first studies carried out in plants that applied electrophoretic analysis of enzymes to assess the amount of genetic divergence correlated with speciation (Gottlieb, 1973, 1974a). The rationale behind these studies has been reviewed by Crawford (1983, 1985) and by me (Gottlieb, 1977, 1981, 1986).

In addition to information about variation (presence, number, frequency) and divergence of alleles at loci coding enzymes, electrophoretic patterns provide evidence about the number of isozymes of particular enzymes and, thereby, the number of coding loci. As more and more species of *Clarkia* were examined, it became apparent that they sometimes differed among themselves or from other diploid seed plants in the number of isozymes of many particular enzymes. Subsequent genetic studies revealed that increased isozyme number resulted from duplications of the coding genes (Gottlieb, 1977; Gottlieb & Weeden, 1979; Pichersky & Gottlieb, 1983).

Examination of the number of isozymes in a broad array of higher plants, including conifers and angiosperms, showed that isozyme number was highly conserved and depended on the number of subcellular compartments in which a particular catalytic reaction occurred (Gottlieb, 1982). For example, in diploid plants, enzymes of glycolysis and the oxidative pentose phosphate pathway are encoded in the nucleus and are generally found as two isozymes, one located in the plastids and the other in the cytosol. When the number of isozymes within a particular compartment is more than one, it probably results from duplication of the structural gene or, in polyploid plants, from additive expression of the genes in the several constituent genomes. Since the conserved number of isozymes reflects the metabolic requirements of plant cells, a reduced number is not possible because it would be lethal. (Failure to observe bands of enzyme activity following electrophoresis of plant extracts should not be taken as evidence that the enzyme is not present in the extract, a common error in many surveys of electrophoretic variation in plants that report the absence of an expected enzyme band as a null allele.) The rules for recognizing duplicate isozymes, following electrophoresis of plant extracts, have been thoroughly described (Gottlieb, 1982). It is worth noting again that subcellular location furnishes the best criterion for recognizing the homology of isozymes from different species, and that the rules apply only to enzymes assayed with natural in vivo substrates. No regularities have been identified in the number of isozymes of enzymes such as esterases, phosphatases, and peroxidases that are generally assayed with artificial substrates.

GENE DUPLICATION IN *CLARKIA*

The first duplicate isozyme discovered in *Clarkia* was that of alcohol dehydrogenase (ADH) in *C. franciscana* (Gottlieb, 1974b). Its absence from the closely related *C. amoena* and *C. rubicunda*, along with the very low genetic identity between *C. franciscana* and these species (Gottlieb, 1973), helped reject the hypothesis (Lewis & Raven, 1958) that *C. franciscana* was a recent derivative of *C. rubicunda*. The genetic evidence for duplication of ADH in *C. franciscana* was based on its exhibiting a true-breeding, three-banded electrophoretic pattern, whereas similar three-banded patterns in the related species resulted from heterozygosity at a single locus as evidenced by segregation patterns in progeny. Since *C. franciscana* did not display polymorphism for ADH, the duplication model was tested by making interspecific hybrids between it and *C. amoena*. The *C. amoena* plants used were homozygous at a single locus for an allele that encoded a slow ADH variant. The F_1 hybrids displayed a five-banded pattern that could only have resulted from the dimeric associations of three different polypeptides and, consequently, they must have possessed three genes (Gottlieb, 1974b). The ADH duplication was the second duplication of a gene encoding an enzyme discovered in plants. The first, in maize, was also an ADH (Schwartz & Endo, 1966).

Seven additional duplications of genes in *Clarkia* have since been described and, for each, the taxonomic distribution within the genus has been determined (Table 1). These duplications are cytosolic phosphoglucose isomerase (PGI) (Gottlieb, 1977; Gottlieb & Weeden, 1979), plastid and cytosolic triose phosphate isomerase (TPI) (Pichersky & Gottlieb, 1983), plastid and cytosolic 6-phosphogluconate dehydrogenase (6PGD) (Odrzykoski & Gottlieb, 1984), and plastid and cytosolic phosphoglucomutase (PGM) (Soltis et al., 1987). Detailed information about them is available in the individual reports. Five of the seven duplications (plastid and cytosolic 6PGD, plastid and cytosolic TPI, and plastid PGM) are present in species of all diploid sections of *Clarkia* (Table 1), suggesting they are at least as old as the genus. But only the duplicated plastid TPI was found in every species.

PLASTID AND CYTOSOLIC 6PGD

Four species of *Clarkia* appear to lack one or both 6PGD duplications (Odrzykoski & Gottlieb, 1984). *Clarkia rostrata* and *C. epilobioides* have a single plastid isozyme and a single cytosolic one and, consequently, lost both duplications. *Clarkia lewisii* and *C. cylindrica* have duplicated plastid 6PGDs but only a single cytosolic 6PGD (Table 1). The four species have been assigned to sect. *Peripetasma*, with the morphologically similar and crossable (Davis, 1970) *C. rostrata*, *C. lewisii*, and *C. cylindrica* to one subsection and the distinctive and highly self-pollinating *C. epilobioides* to a monotypic subsection (Lewis & Lewis, 1955). The close relationship of the former three species suggested that the loss of the duplicated cytosolic 6PGD occurred in their common ancestor and was subsequently followed in *C. rostrata* by an additional mutation or chromosomal deletion that silenced a duplicated gene encoding a plastid 6PGD. Since *C. epilobioides* also lacked both duplications, it seemed reasonable to suggest that it was closely related, although it was not possible to decide if the loss of its plastid 6PGD duplication was independent of the loss in *C. rostrata*.

The matter was settled by a restriction endonuclease analysis of chloroplast DNA carried out on all the species in this section, which revealed that *C. rostrata* and *C. epilobioides* were sister species and that *C. lewisii* and *C. cylindrica* comprised a second pair of sister species (Sytsma & Gottlieb, 1986a). The chloroplast DNA study also showed that the two pairs of species share a common ancestor well removed from the other species of the section. Thus, even though *C. rostrata* is not morphologically similar to *C. epilobioides* and was placed in a different subsection, the two species have a close genealogical relationship. Since this phylogenetic inference was based on evidence from both nuclear genes and chloroplast DNA, it is particularly strong.

PLASTID AND CYTOSOLIC TPI

Both TPI duplications appear to be present throughout *Clarkia* (Table 1), although some uncertainty remains in regard to the cytosolic TPI in sect. *Eucharidium* for which the genetic analysis is incomplete (Pichersky & Gottlieb, 1983). Electrophoretic studies of TPI have also been carried out on a number of species of other genera of Onagraceae to ascertain the taxonomic distribution of the duplications outside of *Clarkia*. Since sufficient (or appropriate) material was not available to conduct genetic analysis, three criteria had to be met to warrant the hypothesis that a given species possessed a TPI duplication. The minimum number of electromorphs per individual for each isozyme had to be at least three (TPI is dimeric), the multiple isozymes had to be located in the same subcellular compartment, and a side-by-side comparison of leaf and pollen extracts had to show the same number of cytosolic isozymes (the criteria are discussed in detail in Gottlieb, 1983). On the basis of satisfying all of these criteria (although sample sizes were very limited), the cytosolic TPI duplication was identified in five of the seven tribes of the family, including Jussiaeeae (*Ludwigia*), Fuchsieae (*Fuchsia*), Hauyeae (*Hauya*), Onagreae (*Clarkia, Heterogaura, Camissonia, Calylophus, Gongylocarpus*, and *Oenothera*), and Epilobieae (*Boisduvalia*) (Pichersky & Gottlieb, unpubl.). The presence of the duplication in both *Fuchsia* and *Ludwigia*, the two most ancient lineages in the family (Raven, 1979), suggests its great antiquity. In contrast, the plastid TPI duplication was not identified outside of *Clarkia* and must have arisen much more recently. Although these results should be regarded as exploratory, they point out the possibility that certain taxonomically widespread duplications may be useful to group genera (and eventually families) into monophyletic assemblages. However, since the time spans in these comparisons are great, it would be appropriate and necessary to validate the conclusions by examination of the nucleotide sequences of the duplicated genes.

PLASTID AND CYTOSOLIC PGM

In contrast to the situation in 6PGD in which the absence of duplicated genes could be assigned to some type of mutation in common ancestors of extant species, the loss of the plastid PGM duplication (Table 1) in *C. concinna* and in *C. lassenensis* (Soltis et al., 1987) must be regarded as independent events in lineages directly ancestral to these species but to no others, since the two species belong to distantly related sections of *Clarkia* (Lewis & Lewis, 1955).

The presence of the cytosolic PGM duplication in *C. arcuata* (sect. *Rhodanthos*) and in all species of sections *Godetia* and *Myxocarpa* (Table 1) is consistent with a taxonomic assignment previously made by Lewis & Lewis (1955). They proposed (p. 261) that sect. *Rhodanthos* (then designated sect. *Primigenia*) was "probably directly ancestral" to sect. *Godetia* and "perhaps" to sect. *Myxocarpa*. Within sect. *Rhodanthos*, the relevant lineage is now represented by *C. arcuata*

TABLE 1. *The phylogenetic distribution of duplicate isozymes in diploid species of* Clarkia. *The PGI data are from Gottlieb & Weeden (1979), the PGM data from Soltis et al. (1987), the 6PGD data from Odrzykoski & Gottlieb (1984), and the TPI data from Pichersky & Gottlieb (1983). The numeral 1 indicates the species has a single isozyme and the numeral 2 indicates duplicated isozymes. For each enzyme, plastid (Pl) and cytosolic (Cy) isozymes are indicated.*

	Isozyme Number						
	PGI	PGM		6PGD		TPI	
Section Species	Cy	Pl	Cy	Pl	Cy	Pl	Cy
Eucharidium							
C. breweri	2	2	1	2	2	2	?
C. concinna	2	1	1	2	2	2	?
Fibula							
C. bottae	2	2	1	2	2	2	2
Peripetasma							
C. cylindrica	2	2	1	2	1	2	2
C. lewisii	2	2	1	2	1	2	2
C. epilobioides	2	2	1	1	1	2	2
C. rostrata	1	2	1	1	1	2	2
C. biloba subsp. *australis*	2	2	1	2	2	2	2
C. dudleyana	2	2	1	2	2	2	2
C. lingulata	2	2	1	2	2	2	2
C. modesta	2	2	1	2	2	2	2
Heterogaura heterandra	2	2	1	2	2	?	2
Phaeostoma							
C. xantiana	2	2	1	2	2	2	2
C. unguiculata	2	2	1	2	2	2	2
Godetia							
C. imbricata	1	2	2	2	2	2	2
C. nitens	1	2	2	2	2	2	2
C. speciosa subsp. *polyantha*	1	2	2	2	2	2	2
C. williamsonii	1	2	2	2	2	2	2
Myxocarpa							
C. mildrediae	1	2	2	2	2	2	2
C. virgata	1	2	2	2	2	2	2
Rhodanthos							
C. arcuata	1	2	2	2	2	2	2
C. lassenensis	1	1	1	2	2	2	2
C. amoena subsp. *huntiana*	1	2	1	2	2	2	2
C. franciscana	1	2	1	2	2	2	2
C. rubicunda	1	2	1	2	2	2	2

which, together with *C. lassenensis*, was placed in a distinct subsection. The other subsection containing diploid species includes *C. amoena*, *C. rubicunda*, and *C. franciscana*, and it then would represent the lineage from which the other four sections of *Clarkia* (Table 1) eventually evolved. Alternatively, the cytosolic PGM duplication may have had independent origins in *C. arcuata* and sections *Godetia* and *Myxocarpa*. Sequence comparisons of the PGM genes will make it possible to distinguish these models.

Regardless of the outcome of such comparisons, the taxonomic distribution of the cytosolic PGM duplication is independent of the sectional phylogeny suggested (Lewis, 1980) following the discovery of the cytosolic PGI duplication (Gottlieb, 1977; Gottlieb & Weeden, 1979), since the two duplications are not present together in any species (Table 1). The PGM evidence suggests that the four sections that have the PGI duplication (Table 1) arose from the lineage within sect. *Rhodanthos* that also gave rise to *C. amoena*, *C. rubicunda*, and *C. franciscana*. It is also an interesting possibility that since the two enzymes catalyze adjacent reactions in glycolysis and gluconeogenesis (PGI interconverts fructose-6-phosphate and glucose-6-phosphate, and PGM interconverts the latter and glucose-1-phosphate), there may be metabolic reasons that select against the occurrence of both duplicated enzymes in the same cytosol.

Overall, the genetic and biochemical evidence from the several gene duplications provides a remarkably consistent and coherent picture of the phylogenetic relationships within *Clarkia*. The evidence is also consistent with the recent discovery based on restriction endonuclease patterns in chloroplast DNA that the monotypic *Heterogaura heterandra* (Table 1) is actually a *Clarkia* and closely related to *C. dudleyana* (Sytsma & Gottlieb, 1986b).

PGI

The PGI duplication in *Clarkia* has been studied intensively because it was one of the first duplications identified that is present in some but not all species of a single genus. Thus, it is possible to compare duplicate PGI genes and their products with their nonduplicate homologues, and the comparisons can be done in species having a relatively similar genomic background. The example provides an unusual opportunity to examine the critical early stages of gene evolution and to test the general model that major changes in gene regulation, structure, and function cannot evolve without the availability of duplicate sequences.

The PGI duplication characterizes all of the species (except *C. rostrata*) in the morphologically advanced and diverse sections *Eucharidium*, *Fibula*, *Phaeostoma*, and *Peripetasma*, and is absent from sections *Godetia*, *Myxocarpa*, and *Rhodanthos* (Table 1). Consequently it identifies a specific branching point in the phylogeny of *Clarkia* and serves to group the former four sections into a monophyletic lineage (Gottlieb & Weeden, 1979; Lewis, 1980). The realignment was effected without having to move any species into or out of any section (Lewis, 1980).

Genetic studies revealed that the duplicate PGI genes assort independently (Gottlieb, 1977; Gottlieb & Weeden, 1979; Weeden & Gottlieb, 1979), which is thought to mean that they arose by a process involving overlapping reciprocal translocations or insertional translocations rather than unequal crossing-over. The relevant arguments were presented in Gottlieb (1983). Many other duplicate genes in plants also assort independently (Tanksley, 1987). The mode of origin is important for phylogenetic reconstructions because chromosomal rearrangement is much more likely than unequal crossing-over to occur only once for a particular chromosome segment in a particular linkage. Linkage relationships for the other duplications in *Clarkia* have not been studied in similar detail, although we do know that the duplicate genes encoding plastid TPIs and one of them and a cytosolic TPI gene also assort independently (Pichersky & Gottlieb, 1983).

A number of biochemical studies were carried out to determine how much and what type of divergence marked the duplicate PGI isozymes. Three results are noteworthy, one having to do with the molecular weight of PGI subunits and the other two with the evolution of regulatory factors that appear to modulate the expression of the duplicate PGI genes.

PGI subunits encoded by the duplicate genes have different apparent molecular weights (apparent because the values were obtained from their electrophoretic mobility on SDS gels), with PGI-2 being 60,400 and PGI-3 59,000, or values closely similar (Gottlieb & Higgins, 1984a). Species in sect. *Myxocarpa* that lack the duplication have PGI subunits with molecular weight of 60,400, and PGIs from sections *Godetia* and *Rhodanthos* weighed in at 59,000. The presence of two molecular weight forms in species with the duplication and each molecular weight form by itself in species without the duplication was unlikely to have come about by chance. The result suggested the novel possibility that the PGI locus in an ancestal *Clarkia* was translocated to different nonhomologous chromosomes, that the genes then accumulated mutational changes that encoded different molecular weight subunits, and that lines carrying the different chromosomes eventually hybridized with both PGI genes becoming segregated into a single genome by a process originally documented in maize (Burnham, 1962) involving overlapping reciprocal translocations. The scenario seems feasible for *Clarkia*, in which species are distinguished by gross amounts of chromosomal rearrangement, and which all have a self-compatible breeding system permitting chromosomal heterozygotes to be made homozygous and true-breeding by self-pollination. The merits of this speculation can be directly tested by comparing nucleotide sequences of PGI genes from species with and without the duplication (see below).

After it became apparent that the catalytic properties of the duplicate and nonduplicate PGIs were alike (Higgins & Gottlieb, 1984), studies turned to questions about increased gene dosage and whether it caused increased levels of cytosolic PGI activity and protein. The PGI levels in clarkias with and without the duplication were assessed by immunological means using an antiserum specific to cytosolic PGI (i.e., one that does not cross-react with plastid PGI). The result was clear-cut. The two types of species had the same levels of cytosolic PGI activity and protein, suggesting that some form of regulation had evolved that "compensated" for the duplicated genes (Gottlieb & Higgins, 1984b). The activity level proved to be the same as that in a number of diploid vegetables, indicating that green plants generally maintain a similar PGI level. This finding provided an important rationale for the evolution of dosage compensation because it restored an activity level characteristic of typical diploid plants having a single cytosolic PGI. Thus a regulatory mechanism had evolved that reduced the impact of the duplication on metabolic function.

To determine whether the regulation operated via metabolic or genetic factors, a series of null activity mutants of each duplicate gene was induced by ethyl methanesulfonate (EMS) treatment of seedlings of *C. xantiana* (Jones et al., 1986). Metabolic factors would be implicated if lesions induced in either gene did not change PGI levels. In homozygous state, each mutant completely lacked the homodimer activity normally specified by the affected gene. The mutants were backcrossed to wildtype for five generations, making it possible to assign changes in PGI activity directly to the mutation and not to unknown factors in the background. Immunological analysis revealed that they reduced PGI activity in direct proportion to the normal contribution of each gene. The homozygous mutants at *Pgi2* reduced cytosolic PGI activity to 36% of wildtype, and the mutant at *Pgi3* to 64%. The effects of the mutations at the two loci were additive. Thus, $Pgi2^{null}2^{null}$, $Pgi3^{a}3^{null}$ plants synthesized in an F_2 progeny from experimental hybrids between the two mutants exhibited only 14% of wildtype activity. The double homozygous null was lethal. The results demonstrated that PGI activity in plants having the duplication is not directly regulated by metabolic factors, warranting the suggestion that the dosage compensation depends on factors that regulate the levels of transcription or translation (Jones et al., 1986). Since *Pgi3* contributes less than *Pgi2* to the total cytosolic PGI activity, the regulatory factors appear to operate to a greater extent on the former locus. Thus, two levels of regulation were identified, one that reduces cytosolic PGI activity in species with the duplication to the level characteristic of species without the duplication, and the second that results in differential accumulation of the products of the duplicate genes.

The genetic and biochemical analyses of PGI in *Clarkia* identified a number of interesting questions that can be answered only with evidence from the sequences of the coding genes. For example, in terms of phylogenetics, it is necessary to test the major hypothesis that the duplication had a unique origin, with the consequence that the four sections that possess it are monophyletic. A corollary hypothesis is that the origin of the duplication involved hybridization between lineages now represented by *Myxocarpa* (which has the higher molecular weight subunit) and *Godetia/Rhodanthos* (with the low molecular weight subunit). The hypotheses can be tested by comparing the sequences of duplicate and nonduplicate PGI genes. On the hypothesis, *Pgi2* from a species with the duplication should be similar to *Pgi* from *Myxocarpa*, and *Pgi3* from the species with the duplication should be similar to *Pgi* from *Godetia/Rhodanthos*. In other words, the duplicate genes should be more similar to genes from different species than they are to each other.

Other questions of interest in a context of evolutionary biology have to do with the extent of PGI sequence divergence in species with the duplication versus those without the duplication, the extent of polymorphism for PGI genes in natural populations of *Clarkia*, and the value of the sequences to demonstrate phylogenetic relationships outside of *Clarkia*, particularly among the diverse genera included in tribe Onagreae.

A different set of questions must be answered to explain how the cytosolic PGI level is reduced in species with the duplication to that characteristic of those without it, to determine the basis for the near 2:1 difference in PGI activities attributable to the duplicate genes, to learn why *Pgi2* encodes a higher molecular weight unit than *Pgi3*, and the nature of the mutations that eliminated PGI activity in the EMS-induced null mutants.

CLARKIA PGI GENE SEQUENCES

Headway on these questions can now be made because we have cloned and sequenced PGI genes from several *Clarkia* genomic libraries. Here I describe how these genes were obtained, evidence that they encode PGI, and their general structure. Detailed characterizations and sequences will be presented separately. To my knowledge, the *Clarkia* PGI genes are the first nuclear genes from wild plants that have been sequenced.

Our first genomic library was constructed with DNA isolated from seedlings of a horticultural strain

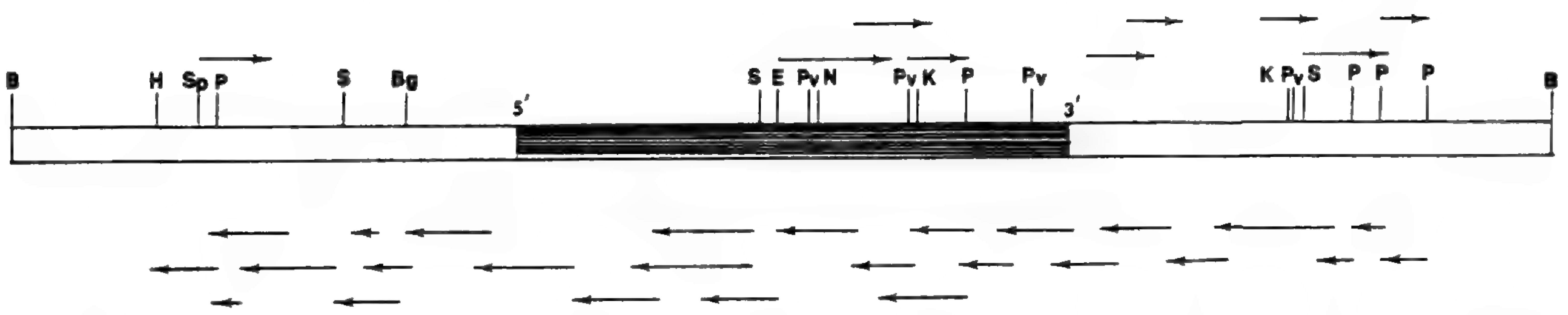

FIGURE 1. *Restriction map and sequencing strategy for the* Clarkia unguiculata *U2 gene which encodes PGI. The gene is present on a 4.45-kb* Bam*H1 fragment. Restriction sites shown are* Bam*H1 (B),* Hpa*I (H),* Sph *(Sp),* Pst*I (P),* Sal*I (S),* Bgl*III (Bg),* Eco*R1 (E),* Pvu*II (Pv),* Nco*I (N), and* Kpn*I (K). The arrows above and below the restriction map show the direction and extent of sequencing for the individual M13 subclones. 3.8 kb including the entire coding region was sequenced on one strand, and 1.6 kb on the complementary strand.*

of *C. unguiculata* (Northrup King "Clarkia Double Mixed Colors"), a species with the PGI duplication. Horticultural material was used because very large amounts of seed could be purchased, permitting us to fine-tune our techniques prior to studying natural populations. The DNA was extracted by a procedure modified from Fischer & Goldberg (1982) that yielded a nuclear pellet that, after lysis, provided high molecular weight DNA fragments (greater than 100 kb). The DNA was partially restricted with *Sau*3a and fragments between 15 and 23 kb obtained by fractionation on a sucrose gradient. After determining optimal ratios of chromosomal DNA and vector arms, the DNA fragments were cloned into the *Bam*H1 site of the lambda replacement vector Charon 35. The resulting library is estimated to contain 1.8 × 10^6 phage with 88% recombinants and represents about seven *Clarkia* genomes.

The library was screened at low stringency (51°C, 5 × SSPE) with an 800-bp DNA fragment of a yeast gene encoding PGI, kindly provided by a biotechnology firm. Since we expected low to very low homology between the yeast and *Clarkia* PGI sequences, the screening conditions were determined in a prior experiment in which the probe was hybridized on a Southern blot to genomic *C. unguiculata* DNA digested with several restriction enzymes. Two positive clones were obtained from the first 30,000 plaques examined. They were purified, and DNA prepared from each was restricted with several enzymes, subjected to agarose gel electrophoresis, and analyzed by Southern blots using the yeast PGI DNA fragment as probe. The two clones had inserts of 13.7 and 15 kb, which proved different. Hybridizing fragments of the former clone, designated U2, were cloned into M13mp10 and partially sequenced. The sequences showed homology to that of the yeast gene. A 4.45-kb *Bam*H1 fragment (Fig. 1) was then subcloned into pUC19 and deletion fragments constructed using the exonuclease III-S1 protocol of Henikoff (1984). One strand of 3.8 kb including the entire coding region was completely sequenced, and 1.6 kb was sequenced on the complementary strand by the dideoxy sequencing protocol (Messing, 1983). The U2 sequence revealed an uninterrupted open reading frame of 1,644 nucleotides encoding a protein of 548 amino acids.

TABLE 2. *Homology between predicted amino acid sequences from nucleotide sequences of U2 and U8, cloned from a genomic library of* Clarkia unguiculata *and amino acid sequences of cyanogen-bromide peptides purified from pig muscle PGI (Achari et al., 1981).*

Sequence	Number Identical Amino Acids / Total Number of Amino Acids	Homology
U2 vs. U8	319/548	58%
U2 vs. Pig	110/166	66%
U8 vs. Pig	108/166	65%
U2 vs. U8 (in sequences covered by Pig peptides)	89/165	54%

The identity of U2 was established by comparing its predicted amino acid sequence with the amino acid sequences of five cyanogen-bromide peptides obtained from pig muscle PGI (Achari et al., 1981). These are the only PGI sequences, protein or DNA, that are published for any organism. The five pig peptides identify a total of 166 amino acids, about 30% of the complete protein. The U2 gene encodes amino acids that are identical to those in pig PGI at 110 of these 166 residues, or 66% of the total (Table 2). A second PGI gene, called U8, also obtained from the *C. unguiculata* genomic library, using U2 as the probe, was found that contains the same sequence present in the 15-kb insert noted above. A similar isolation and sequencing strategy was used to characterize the U8 clone as was used for U2. U8 proved to have a 65% ho-

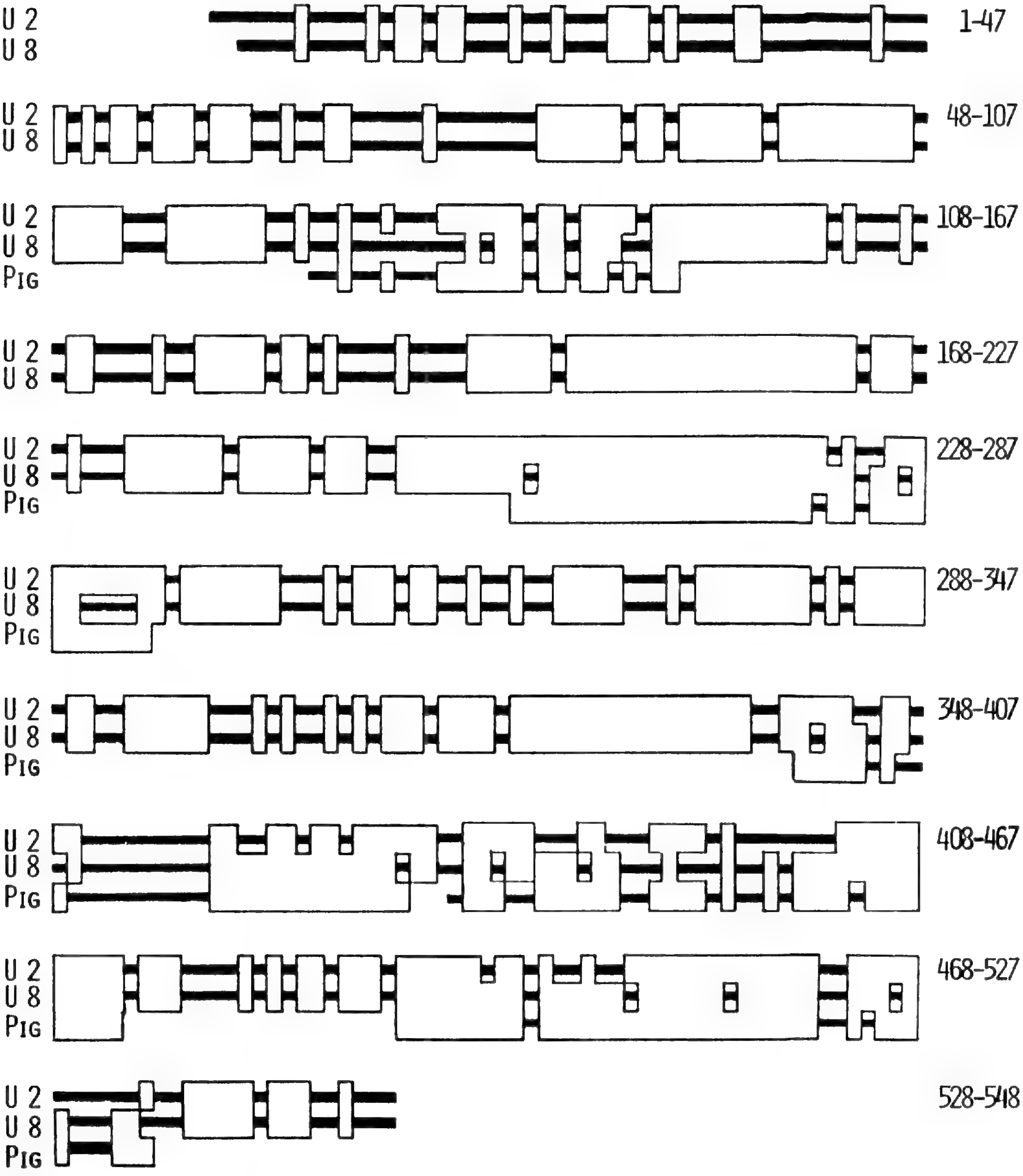

FIGURE 2. *Comparison of the predicted amino acid sequences encoded by* Clarkia unguiculata *U2 and U8 genes with the amino acid sequences from five cyanogen-bromide peptides from pig muscle PGI (Achari et al., 1981). An open box drawn across the black bars indicates the same amino acid appears in the corresponding position on two or three of the sequences. The amino acids are numbered on the right beginning with the first methionine in the U2 sequence. U2 encodes 548 amino acids, U8 encodes 543 amino acids, and the total number of amino acids identified in the pig peptides is 166. The diagram represents the best fit by eye, taking into account several short insertions and deletions in the sequences.*

mology to pig PGI (Table 2), and encodes a protein of 543 amino acids.

The predicted amino acid sequences show that U2 and U8 are 58% homologous over their entire coding regions. Comparing U2 and U8 only in the regions covered by the pig peptides, the two sequences are 54% identical (Table 2). Thus, the two *Clarkia* PGI genes differ more from each other than either does from pig PGI. The homology of the *Clarkia* and pig sequences is diagrammed in Figure 2. The two *Clarkia* proteins exhibit large blocks of very high amino acid identity as well as many shorter regions of nonidentity. Several lengthy portions of the three sequences show complete identity. Overall, the high homology between the pig PGI amino acid sequences and the predicted *Clarkia* amino acid sequences establishes with certainty that both *Clarkia* genes encode PGI.

On the basis of lack of interruption in their open reading frames and the lengths of their sequences, which encode proteins that have closely similar molecular weights to that previously determined for *Clarkia* PGI, neither *Clarkia* gene appears to include introns (and see below). Otherise, both genes have many features expected of eukaryotic genes, including potential TATA boxes and other upstream regions similar to known regulatory sequences. A complete transcriptional characterization of the genes will be reported separately.

Clarkia unguiculata possesses the PGI duplication, and its genome must include two loci encoding cytosolic PGIs and one locus encoding plastid PGI. Since a heterologous probe was used to obtain the U2 and U8 PGI genes, it was necessary to determine which isozyme is encoded by each gene. A priori, the expectation was that sequences encoding the cytosolic PGIs would be more similar to each other than either would be to the plastid PGI. Genes encoding plastid and cytosolic glycolytic isozymes have been cloned and sequenced in plants only for tobacco glyceraldehyde-3-phosphate dehydrogenase (G3PD) (Shih et al., 1986), and the results of that study are closely relevant to our research with PGI. Comparison of predicted amino acid sequences from cDNAs showed that the tobacco cytosolic G3PD was more similar to other eukaryotic G3PD enzymes, with about 65% homology, than it was to the tobacco plastid isozyme, with 45% homology. The homology of U2, U8, and pig PGI are roughly similar to these values, but we were able to compare only a few sequences.

Our initial attempt to identify the isozymes encoded by the *Clarkia* genes centered on the search for correlation between restriction length fragments and allelic segregation. This could be followed by PGI activity staining on starch gels following electrophoresis of leaf extracts and correlated with the RFLP segregation. To date, we have examined a number of DNAs from single *C. unguiculata* plants by restriction analysis followed by electrophoresis and Southern blotting. The DNAs proved highly polymorphic, but we have been able to match restriction fragments to U2. U8 and several other genes cloned from the *C. unguiculata* library have not yet been similarly matched, but this is not unexpected, since the library was made from DNA isolated from a bulk of hundreds of individual seedlings and this commercial strain is highly polymorphic.

However, a different procedure suggests that U8 encodes the slowly migrating allozyme PGI-3B, a cytosolic isozyme. The U8 sequence was inserted in pUC18, downstream from the beta-galactosidase promoter. When the operon was induced by IPTG, the *E. coli* host synthesized very large quantities of PGI protein. The PGI was catalytically active and had a very slightly faster electrophoretic mobility on starch gels than the slow allozyme PGI-3B of *C. unguiculata*, a difference probably caused by different post-translational protein modification between *Clarkia* and *E. coli*. By the same procedure, a large quantity of protein with the molecular weight of PGI was also synthesized from U2, and its electrophoretic mobility was similar to that of *Clarkia* plastid PGI. The expression of these genomic clones in *E. coli*, apparently by virtue of fortuitous promoters in their 5′ noncoding region, provides convincing evidence that introns are not present in these genes. Whether other PGI genes also lack introns remains to be determined. Their absence is surprising, since other genes encoding glycolytic enzymes in plants such as maize *Tpi* has eight introns (Marchionni & Gilbert, 1986) and maize *Adh* has nine introns (Dennis et al., 1984).

To summarize the molecular studies, we have cloned and sequenced two PGI genes from a genomic library of *C. unguiculata*, a species with the PGI duplication. The genes have a homology of 58%; one of them (U8) appears to encode a cytosolic PGI-3 isozyme; the other is thought to encode a plastid PGI. We have also constructed genomic libraries from *Clarkia* species without the PGI duplication and have obtained clones of a number of sequences homologous to the PGI probes from *C. unguiculata*. The molecular genetics studies of PGI in *Clarkia* constitute one of the first analyses of the evolution of a plant nuclear gene. Many additional molecular studies are called for to understand gene evolution and to improve phylogenetic reconstructions.

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CHLOROPLAST DNA VARIATION AND PLANT PHYLOGENY[1]

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ABSTRACT

Several features, foremost its conservative mode of evolution, make chloroplast DNA an extremely valuable molecule for phylogenetic studies. Its conservatism is also its only serious drawback, as this can limit the amount of useful DNA variation at the intraspecific level. Comparative restriction site mapping is currently the preferred molecular method for examining interspecific relationships. At this level, one typically encounters less than 5% homoplasy. Furthermore, the predominantly uniparental inheritance of chloroplast DNA provides unique insights into the origin of hybrid and polyploid complexes, as illustrated by examples from the genus Brassica. *In many families of angiosperms, such as the Asteraceae and Orchidaceae, restriction site mapping can also be used to determine intergeneric relationships. The greater expense of DNA sequencing makes it most appropriate only at those higher taxonomic levels—above the family level—where restriction site mapping fails. Within angiosperms, the* rbcL *gene appears to be the chloroplast gene of choice for phylogenetic studies. Twenty-five* rbcL *sequences have already been accumulated, and several laboratories are making a coordinated effort to sequence this gene widely among angiosperms and gymnosperms. The more conservatively evolving ribosomal RNA genes hold the greatest promise for resolving the deepest branchings of plant evolution and, indeed, have already settled the ultimate question of chloroplast evolution, namely, its endosymbiotic origin. A third approach to extracting phylogenetic information from chloroplast DNA is by analyzing the distribution of major structural rearrangements, such as inversions and the loss or gain of genes and introns. Although such rearrangements are rare relative to point mutations, their great rarity and freedom from homoplasy also make them extremely powerful characters. Examples to be discussed include an inversion defining the most ancient branching in the Asteraceae, rearrangements that mark several major divisions within the Fabaceae, and events that identify the green algal ancestors of land plants.*

The confounding diversity and plasticity of plant morphologies have prompted plant systematists to search for more reliable characters to use in phylogenetic reconstruction. In recent years, these characters often have been chemical ones. A large body of comparative data has been gathered on secondary plant chemicals (reviewed in Harborne & Turner, 1984; Giannasi & Crawford, 1986, in press), yet the ultimate systematic value of these compounds remains unclear, particularly at higher taxonomic levels (Giannasi & Crawford, 1986, in press). The examination of plant protein variation by enzyme electrophoresis continues to be a powerful tool for inferring relationships within species and for studying mechanisms of speciation (Gottlieb, 1981; Crawford, 1983; Harborne & Turner, 1984; Giannasi & Crawford, 1986, in press). However, early attempts to infer broader patterns of plant phylogeny by amino acid sequencing were largely unsuccessful (Boulter, 1980; Harborne & Turner, 1984; Giannasi & Crawford, 1986, in press). While a recent review concluded that plant "amino acid sequencing is an approach whose time has come and gone" (Giannasi & Crawford, 1986), recent studies by Martin and collaborators (e.g., Martin & Dowd, 1986; Martin et al., 1986) demonstrate that this approach does indeed have phylogenetic merit.

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The tremendous power of modern molecular biology has revolutionized our ability to analyze and compare large stretches of chromosomes and DNA sequences. Literally millions of discrete DNA characters, i.e., base pairs, are present in the genomes of all organisms. Moreover, the underlying basis of changes in the states of these characters can be understood in the most satisfying way possible—as mutations in the genetic material itself. The application of DNA comparisons to systematic questions is now being actively pursued for most life forms. The power and promise of DNA systematics has already been demonstrated in studies whose emphases range from the primary lines of descent of life on Earth (Pace et al., 1986) to population dynamics and the speciation process in higher animals (Avise et al., 1987; Moritz et al., 1987).

Although the field of chloroplast DNA (cpDNA) systematics is only 12 years old (Atchison et al., 1976; Vedel et al., 1976), it has already provided significant insights into a number of phylogenetic problems, and, together with parallel studies of nuclear DNA variation, offers the best hope of producing an accurate phylogeny of the major lines of plant descent. Several reviews of the field have appeared recently (Cattolico, 1985; Palmer, 1985a, 1986a, 1987; Giannasi & Crawford, 1986, in press). This article will review approaches for extracting useful phylogenetic information from chloroplast DNA comparisons as practiced in this laboratory and also results obtained from such studies.

THE CHLOROPLAST CHROMOSOME

An understanding of certain basic properties of the cpDNA molecule is critical to a proper appreciation of its utility in systematic studies. The following overview is based primarily on several review articles (Sears, 1980; Gillham et al., 1985; Palmer, 1985b, c, 1987; Rochaix, 1985; Ritland & Clegg, 1987; Zurawski & Clegg, 1987; Wolfe et al., 1987), which should be consulted for details beyond this brief synopsis and for relevant references. In addition, the recently completed sequences of the entire chloroplast genomes of an angiosperm (*Nicotiana tabacum*; Shinozaki et al., 1986) and a liverwort (*Marchantia polymorpha*; Ohyama et al., 1986) provide a wealth of specific information on chloroplast gene content and organization.

STRUCTURE AND GENE CONTENT

Figure 1 shows the structure and gene arrangement of a representative and well-understood chloroplast genome, that of tobacco. This circular chromosome is 156 kilobase (kb) pairs in size (155,844 base pairs, to be exact) and is arranged in four parts; there are two identical 25-kb segments that form an inverted repeat separating the rest of the molecule into single-copy regions of 87 kb and 18 kb. The typical chloroplast genome of land plants is densely packed with approximately 120 genes, some of which are shown in Figure 1. These genes encode four ribosomal RNAs, 30–31 transfer RNAs, approximately 55 proteins of known function, and about 30 unidentified proteins. Chloroplast gene products function primarily in photosynthesis and in transcription-translation. The former category includes many of the critical polypeptides of the major thylakoid protein complexes (see legend to Fig. 1) and also the large subunit of the primary CO_2 fixing enzyme, ribulose-1,5-bisphosphate carboxylase. Gene products involved in transcription-translation include the ribosomal and transfer RNAs, approximately a third of the chloroplast ribosomal proteins, four subunits of RNA polymerase, and initiation factor 1. Surprisingly, tobacco and *Marchantia* cpDNAs contain six genes similar in sequence to those encoding subunits of *mitochondrial* NADH dehydrogenase, although their function in the chloroplast remains a mystery.

Both strands of the chloroplast genome are actively expressed, indeed transcription switches strands over 30 times. Many chloroplast genes are grouped functionally into polycistronic operons, such as those containing the four ribosomal RNA genes, *atp*I-H-F-A, *atp*B-E, and a cluster of eight ribosomal proteins extending from *rpl*23 through *rps*8 (Fig. 1). The order and mode of expression of genes in these operons are highly similar to those found in prokaryotes. A major structural difference between certain chloroplast genes and those of prokaryotes is the presence of introns, which in tobacco occur in six tRNA genes and ten protein genes, but which are absent from eubacterial genes.

EVOLUTION AND INHERITANCE

Land plant cpDNAs evolve quite slowly in all respects. They vary in size less than two-fold (120–217 kb), with most of this variation resulting from a few major expansions or contractions of the large inverted repeat, so that the range of sequence complexities is only 110–150 kb. Most length mutations are quite short (1–10 bp), although larger ones on the order of 50–1,200 bp occur frequently enough to be a major component of the variation encountered in restriction fragment and map comparisons (see below). Gene content is highly con-

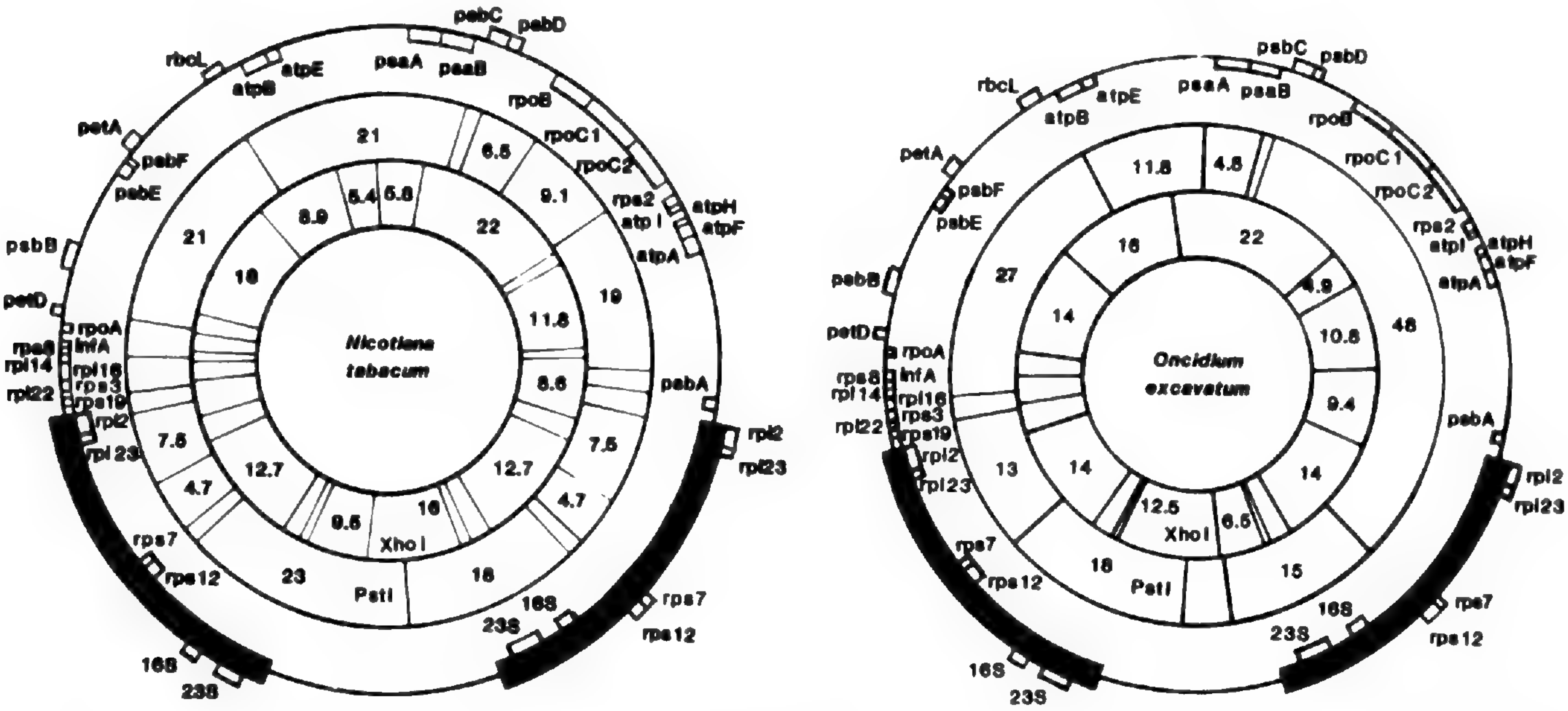


FIGURE 1. *Physical and gene maps of typical cpDNAs from a dicot (*Nicotiana tabacum; *Solanaceae) and monocot (*Oncidium excavatum; *Orchidaceae). Heavy black lines centered on the circles indicate large inverted repeats. Ribosomal RNA genes are indicated by 16S and 23S. Genes for the 50S and 30S ribosomal proteins are given as* rpl *and* rps, *respectively, followed by the number of the corresponding* E. coli *protein. Genes for RNA polymerase subunits are indicated by* rpo, *followed by a subunit-specific letter.* Inf*A encodes initiation factor 1.* Rbc*L encodes the large subunit of ribulose-1,5-bisphosphate carboxylase. Subunits of the thylakoid membrane complexes ATP synthase, photosystem I, photosystem II, and cytochrome b_6/f complex are encoded by* atp, psa, psb, *and* pet, *respectively, followed by a subunit-specific letter. Only selected genes are shown for the completely sequenced cpDNA of tobacco; see Shinozaki et al. (1986) for a more complete map. Orchid data are from M. Chase & J. Palmer (unpublished data).*

served; only two differences are known among the 120 genes present in the cpDNAs of tobacco and *Marchantia*, which diverged some 400 million years ago. The order of chloroplast genes is also highly conserved. The tobacco gene order is found in most other angiosperms (e.g., an orchid, Fig. 1) and in at least one fern and one gymnosperm, and differs by only one inversion from the *Marchantia* order. With the exceptions so far of only two groups of plants (some legumes and *Pelargonium*), most of the changes in gene order found among angiosperm cpDNAs can be accounted for by one or two simple inversions.

Sequence comparisons of several kinds reveal a low rate of nucleotide substitution in land plant cpDNA as a whole, although direct sequence studies reveal rate differences among specific chloroplast genes. On average, the rate of silent substitution in chloroplast genes is two to three times lower than in nuclear genes and 20 times lower than in animal mitochondrial genes, but three to four times higher than in plant mitochondrial genes. Transitions outnumber transversions in chloroplast genes by a factor of somewhat less than two relative to random expectations, a much smaller bias than that found in animal mtDNA.

A critical feature of cpDNA from the standpoint of phylogenetic studies at lower taxonomic levels is its mode of inheritance. In all land plants examined thus far, it is inherited clonally, through the maternal parent in most angiosperms and the paternal parent in gymnosperms. In those plants where both parents contribute chloroplasts to their offspring, the chloroplasts and their genomes have never been seen to recombine, but simply sort out somatically.

APPROACHES TO DETECTING AND ANALYZING CHLOROPLAST DNA VARIATION

Mutations in cpDNA are fundamentally of two types—point mutations (single nucleotide pair substitutions) and rearrangements, with several kinds of rearrangements recognized. By far the most frequent mutations are point mutations and deletions/insertions in noncoding regions. Whereas point mutations can profitably be used for phylogenetic studies at all taxonomic levels, the systematic use of noncoding deletions/insertions is often inappropriate, as will be discussed in the section on restriction site mapping. Other classes of rearrangements (inversions and deletions/insertions of genes, introns, and one copy of the large inverted repeat) occur rarely during cpDNA evolution. Because of their rarity, these changes are often extremely useful in phylogenetic reconstruction.

In the following sections, we discuss the kinds of approaches available for comparing cpDNAs and revealing phylogenetically informative mutations. The three major approaches will be discussed in terms of the methodologies involved, the kinds of mutations detected, and the taxonomic levels at which they are most appropriate. Before discussing these approaches, we first review methods for preparing cpDNA and total DNA for use in phylogenetic studies.

ISOLATION OF CHLOROPLAST AND TOTAL DNA

The most generally applicable procedure for preparing purified cpDNA is the sucrose gradient procedure described in Palmer (1986b). For some plants, such as members of the Geraniaceae, substantially higher yields are obtained by substituting for the aqueous blending used in Palmer (1986b) a two-step homogenization procedure, consisting of powdering of liquid nitrogen-frozen tissue in a coffee mill (Calie & Hughes, 1987a), followed by Polytron-grinding of the powder in aqueous buffer. A large number of alternative procedures for preparing cpDNA are reviewed in Palmer (1986b). We particularly call the reader's attention to a NaCl-isolation technique (Bookjans et al., 1984) that works extremely well with many recalcitrant legumes and Malpighiaceae, to recently developed techniques for extracting cpDNA from conifers (White, 1986) and mosses (Calie & Hughes, 1987a), and to a promising modification (Dally & Second, submitted) of the nonaqueous procedure of Bowman & Dyer (1982), which eliminates the use of highly dangerous organic chemicals.

In many cases it may be convenient, if not preferable, to analyze cpDNA variation in preparations of total cellular DNA, rather than purified cpDNA. The major advantages of using total DNA are *yield* (total DNA extraction efficiencies are nearly quantitative and provide 5–100 times higher yields of cpDNA than cpDNA extraction procedures; 1–2 grams of fresh leaf tissue will usually provide sufficient total DNA for 10–30 restriction enzyme digests, enough for most comparisons of cpDNA variation), *flexibility* (total DNA preparations can obviously be used to study variation in all three plant genomes), and *adaptability* (total DNA has been extracted from several groups of plants in which common methods of cpDNA extraction did not work). The small amount of starting material needed for total DNA extractions has proved critical in our studies on orchids, many of which are rare or minute plants that at maturity may weigh only 0.3–0.6 grams.

Since cpDNA is present in several thousand copies in the typical leaf cell (Bendich, 1987), it is easy to visualize and map cpDNA fragments by hybridizing cloned cpDNA fragments to filter blots containing restriction enzyme digests of total DNA. Indeed, most current studies of cpDNA restriction site variation have employed total DNA (e.g., Sytsma & Gottlieb, 1986a, b; Coates & Cullis, 1987; Jansen & Palmer, 1988). The use of purified cpDNA is of somewhat greater advantage in DNA sequencing and rearrangement studies, as described in the relevant sections below.

An extremely effective procedure for preparing total cell DNA is Doyle & Doyle's (1987) modification of the CTAB isolation method of Saghai-Maroof et al. (1984). This method typically yields 20–100 micrograms of high molecular weight DNA from 0.5–2 grams of fresh (or fresh frozen) leaves. We find that higher yields of total cellular DNA are often obtained from species, particularly orchids, with succulent tissues by increasing the CTAB buffer from 2× (Doyle & Doyle, 1987) to 3× concentration. Also, fibrous leaves are often homogenized more efficiently by grinding in liquid nitrogen (either with mortar and pestle or in a coffee mill), followed by addition of CTAB buffer, rather than directly in the buffer. The CTAB method sometimes gives an enrichment of cpDNA (relative to nuclear) if the alcohol-precipitated DNA is spun down rather than spooled out of the aqueous solution. The CTAB method has also proven successful in the extraction of usable DNA from recently dried herbarium specimens (Doyle & Dickson, 1987). A variation on this CTAB procedure was reported by Rogers & Bendich (1985) to give good results with fresh tissues from a wide variety of plants, but to yield only degraded DNA from older herbarium specimens and mummified tissues.

RESTRICTION SITE MAPPING

The cpDNAs of closely related species (from the same or related genera) are most easily compared by examining the pattern of fragments produced upon digestion of the DNAs with restriction endonucleases and subsequent electrophoresis in agarose gels. The restriction fragment phenotypes that are diagnostic for three types of mutations—base substitutions (point mutations), deletions/insertions (length mutations), and inversions—have been described in earlier papers (Upholt, 1977; Palmer et al., 1985; Palmer, 1986a). Point mutations (detected as the gain or loss of restriction enzyme cleavage sites) and length mutations (detected as fragment size differences) are common, whereas inversions are rare. The length mutations detected

FIGURE 2. *Hypervariation in cpDNA resulting from length mutations. DNAs from 1–4 populations of each of four species in the genus* Pisum *(*P. sativum, *lane S;* P. elatius, *lanes E;* P. humile, *lanes H;* P. fulvum, *lanes F) were digested with the restriction enzymes XhoI, and fragments were separated by electrophoresis in a 0.7% agarose gel. Fragments were transferred from the gel to a nitrocellulose filter and hybridized with a ^{32}P-labeled XhoI fragment of 3.2 kb from pea cpDNA. Sizes indicated at left are in kb. Modified from Palmer et al. (1985).*

in restriction enzyme studies usually occur in spacers between genes and pose problems for phylogenetic analysis because they tend to cluster in "hotspot" regions having high levels of variability and because the assignment of exact homology is often difficult (e.g., Fig. 2). In combination, these two factors can result in high degrees of homoplasy (i.e., parallelism and convergence). Therefore, spacer length mutations are usually not included in a formal phylogenetic analysis (Perl-Treves & Galun, 1985; Palmer et al., 1985; Sytsma & Gottlieb, 1986a), although it is critical that they be properly recognized and distinguished from restriction site mutations.

In early studies cpDNA restriction site mutations were inferred indirectly by the inspection of restriction fragment profiles of total, purified cpDNA (e.g., Palmer & Zamir, 1982; Erickson et al., 1983; Clegg et al., 1984). This approach is limited to situations in which 1) cpDNA can be readily prepared (requiring both large amounts of tissue, 10–100 g fresh weight, and amenability of the tissue to cpDNA purification techniques) and 2) levels of base sequence divergence are low enough (less than 0.5–1.0%) to permit the critical interpretation of fragment pattern differences in terms of specific mutations. Currently, most researchers in the field analyze cpDNA variation by a filter hybridization approach, in which cloned fragments of one chloroplast genome are hybridized to filter blots containing digests of all the DNAs under study (e.g., Sytsma & Gottlieb, 1986a, b; Coates & Cullis, 1987; Jansen & Palmer, 1988). The hybridization approach enables the direct ordering, or mapping, of restriction enzyme cleavage sites and permits a more critical analysis of mutations and discrimination between site mutations and length mutations. In addition, it allows one to use total DNA, which offers several advantages over the use of purified cpDNA (see previous section).

The choice of cpDNA clones to use as hybridization probes in mapping studies depends on several factors (reviewed in Palmer, 1986b). "Homologous" clones, i.e., those from one of the taxa under study, give the best results but can be a lot of work to make if not already available. The use of "heterologous" clones requires sufficient conservation of 1) base sequence to ensure a significant level of cross-hybridization and 2) linear arrangement of the chromosome to permit alignment of the cross-hybridizing fragments and interpretation of the hybridization signals. Fortunately, the great majority of cpDNAs are highly conserved in sequence and arrangement (Palmer, 1985b, c; Zurawski & Clegg, 1987), and heterologous probes have been shown to work effectively across subclasses of angiosperms (e.g., Perl-Treves & Galun, 1985; Sytsma & Gottlieb, 1986a). The relevant properties of 15 angiosperm cpDNA clone banks were tabulated in Palmer (1986b). Additional clone banks have been developed for a number of other angiosperms (tobacco, Sugiura et al., 1986; tomato, Phillips, 1985; potato, Heinhorst et al., 1988; soybean, Singh et al., 1984; lettuce, Jansen & Palmer, 1987a; a poplar, *Populus nigra,* R. Smith & K. Sytsma, unpublished data; sorghum, Dang & Pring, 1986; an orchid, *Oncidium excavatum,* M. Chase & J. Palmer, unpublished data), two ferns (Stein et al., 1986; D. Stein, unpublished data), a conifer (C.-H. Tsai & S. Strauss, unpublished data), and the liverwort *Marchantia polymorpha* (Ohyama et al., 1986). Most of these clone banks are freely available for use.

An outline of the approach we currently use for comparative mapping of cpDNA restriction site mutations is as follows: 1) Total DNAs are prepared from 1–2-g leaf samples by the procedure of Doyle & Doyle (1987) or by one of the modifications of this procedure described in the preceding section. 2) The DNAs are digested with each of 10–20 different restriction enzymes that cut the genome 20–100 times. 3) The digests are separated electrophoretically in 1.0% agarose gels in which the bromophenol blue dye marker is run 10 cm. (Most of the details of the electrophoresis and hybridization conditions are given in Palmer, 1986b; plans for the gel rigs we use are available upon request of the senior author.) The use of narrow tooth gel combs permits 35 samples (e.g., 33 plant DNAs and two lanes of size markers) to be run across a 20 cm width corresponding to the width of standard 8″ × 10″ X-ray film. The DNAs are arranged on the gel (or gels) according to presumed relatedness. By running the gels no farther than 10 cm, we accommodate two gel-sized filters (each 20 cm × 12.5 cm), or 66 experimental lanes, on each X-ray film exposure. 4) Two replica filters of each gel are made using the bidirectional blotting procedure of Smith & Summers (1980) as modified for greater sensitivity by the alkaline transfer procedure (Reed & Mann, 1985). We use durable nylon filters (Zetabind; manufactured by AMF Cuno), which in our experience can be readily reused 15 or more times. 5) The two identical sets of 8–12 filters (one filter per enzyme in the case of a 33-DNA study) are hybridized in plastic buckets using the BLOTTO (nonfat dry milk) hybridization buffer of Johnson et al. (1984). Hybridization probes consist of cloned fragments of an appropriate chloroplast genome (see above). Using two probes at a time, and taking a week for each cycle of hybridization and autoradiographic exposure, we require about two to three months to perform the entire set of hybridizations once all the gels have been run and blotted (each hybridization cycle requires only about two person-days of work per week).

The most time-consuming and difficult part of such studies, particularly those in which levels of divergence are on average greater than 1%, can be the interpretation in terms of individual mutations of the fragment pattern differences revealed by the autoradiographs. We recommend the construction of complete restriction site maps for each enzyme for one of the taxa under study. This comprehensive mapping is aided by including on each enzyme gel a double digest of the reference DNA with the enzyme specific to that gel and an enzyme used in common in all the double digests. The double digest hybridizations allow one to place the single enzyme maps in register with one another and thereby to construct a single unified restriction map. Mutations relative to this basic map can then be recognized by comparing the patterns across the autoradiographs and then identifying and localizing on the map fragment changes consistent with the loss/gain of specific cleavage sites (i.e., the presence in one taxon of two adjacent fragments which are replaced in a second taxon by a single fragment equal in size to the two missing ones). Restriction site mutations are studied by grouping the X-ray films by enzyme and "walking" along the chloroplast chromosome from cloned hybridization probe to adjacent probe fragment. Resorting the films according to probe fragment facilitates detection and confirmation of length mutations, as well as the resolution of most ambiguities noted in the first level of analysis.

The phylogenetic analysis of restriction site mutations is easily accomplished within the framework of parsimony-based cladistic analysis. Each site can be treated as a single two-state character, whose polarity can be assessed by outgroup comparisons (Watrous & Wheeler, 1981). Algorithms based on both Wagner parsimony (PAUP, developed by D. Swofford) and Dollo parsimony (PHYLIP, developed by J. Felsenstein) can be employed to analyze cpDNA data. Wagner parsimony gives equal weight to parallel gains and losses, whereas Dollo parsimony prohibits the former class of events. The justification for the use of Dollo parsimony is that parallel site losses are in fact much more probable than parallel site gains (DeBry & Slade, 1985). The bootstrap algorithm of Felsenstein (1985) is useful for evaluating the statistical significance of the monophyletic groups defined by parsimony analysis. The application of parsimony and bootstrap programs to large sets of cpDNA site mutations is best exemplified by the studies of Sytsma & Gottlieb (1986a) and Jansen & Palmer (1988).

DNA SEQUENCING

DNA sequence analysis allows one to compare bases individually and results in much lower levels of homoplasy than site mapping, where changes at any of six positions can cause a site loss. By sequencing a gene, one effectively avoids the problem of length mutations and also gains resolution at greater phylogenetic distance, since many genes are more conserved than the genome as a whole. The trade-off relative to restriction site mapping is that sequencing is currently a significantly slower and more expensive way of gathering phylogenetic information. Therefore, sequencing is presently most appropriate at the family level and above, where restriction site mapping is plagued by excessive homoplasy and length mutation.

No major studies on chloroplast gene sequences and plant phylogeny have been published. However, one chloroplast gene (*rbc*L, encoding the large, catalytic subunit of ribulose-1,5-bisphosphate carboxylase) has, because of its fundamental importance in photosynthesis, been sequenced widely enough to demonstrate the phylogenetic utility of this approach. Members of each of the four angiosperm families for which multiple *rbc*L genes have been sequenced cluster as natural groups, while representatives of three subclasses of dicots group together at an appreciable molecular dis-

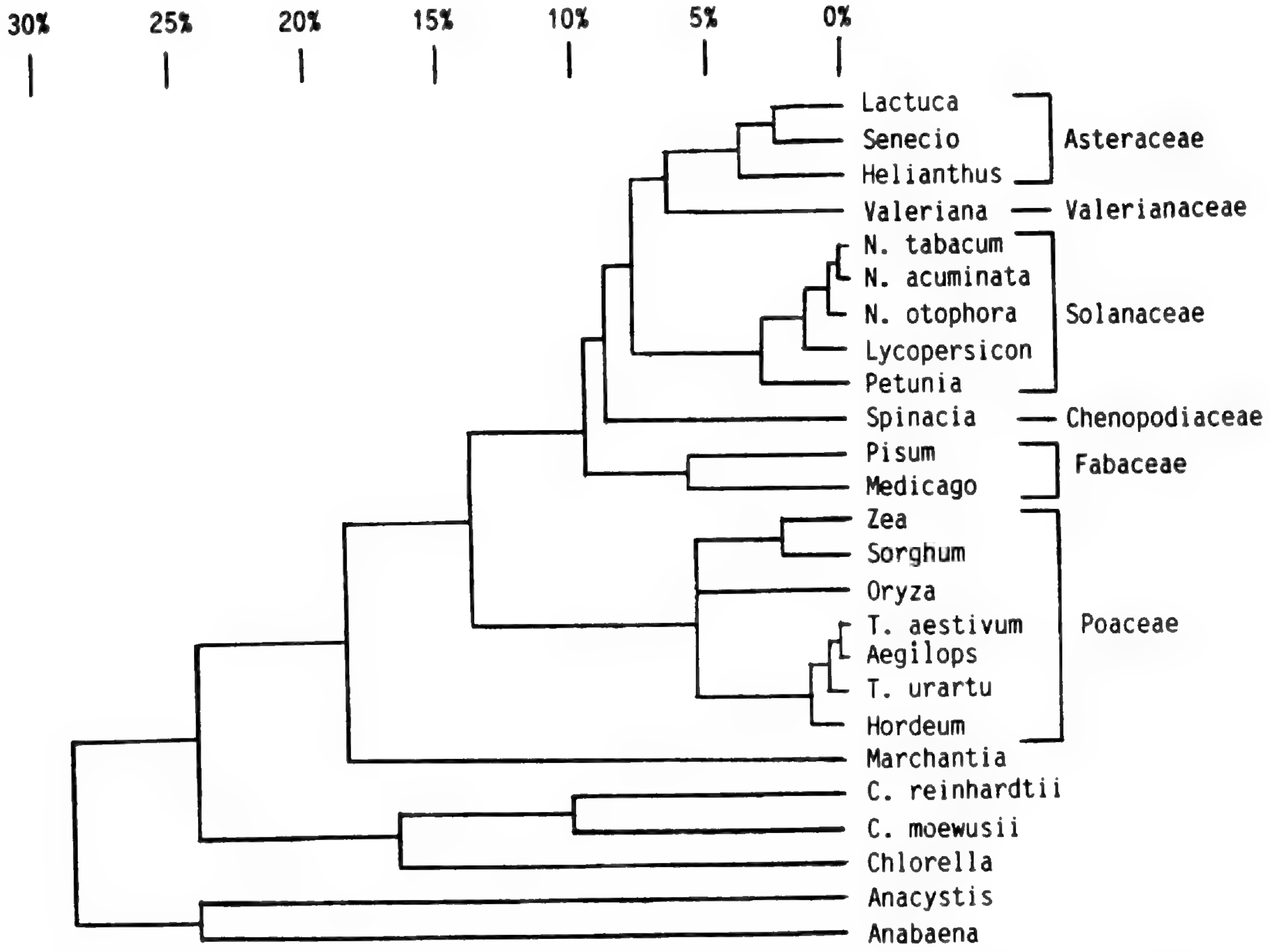


FIGURE 3. *Phenogram of* rbcL *sequence relationships. The diagram is based solely on the percent nucleotide sequence divergence (top scale) between* rbcL *genes of the indicated taxa. No corrections have been applied for multiple substitutions at a position. As yet, no phenetic or cladistic algorithms have been applied to this data set. References for eight of the sequences are given in Ritland & Clegg (1987); the others are* Nicotiana acuminata *and* N. otophora *(Lin et al., 1986)*, Lycopersicon *(W. Gruissem, pers. comm.)*; Petunia *and* Medicago *(Aldrich et al., 1986a, b)*; Lactuca, Senecio, Helianthus, *and* Valeriana *(H. Michaels, R. Jansen & J. Palmer, unpublished data)*; Oryza *(Nishizawa & Hirai, 1987)*; Sorghum *(J. Doebley pers. comm.)*; Aegilops *(Terachi et al., 1987)*; Triticum aestivum *and* T. urartu *(T. Dyer, unpublished data)*; Marchantia *(Ohyama et al., 1986)*; Chlamydomonas moewusii *(Yang et al., 1986); and* Chlorella *(Yoshinaga et al., 1988)*.

tance from the grasses (Fig. 3). A liverwort, three green algae, and two cyanobacteria appear as successive outliers to the angiosperms. With certain minor exceptions, discussed below in "Familial Relationships," all of the relationships expressed in Figure 3 are consistent with widely accepted concepts of plant phylogeny. Such correspondence is encouraging relative to the problematic early history of protein sequencing and plant phylogeny (see introductory paragraphs).

For a variety of reasons, we feel that *rbc*L is the chloroplast gene of choice for examining phylogenetic relationships within vascular plants: 1) The *rbc*L gene is by far the most widely sequenced chloroplast gene. This provides not only a reservoir of data that can be compared with data from future studies but also confidence that the gene is a reliable one for phylogenetic purposes (Fig. 3). 2) A number of plant molecular systematists have started to or are planning on using *rbc*L (we are sequencing *rbc*L in the Asteridae and other subclasses of dicots; M. Clegg, D. Giannasi, D. Soltis, and P. Soltis are conducting a broad survey of *rbc*L in several subclasses of angiosperms; M. Chase in Rosidae and Liliidae; K. Sytsma in Myrtales; R. Jansen in Asteraceae; G. Furnier in gymnosperms). In a few years, accumulated *rbc*L data should permit the construction of a broad framework of phylogenetic relationships among angiosperms and gymnosperms. 3) The *rbc*L gene is large enough (1,431 bp; only eight of the 120 chloroplast genes are significantly larger) to provide a sufficient number of characters (i.e., base pairs) for phylogenetic studies. 4) Its rate of evolution appears appropriate for questions of angiosperm phylogeny, whereas other obvious candidates such as the 16S and 23S ribosomal RNA genes change too slowly (the 16S gene is only 4% divergent between monocots and dicots, compared with 3–6% *rbc*L divergence within each of three angiosperm families in Fig. 3).

Our current *rbc*L sequence studies rely on three technical factors to enable collection of large amounts of sequence data in a rapid and efficient manner. First, rather than screen large shotgun clone banks of total cellular DNA or total cpDNA for *rbc*L-containing clones, we isolate directly a *rbc*L-containing fragment (first identifying it by blot hybridization) from a cpDNA digest separated in a low-melting-temperature agarose gel and then ligate the fragment directly in the melted agarose to a suitable cloning vector. In the case of most taxa examined in the Asteridae and Rosidae, digestion with EcoRI, BamHI, SacI, XhoI, or various double-digest combinations of these enzymes produces a conveniently sized fragment (1.5–5 kb) containing the entire *rbc*L gene. The use of purified cpDNA considerably simplifies this cloning step as compared with total DNA. The second savings results from our use of the plasmid-phage cloning vector BLUESCRIPT M-13 (Strategene Inc.). This allows us to clone the gel-isolated *rbc*L-containing fragment in a double-stranded form and then obtain single-stranded DNA for dideoxy chain termination sequencing without the need for recloning into a single-stranded phage vector. Third, we use synthetic oligonucleotides (20–25 bases in length) complementary to conserved regions of *rbc*L as primers in dideoxy sequencing reactions. These primers were synthesized by G. Zurawski, who generously has made them widely available to molecular systematists. By using synthetic primers of this nature, we avoid perhaps the most time-consuming aspect of sequencing, i.e., preparing multiple subclones from each primary clone.

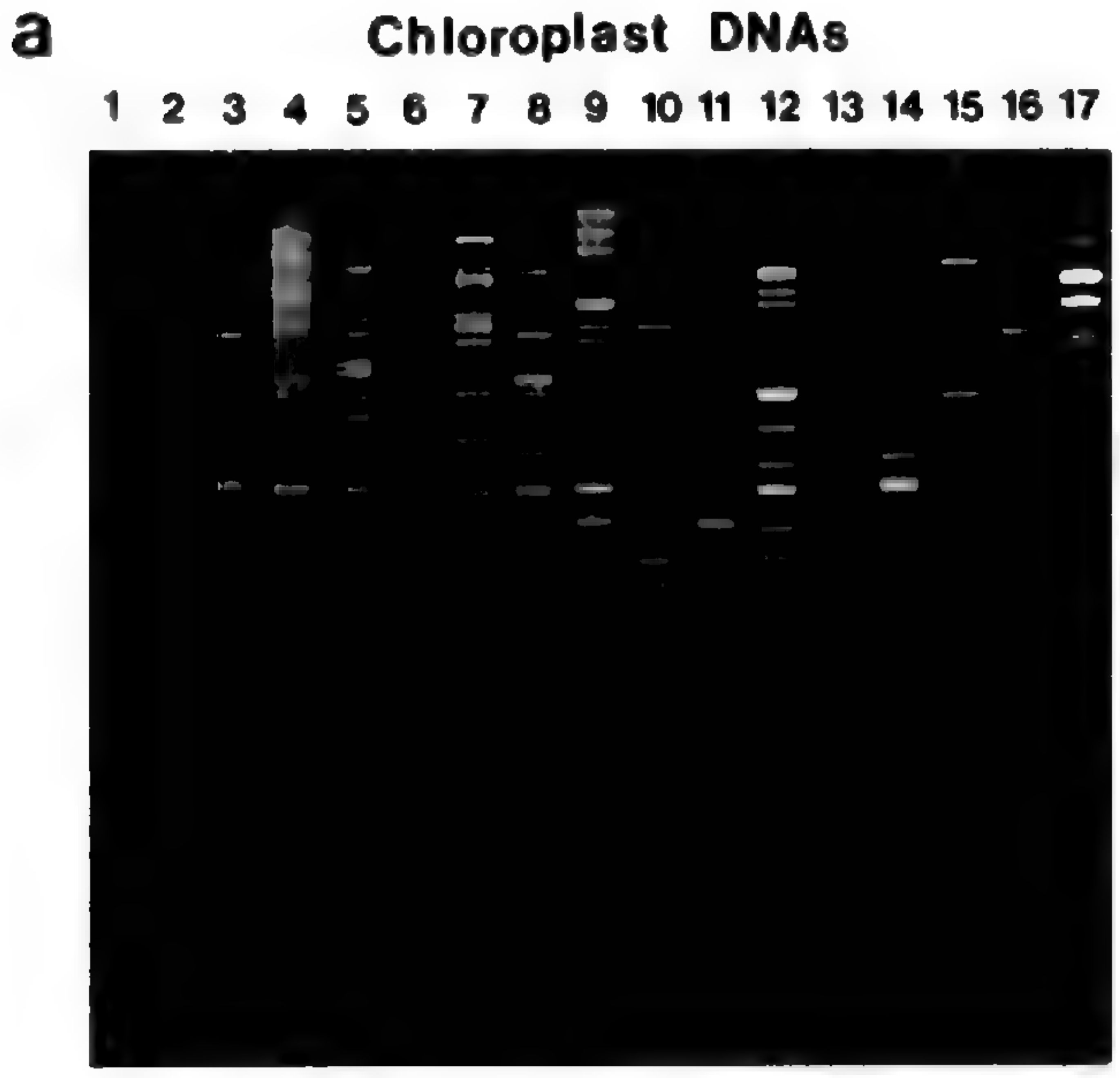
The technology for DNA sequencing is rapidly advancing at present. Significant future savings in time should derive from the use of 1) double-stranded dideoxy sequencing protocols (Korneluk et al., 1985; Zhang et al., 1988); 2) optimized sequencing reactions permitting sequence reading up to 1 kb from a priming site (Johnston-Dow et al., 1987); 3) the polymerase chain reaction to amplify a DNA fragment many thousands of times in vitro, which either facilitates the cloning step or obviates it altogether (Erlich et al., 1988; Oste, 1988); and 4) automated DNA sequencing machines (Connell et al., 1987; Prober et al., 1987).

Once obtained, DNA sequence data are aligned and compared using standard DNA sequence analysis software programs, a large number of which are now commercially available. Cladistic analysis of the sequence data (each nucleotide position is treated as a single four-state character) can be performed using the same parsimony programs and statistical tests as described for restriction site data. In addition, maximum likelihood programs have been developed specifically for nucleotide sequence data (Felsenstein, 1981, 1983), and Nei (1987) reviewed a number of tree-building algorithms that use sequence data.

REARRANGEMENT ANALYSIS

A second class of DNA mutations useful for phylogenetic inference is major rearrangements (the first class being the base substitutions detected by sequencing and site mapping). Major rearrangements are defined here as inversions and deletions/insertions of introns, of the coding region of genes, and of one segment of the large inverted repeat characteristic of most chloroplast genomes. The analysis of major cpDNA rearrangements is in several ways a complementary approach to comparative sequencing for studying higher levels of plant phylogeny. An advantage of sequencing is that large numbers of characters (1,431 in the case of *rbc*L) can be surveyed with reasonably predictable expectations as to the number of differences that will be found (Fig. 3). Many fewer DNA rearrangements can be expected and a preliminary survey is needed to find them. However, once found, they are often easy to survey widely (Fig. 4). The extreme rarity and lack of homoplasy of major rearrangements (Fig. 5) makes each one a signal character in a way that nucleotide substitutions, which inevitably will be afflicted with certain levels of homoplasy, can never be. Each rearrangement is therefore a much more powerful character, one that in our opinion should be weighted much more heavily than a single nucleotide substitution or restriction site mutation. Large amounts of sequence data may not suffice to resolve relatively ancient and compressed evolutionary radiations, whereas each rearrangement generally resolves with confidence a particular branching point in a phylogeny.

The existence of inversions and deletions of the cpDNA inverted repeat has been known for several years (Palmer, 1985c; Palmer et al., 1987). However, it is only with the recent acquisition of the complete sequences of the chloroplast genomes of the angiosperm *Nicotiana tabacum* (Shinozaki et al., 1986) and the liverwort *Marchantia polymorpha* (Ohyama et al., 1986) that it became possible to uncover and exploit significant numbers of the two other major classes of rearrangements,



Lane Number	Species	Family	Subclass
1	Zea mays	Poaceae	Commelinidae
2	Narcissus tazetta	Amaryllidaceae	Liliidae
3	Aristolochia durior	Aristolochiaceae	Magnoliidae
4	Delphinium grandiflorum	Ranunculaceae	Magnoliidae
5	Eschscholtzia californica	Papaveraceae	Magnoliidae
6	Pilea microphylla	Urticaceae	Hamamelidae
7	Spinacia oleracea	Chenopodiaceae	Caryophyllidae
8	Rumex obtusifolius	Polygonaceae	Caryophyllidae
9	Glycine max	Fabaceae	Rosidae
10	Medicago sativa	Fabaceae	Rosidae
11	Trifolium subterraneum	Fabaceae	Rosidae
12	Pisum sativum	Fabaceae	Rosidae
13	Aesculus californica	Hippocastanaceae	Rosidae
14	Pelargonium Xhortorum	Geraniaceae	Rosidae
15	Brassica campestris	Brassicaceae	Dilleniidae
16	Nicotiana tabacum	Solanaceae	Asteridae
17	Lactuca sativa	Asteraceae	Asteridae

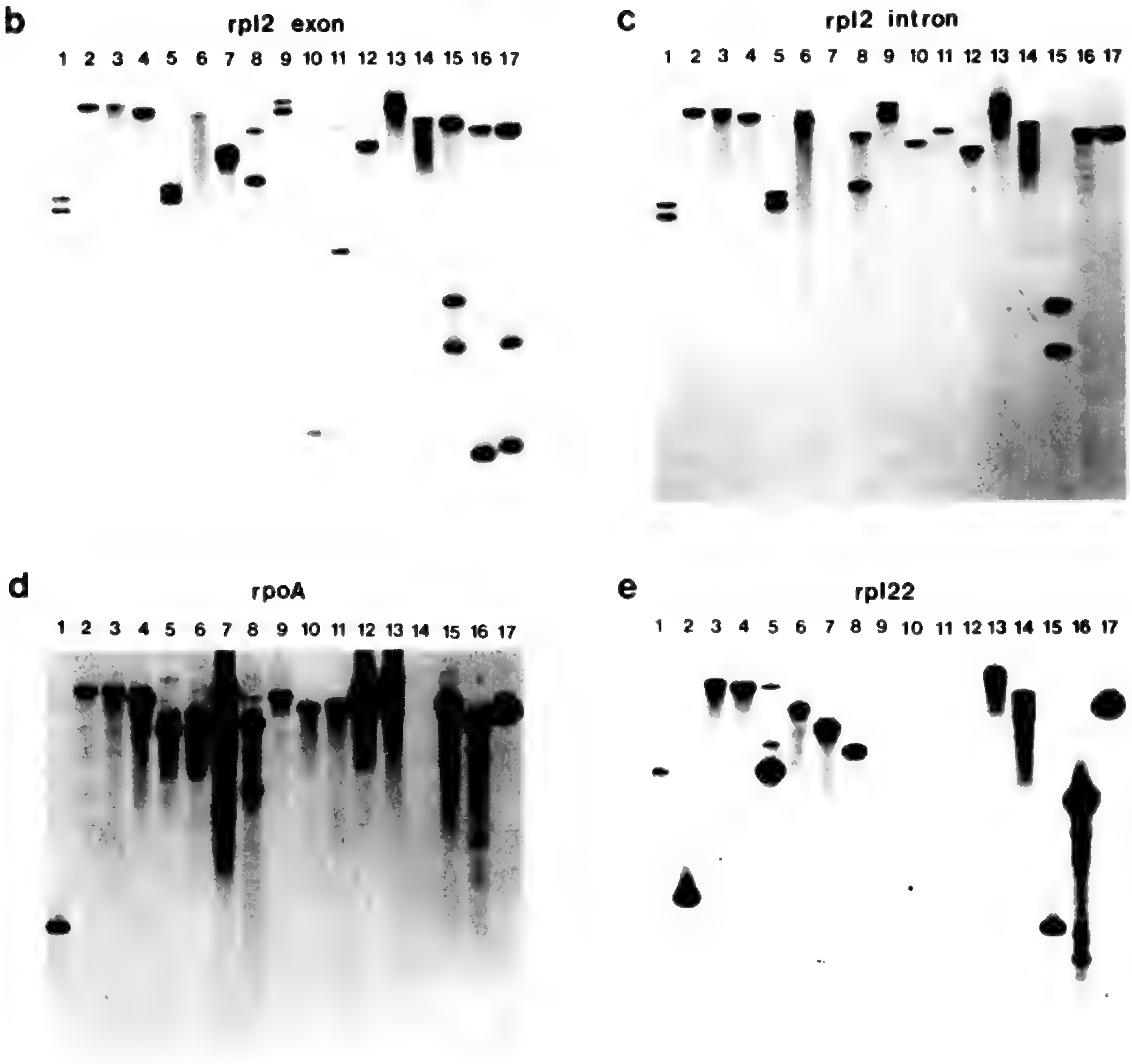


FIGURE 4. *Detection of intron and gene losses during angiosperm cpDNA evolution.—a. Electrophoresis in a 0.9% agarose gel of cpDNA fragments produced by digestion with EcoRI (lanes 1 and 11), SacI-PvuII (lanes 2–6, 8, 9, 13, and 14), SacI-PsstI (lanes 7, 12, and 15), and HindIII (lanes 10, 16, and 17). Two Zetabind filter replicas of the gel were made by bidirectional blotting and then hybridized sequentially with the gene probes indicated in panels b–e.—b. Hybridization with a 772-bp fragment internal to and containing 90% of the coding region of the* rpl2 *gene from spinach.—c. Hybridization with a 545-bp fragment internal to and*

namely gene and intron losses/gains. All four of these rearrangement classes are usually detected by Southern hybridization experiments using defined segments of chloroplast genes as probes. In some cases, follow-up DNA sequencing analysis may be called for if the results of the hybridization experiments are ambiguous.

As illustrated in Figure 4, gene and intron losses/gains are easily detected by a simple presence/absence test. For example, a cloned fragment internal to the intron of the gene *rpl*2 hybridizes to all angiosperm cpDNAs tested except to that of spinach (Fig. 4d). This result and similar hybridizations to other cpDNAs have led to the conclusion that this intron was lost in the common ancestor of the order Caryophyllales (J. Palmer & G. Zurawski, unpublished data). Similarly, hybridization studies reveal that the gene *rpo*A is absent from the chloroplast genome of *Pelargonium* × *hortorum* (Fig. 4d) and all other species of *Pelargonium* (P. Calie & J. Palmer, unpublished data), while the *rpl*22 gene is absent from the chloroplast genomes of all legumes (Fig. 4e; J. Palmer, B. Milligan, J. Doyle, unpublished data). It should be noted that all three of these intron/gene absences have been confirmed by sequencing the region of the suspected absence in at least one of the relevant taxa (Zurawski et al., 1984; B. Milligan, P. Calie, J. Palmer, unpublished data). The "gene losses" should, in the larger biological context, be viewed as "gene transfers," since genes that are missing from the chloroplast genome appear to have been transferred to the nucleus (S. Baldauf, S. Gantt, J. Palmer, unpublished data).

The detection of inversions and inverted repeat loss/gains is somewhat more complicated than for gene or intron loss/gains. Inversions can be diagnosed in two ways. Two nearby fragments in an uninverted genome that have become separated by virtue of inversion will consistently hybridize to different fragments in the inverted genome. Conversely, two fragments that are widely separated in a genome lacking an inversion will each hybridize to the same two fragments in a genome containing a derived inversion, indicating a new linkage relationship (e.g., see figs. 2 and 3 of Jansen & Palmer, 1987a). The presence or absence of the large inverted repeat shown in Figure 1 is diagnosed as follows (Palmer et al., 1987; Lavin et al., 1988). In digests produced by enzymes that cut rarely (10–20 times per genome), short, single copy fragments flanking a deleted repeat will normally hybridize to different fragments in genomes retaining the repeat, but to the same fragment in genomes lacking the repeat. Also, with most rarely cutting enzymes, short fragments near the end of the repeat will hybridize to two fragments in genomes retaining the repeat, but to only one fragment in those lacking it.

In a typical survey for rearrangements, we digest each cpDNA with four enzymes only (compared with the 10–20 used for restriction site studies), each cutting on the order of 40–100 times. This provides resolution sufficient to detect small inversions without unduly increasing the size of the study. In contrast to restriction site studies, where it is most useful to arrange all the digests for a given enzyme on a single gel or set of gels, all four digests for a given DNA are placed together on the same gel. This facilitates rapid diagnosis of rearrangements. Eight DNAs can be analyzed conveniently on a single gel with 35 lanes, including three for size markers. Double-sided blotting (Smith & Summers, 1980) allows one to make two filter replicas for each gel, which then can be probed sequentially over a period of weeks, months, and even years.

For hybridization probes, we use small cloned fragments 0.2–3.0 kb in size that we have prepared from several angiosperm chloroplast genomes (Jansen & Palmer, 1987a). These clones are available upon request of J. Palmer for use in molecular systematic studies. In addition, we currently are making probes specific for many of the genes from the completely sequenced tobacco chloroplast genome (Shinozaki et al., 1986), using a starting set of large cloned fragments provided by M. Sugiura (Sugiura et al., 1986). Smaller probes (0.2–1.0 kb) are most useful as internal, gene- and intron-specific markers to detect gene and intron losses. These smaller probes, plus somewhat larger ones (1–3 kb) containing spacer and tRNA genes, are useful to detect inversions because many cpDNA inversions have their endpoints in tRNA-spacer-rich regions of the genome (Palmer, 1985c; Jansen & Palmer, 1987a).

←

containing 82% of the intron of the rpl2 *gene from tobacco.—d. Hybridization with a 1,040-bp fragment containing 96% of the coding region of the* rpo*A gene from spinach and 78 bp of 5′ noncoding sequence.—e. Hybridization with a 209-bp fragment internal to and containing 45% of the coding region of the* rpl22 *gene from tobacco. Unpublished data of J. Palmer, B. Milligan and P. Calie.*

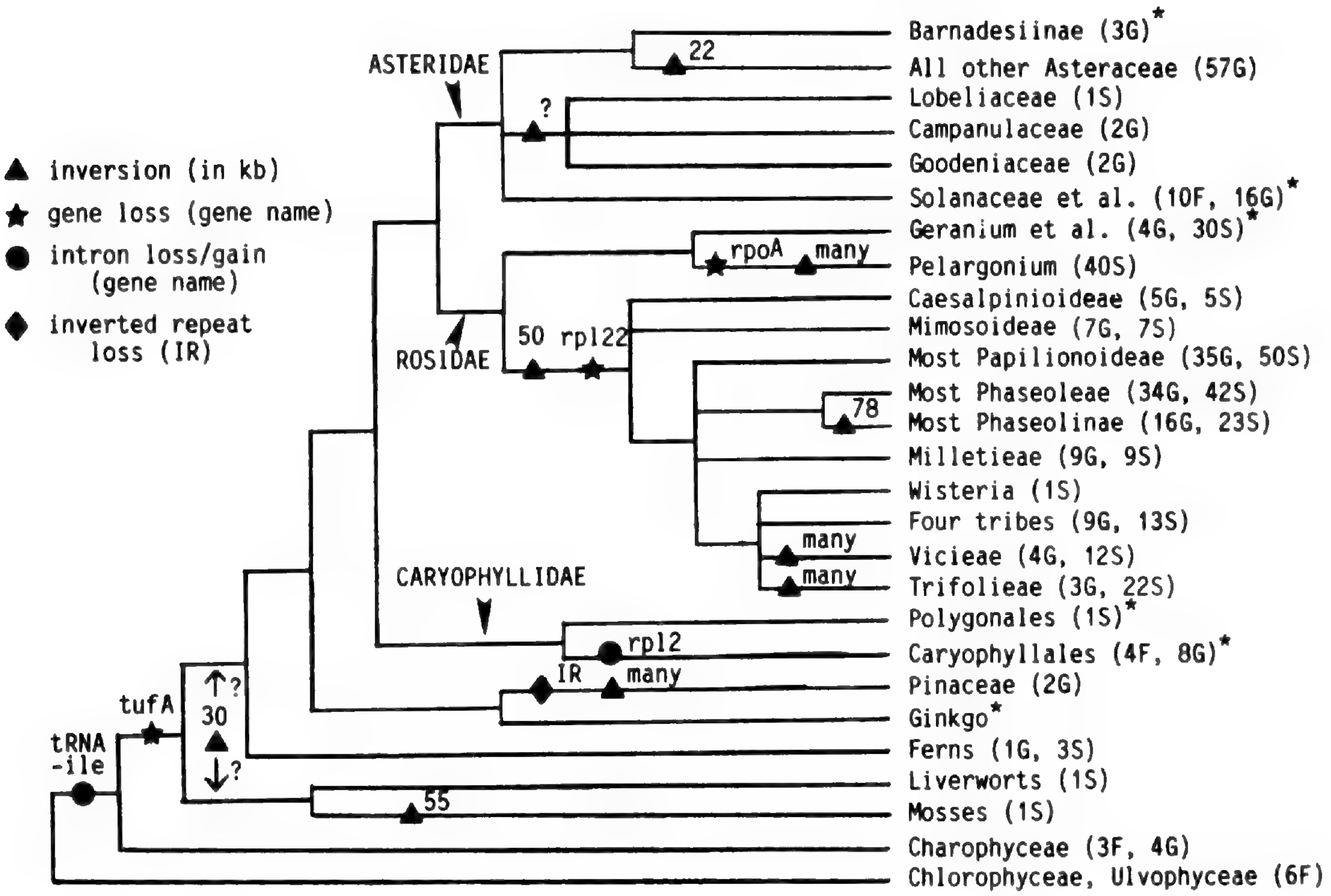


FIGURE 5. *Evolutionary tree based on the distribution of selected cpDNA rearrangements. Not all known rearrangements are shown (see text and Palmer, 1985c, 1987, for more complete listing and for references). Asterisks denote genomes with the consensus vascular plant gene order. Numbers in parentheses indicate numbers of taxa examined (F = family; G = genus; S = species). Question marks denote rearrangements of uncertain nature and/or phylogenetic distribution and direction. Four charophytes have been examined for the* tufA *gene loss, but only one for the tRNA-ile intron gain.*

APPLICATIONS OF CHLOROPLAST DNA DATA TO SYSTEMATIC QUESTIONS

Most cpDNA comparisons have been made within and between congeneric species using the approach of restriction site analysis. The utility of this approach at these levels has already been well documented in a number of papers and reviews (for reviews, see Palmer, 1985a, 1986a, 1987; Giannasi & Crawford, 1986, in press). Consequently, the following discussion will emphasize recent developments and results obtained in studies at higher taxonomic levels.

INTRASPECIFIC RELATIONSHIPS

The ultimate utility of cpDNA as a marker within and among populations of a species remains unclear. Relatively little cpDNA differentiation was obtained in the two most extensive intraspecific studies (of 371 individuals and 147 populations of two pine species (Wagner et al., 1987) and 100 individuals and 21 populations of *Lupinus texensis* (Banks & Birky, 1985)). In a number of more limited studies (reviewed in Palmer, 1987; Giannasi & Crawford, in press), multiple populations from the same species often had indistinguishable cpDNAs. However, when found, intraspecific differences have been quite informative, particularly regarding the origins of several crop plants (Palmer et al., 1983; Clegg et al., 1984; Palmer et al., 1985; Doebley et al., 1987). A recent study demonstrated extensive intraspecific variation within *Heuchera micranthra* sufficient to document multiple origins of autopolyploidy (Soltis et al., in press). In this case, cpDNA variation actually provided greater resolution at the populational level than nuclear isozyme markers.

It is not surprising that intraspecific variation in cpDNA is often limited, given the overall conservatism of the chloroplast molecule (Palmer, 1985b, c; Zurawski & Clegg, 1987). By pushing the molecular approaches to their extreme in terms of the number of nucleotides sampled, it may be possible to address many microevolutionary questions using cpDNA. By using more enzymes, especially ones that cut frequently, the sample size could readily have been increased by a factor of ten or more in many of the studies in which little or no variation was found. It is unlikely, however, that the cpDNA molecule will ever be as useful for populational studies as the rapidly evolving mitochondrial genome of animals (Avise et al., 1987; Moritz et al., 1987), although the *Heuchera* case (Soltis et al., in press) begins to approach the animal mitochondrial situation.

INTERSPECIFIC RELATIONSHIPS

Over 40 studies have now been published in which cpDNA restriction site variation has been used to assess phylogenetic relationships at the interspecific level (many of these are reviewed in Palmer, 1986a; Giannasi & Crawford, 1986, in press), and at least 30 laboratories are now engaged in such pursuits. The molecular phylogenies constructed using cpDNA data have been remarkably untroubled by homoplasy, which ranged from 0% in *Pisum* (Palmer et al., 1985) and *Lisianthius* (Sytsma & Schaal, 1985), to 2.5% in *Lycopersicon-Solanum* (Palmer & Zamir, 1982), 3.3% in *Zea* (Doebley et al., 1987), 3.8% in *Brassica* (Palmer et al., 1983), 4.8% in *Clarkia* sect. *Peripetasma* (Sytsma & Gottlieb, 1986a), and 4.9% in *Cucumis* (Perl-Treves & Galun, 1985). The overall level of homoplasy in these seven studies is 3.9%, i.e., only 12 convergences and parallelisms were necessary to account for the observed distribution of 299 variant cpDNA restriction sites.

To illustrate the kinds of insights cpDNA analysis can provide, we briefly review results obtained in the genus *Brassica*. This is an excellent group to examine in this context for a number of reasons. First, relationships within the genus have already been studied using a wide variety of morphological, genetical, and biochemical approaches (reviewed in Vaughan, 1977; Prakash & Hinata, 1980), and therefore an excellent opportunity exists to evaluate the merits of a cpDNA analysis. Second, *Brassica* features one of the classic cases of a polyploid, hybrid species complex, one that was already well understood at the nuclear level, but where additional, sometimes surprising, findings emerged from the cpDNA analysis. Finally, the *Brassica* work exemplifies the reproducibility of most molecular analyses. Two different groups independently studied cpDNA restriction site variation in *Brassica* (and coincidentally published their results in the same issue of the same journal) and reached largely similar conclusions (Erickson et al., 1983; Palmer et al., 1983).

Figure 6 is a cladogram based on the analysis of cpDNAs from eight species and 21 populations of *Brassica* and *Raphanus sativus* (Palmer et al., 1983). Six of the eight species (those whose genome designations are given in Fig. 6) comprise the three diploids and three tetraploids whose nuclear relationships were first expressed in the famous triangle diagram of U (1935). One unexpected finding is the placement of *Raphanus sativus* (radish) within one of the two major sections of *Brassica*. This placement was first made (Palmer et al., 1983) without the use of an outgroup by invoking the molecular clock assumption (Wilson et al., 1977), which now appears to not hold for cpDNA (see Fig. 8 and "Directions and Prospects") but has since been validated by outgroup comparison (J. Palmer, unpublished data). A similar contrast between molecular and morphological data, suggesting the need for reassessment of generic boundaries, has recently been made in the case of *Clarkia* and the monotypic genus *Heterogaura*. *Heterogaura heterandra* is clearly a derivative of *Clarkia* at the molecular level but features a very divergent morphology from all *Clarkia* species (Sytsma & Gottlieb, 1986b; also see papers in this volume by K. Sytsma & J. Smith and L. Gottlieb).

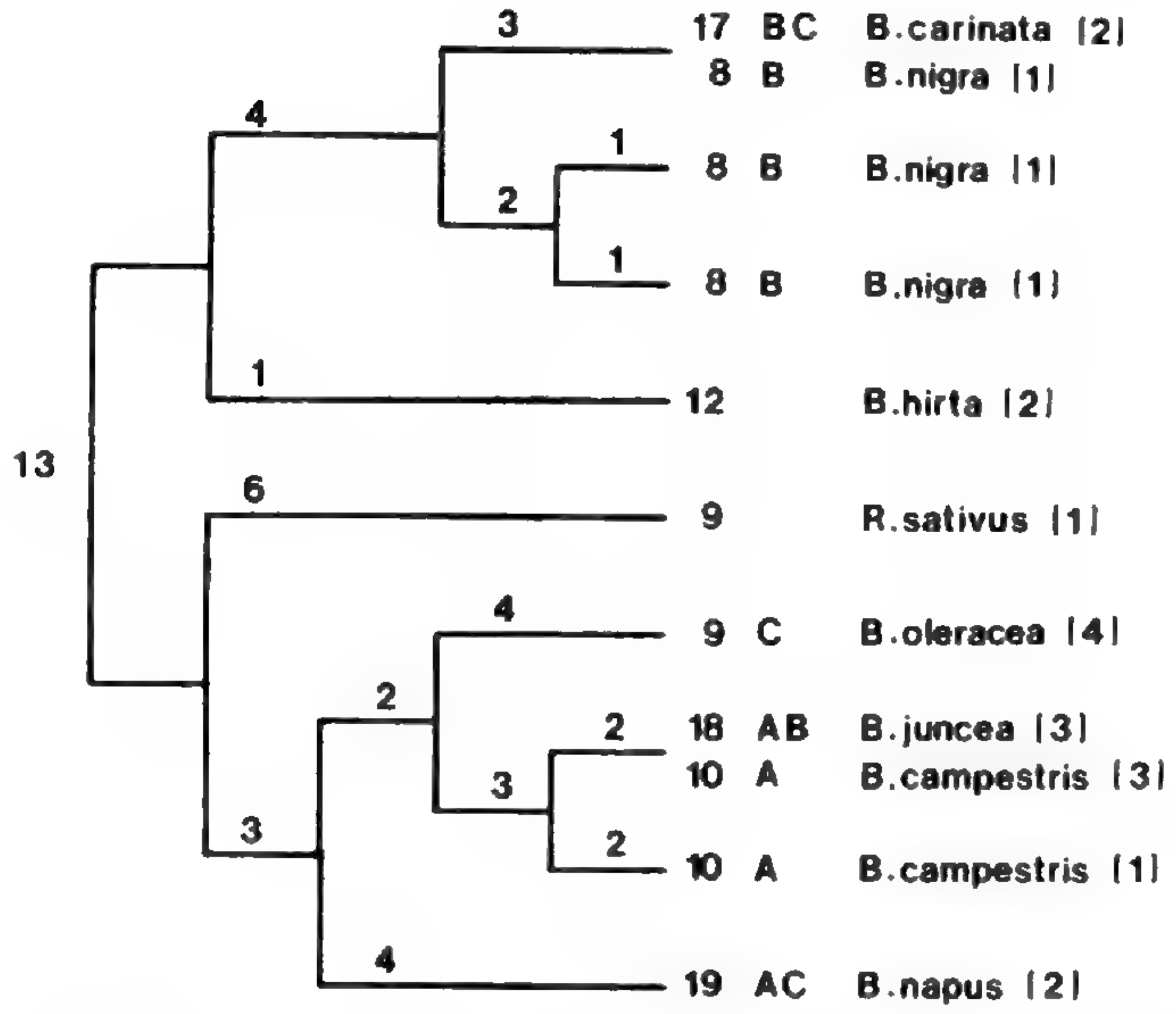


FIGURE 6. *Evolutionary tree of eight cultivated species of* Brassica *and* Raphanus *based on a parsimony analysis of cpDNA restriction site mutations. Numbers on branches indicate number of derived mutations. Numbers at termination of branches indicate nuclear chromosome number, followed by genome designation. Numbers in parentheses indicate number of accessions examined. Redrawn from Palmer et al. (1983).*

Both Erickson et al. (1983) and Palmer et al. (1983) obtained considerable insight into the origins of the amphidiploid species *B. carinata*, *B. juncea*, and *B. napus*. The cpDNAs of *B. carinata* and *B. juncea* were essentially identical to those of the diploids *B. nigra* and *B. campestris*, respectively (Fig. 6). Since cpDNA is maternally inherited in

Brassica (Erickson et al., 1983), one can conclude that these latter two species served as the maternal parents in the interspecific hybridizations that gave rise to the two amphidiploids. By subtraction, *B. oleracea* and *B. nigra* must have served as the paternal parents in these crosses. The cpDNA data permitted two quantitative conclusions regarding the timing of hybridization, although it should be kept in mind that these conclusions rest on an implicit assumption of rate constancy. *Brassica carinata* and *B. juncea* were judged to result from recent hybridization events since their cpDNAs were identical at all 3,000 base pairs compared with those of specific parental lines (Fig. 6; Palmer et al., 1983). However, these recent hybridizations must have taken place after a substantial period of separation and diversification of the parents, since the two pairs of parental cpDNAs were substantially diverged (29–30 mutations distinguish the *B. nigra* genome from those of *B. oleracea* and *B. campestris*; Fig. 6).

Surprisingly, the chloroplast genome of the third amphidiploid, *B. napus*, is less closely related to those of its uncontested nuclear parents, *B. campestris* and *B. oleracea*, than they are to each other (Fig. 6). To resolve this conflict between nuclear and cytoplasmic phylogenies, Palmer et al. (1983) hypothesized that *B. napus* gained its cytoplasm by introgression from some unidentified species. In contrast, in *Helianthus* concordant results obtained using both cpDNA and nuclear DNA do not support a morphologically based hypothesis of introgression (Rieseberg et al., 1988).

FAMILIAL RELATIONSHIPS

A great challenge to plant sytematists is to reconstruct phylogeny among genera and at higher levels, where relationships are in general much more poorly understood than among congeneric species. Although little has yet been published on higher level cpDNA systematics, results are encouraging from several studies in progress, and therefore we feel it important to discuss these in some detail. In addition, the reader should consult the article in this volume by Sytsma & Smith, which discusses their ongoing work on the Onagraceae (also see Sytsma & Gottlieb, 1986a, b).

Asteraceae. The Asteraceae make up one of the largest and most successful flowering plant families, consisting of 12–17 tribes, approximately 1,100 genera, and 20,000 species (Cronquist, 1981). A combination of specialized floral characters (capitula, reduced and modified floral parts, inferior ovaries, basal and erect ovules, and syngenesious anthers) support the monophyly of the family. Recent classifications (Thorne, 1983; Dahlgren, 1980; Takhtajan, 1980; Cronquist, 1981) emphasized the distinctness of the family by placing it in a monotypic order at the most advanced position in the Dicotyledonae. Although there is some controversy concerning the age of the family (Turner, 1977), fossil evidence (Cronquist, 1977; Muller, 1981) and biogeographical considerations (Raven & Axelrod, 1974) suggest that the Asteraceae originated in the middle to upper Oligocene (30 million years ago) and subsequently underwent rapid and extensive diversification.

During the past 30 years, six different schemes of phylogenetic relationships among the subfamilies and tribes have been proposed (Cronquist, 1955, 1977; Carlquist, 1976; Wagenitz, 1976; Jeffrey, 1978; Thorne, 1983; Bremer, 1987). Most of these recent classifications agree that two distinct subfamilies (Asteroideae and Cichorioideae) should be recognized; however, there is no consensus concerning the circumscription of the subfamilies, the number of monophyletic tribes, and the relationships among tribes. Two reasons account for the lack of agreement on intrafamilial relationships in the Asteraceae. First, previous studies have relied almost completely on morphological characters, which have undergone repeated parallel and convergent evolution. Second, only the most recent reassessment of relationships (Bremer, 1987) has applied cladistic approaches to phylogenetic reconstruction, and even that study is limited by high levels of homoplasy and a lack of statistical testing of alternative trees.

To provide new characters to aid in clarifying relationships in this complex family, we have analyzed cpDNA variation within the Asteraceae and putatively related families. We have completed studies using two approaches to the study of cpDNA evolution, the assessment of genome arrangement and comparative restriction site mapping, and recently initiated a comparative study of *rbc*L sequences.

Our studies have revealed two genome arrangements in the Asteraceae that differ by a single inversion (Jansen & Palmer, 1987a, b). Chloroplast DNAs from the subtribe Barnadesiinae (tribe Mutisieae) are colinear with those of most other land plants, including ten families putatively related to the Asteraceae. All other Asteraceae examined (57 genera from 16 tribes) share a derived 22-kb inversion. This rearrangement defines a basal evolutionary dichotomy within the family and has two important phylogenetic implications. First, the Mutisieae are paraphyletic, as previously hypothesized on the basis of morphological evidence (Small, 1918; Wodehouse, 1928; Cabrera, 1977; Bremer, 1987). Second, the Barnadesiinae represent the sister group to the rest of the family, which resolves one of the most controversial systematic issues within the Asteraceae. Five different tribes—Cardueae, Heliantheae, Mutisieae, Senecioneae, and Vernonieae—have previously been suggested as the most primitive lineage (Cronquist, 1955, 1977; Carlquist, 1976; Wagenitz, 1976; Jeffrey, 1977). The identification of the earliest lineage provides indirect support for previous hypotheses concerning the origin of the Asteraceae in the Andes of northern South America (Raven & Axelrod, 1974; Turner, 1977) and the primitive woody habit and bilabiate flowers of the ancestors of the family (Carlquist, 1976; Jeffrey, 1977).

Our restriction mapping study has been carried out in two stages. We first examined taxa primarily from the tribe Mutisieae (Jansen & Palmer, 1988) and then studied representatives of the entire family (R. Jansen, H. Michaels, J. Palmer, unpublished data). Initially, cpDNAs from 13 genera of the Mutisieae, one genus from each of three other tribes, and two genera from two outgroup families were analyzed with ten restriction enzymes. A total of 211 restriction site mutations were detected, 55 of which were phylogenetically informative. Wagner and Dollo parsimony trees constructed with these data were very similar; only the Wagner tree is discussed here. The Wagner parsimony analysis resulted in a single most parsimonious tree (Fig. 7, top) with 247 steps and 15% homoplasy. Four major phylogenetic relationships are depicted in this tree. The most significant is the initial dichotomy separating the subtribe Barnadesiinae (Mutisieae) from the rest of the Asteraceae, including the three other subtribes of the Mutisieae. This is the same dichotomy defined by the inversion described above. The robustness of this initial dichotomy has strong statistical support (98% confidence interval) by the bootstrap analysis of Felsenstein (1985). Furthermore, a recent cladistic analysis (Bremer, 1987) based primarily on morphological data, but also including the 22-kb cpDNA inversion (Jansen & Palmer, 1987b), placed the Barnadesiinae at a basal position within the Asteraceae. Also in accord with the inversion result, the restriction site data indicate the Mutisieae as paraphyletic, since three of the four subtribes are more closely related to the three other examined tribes of the Asteraceae than to subtribe Barnadesiinae. The molecular phylogeny (Fig. 7, top) also provides support for the monophyly of three of the four currently recognized subtribes of the Mutisieae (sensu Cabrera, 1977). Only the morphologically diverse and geographically widespread subtribe Gochnatiinae is shown to be paraphyletic, a conclusion also reached by Bremer (1987).

To clarify further relationships within the Mutisieae, a more extensive analysis was performed in which 12 of the 16 genera of Asteraceae examined above were analyzed using 19 restriction enzymes (Jansen & Palmer, 1988). A total of 390 restriction site mutations were detected, 117 of which were phylogenetically informative. Wagner and Dollo parsimony analyses again gave similar results. The Wagner analysis (Fig. 7, bottom) resulted in a single most parsimonious tree of 454 steps and 14% homoplasy. The tree provides further support for the relationships indicated by the ten-enzyme tree (Fig. 7, top). This is reflected in the higher confidence intervals for a number of monophyletic groups, including all taxa that share the cpDNA inversion, the three subtribes of the Mutisieae with the inversion, and the subtribes Mutisiinae and Nassauviinae. The 19-enzyme tree also indicates that subtribe Gochnatiinae is paraphyletic.

More detailed phylogenetic comparisons were performed using 11 enzymes and 57 genera of the Asteraceae, representing all currently recognized tribes. A total of 926 restriction site mutations were mapped, 328 of which were phylogenetically informative. Wagner parsimony analyses using the global swapping option of PAUP generated 12 equally parsimonious trees of 1,315 steps, all of which support the monophyly of the subfamily Asteroideae (sensu Thorne, 1983). Phylogenetic analyses of the data using the same options in PHYLIP gave six equally parsimonious trees of 1,316 steps, all of which support two monophyletic subfamilies (Asteroideae and Cichorioideae sensu Thorne, 1983). A bootstrap analysis (Felsenstein, 1985) produced a majority rule consensus tree (Fig. 8) with 1,318 steps and 30% homoplasy. Although this tree is three steps longer than the most parsimonious tree, it is presented here because it shows the groups that are best supported statistically.

The most significant implications of the cpDNA phylogeny for the Asteraceae (Fig. 8) concern the circumscription of tribes and subfamilies and phylogenetic relationships among tribes. There is strong support for the monophyly of the subfamily Asteroideae, which includes the eight tribes Tageteae, Heliantheae, Eupatorieae, Calenduleae, Senecioneae, Inuleae, Anthemideae, and Astereae. This group occurs in all most parsimonious trees generated by both PAUP and PHYLIP and has a confidence interval of 86%. The remaining tribes

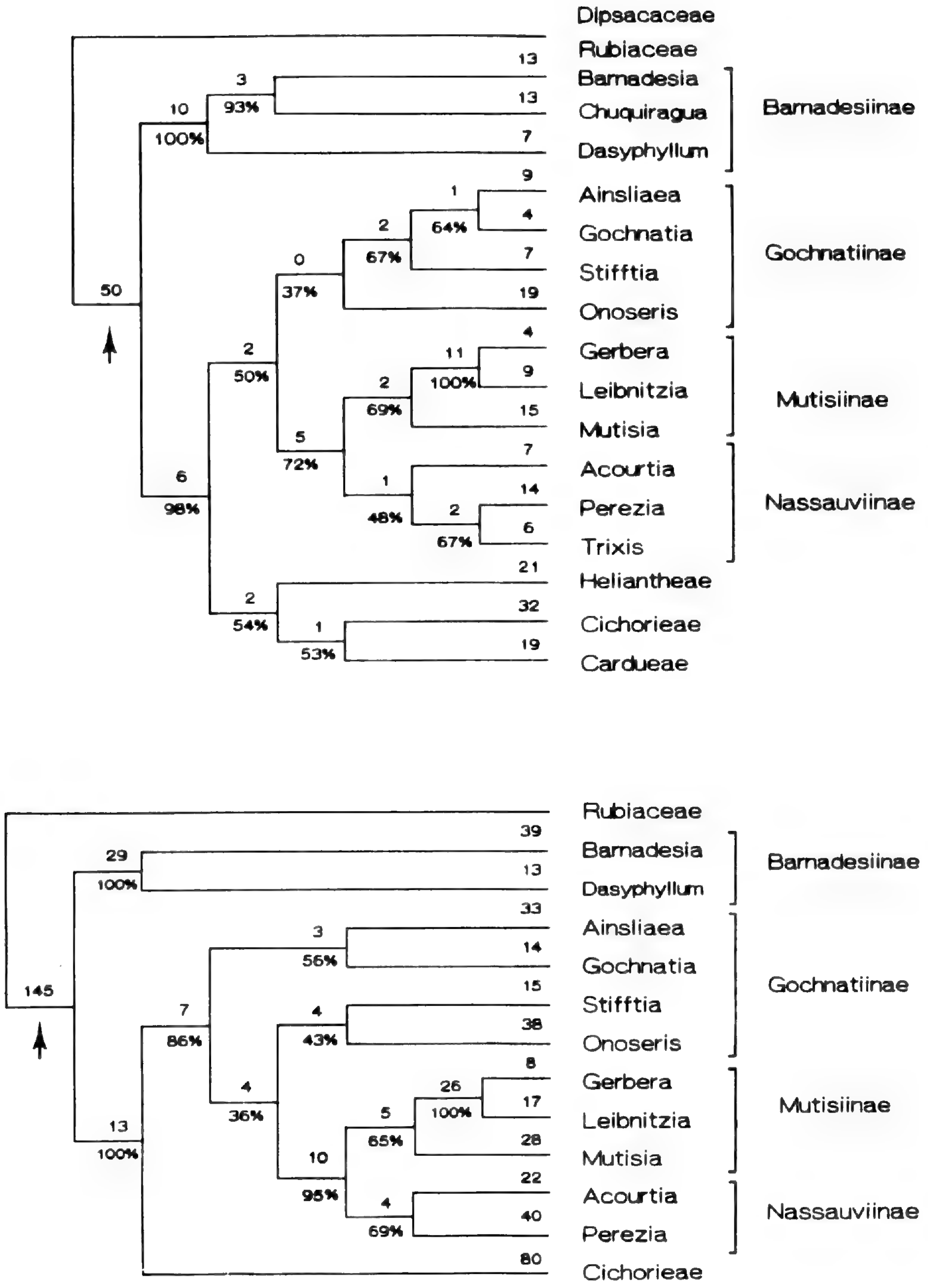


FIGURE 7. *Wagner parsimony trees of genera in the Mutisieae and other Asteraceae. The numbers at each node and along each lineage indicate the number of site mutations. The percentages indicate the number of times that a monophyletic group occurred in 100 bootstrap samples (Felsenstein, 1985). The arrows indicate the occurrence of a 22-kb cpDNA inversion (Jansen & Palmer, 1987b). A single species was examined from each genus, which are as shown for the Mutisieae, and for the other taxa are: Dipsacaceae,* Cephalaria *and* Dipsacus; *Rubiaceae,* Pentas *and* Psychotria; *Heliantheae,* Helianthus; *Cichorieae,* Lactuca; *Cardueae,* Carthamnus. *(Top) Single most parsimonious tree for 16 species of Asteraceae using 211 cpDNA restriction site mutations identified with 10 enzymes. The tree has 247 steps and 15% homoplasy, including 27 parallel losses, two parallel gains, five gains/losses, and two losses/gains. (Bottom) Single most parsimonious tree for 12 species of Asteraceae using 390 cpDNA restriction site mutations identified with 19 enzymes. The tree has 454 steps and 14% homoplasy, including 41 parallel losses, six parallel gains, nine gains/losses, and eight losses/gains. Reprinted with permission from Jansen & Palmer (1988).*

form a paraphyletic group, indicating that the Cichorioideae as circumscribed by most recent workers (Carlquist, 1976; Wagenitz, 1976; Jeffrey, 1978; Thorne, 1983) may not be a strictly natural group. This conclusion is consistent with the recent morphologically based cladistic study of Bremer (1987). The molecular phylogeny indicates that 11 of 14 currently recognized tribes are monophyletic, with the Heliantheae, Mutisieae, and Tageteae being paraphyletic. The cpDNA data (Fig. 8) reveal that the Liabeae and Vernonieae are monophyletic, in agreement with the finding of Bremer (1987). Relationships among the eight tribes in subfamily Asteroideae are clearly resolved in some instances. The previously recognized tribes Cotuleae and Ursinieae (sensu Jeffrey, 1978; Robinson & Brettell, 1973) are closely allied to the Anthemideae, which agrees with their placement in this tribe by Bremer & Humphries (in press). The Tageteae are paraphyletic with respect to the Heliantheae and both tribes are paraphyletic with respect to the Eupatorieae. The very close relationship between the Eupatorieae and Heliantheae does not agree with Bremer's (1987) placement of the former tribe close to the Astereae. Except for the close relationship of the Calenduleae and Senecioneae, there is little resolution of tribal affinities for the remaining members of the Asteroideae. Further phylogenetic analyses using Dollo parsimony and a careful reassessment of character homology are under way to resolve more fully the relatedness of these tribes. For example, an analysis in which statistical approaches were used to eliminate the six most homoplasious characters produced a single most parsimonious tree which again strongly supported the Asteroideae as monophyletic but also weakly supported the monophyly of the Cichorioideae.

The substitution rate in cpDNA (as measured indirectly by the number of restriction site mutations) is markedly faster in the derived subfamily Asteroideae than in the basal, paraphyletic Cichorioideae (Fig. 8). At the extremes, tracing back to the node defined by the 22-kb inversion, only 14 site mutations are derived in the lineage leading to *Stifftia* (Gochnatiinae), compared with 116 in *Santolina* (Anthemideae). This greater than eight-fold discrepancy is not in accord with the molecular clock hypothesis (Wilson et al., 1977) but is consistent with recent findings of rate inequities in the evolution of nuclear DNA (Britten, 1986) and mitochondrial DNA (Wolfe et al., 1987; Palmer & Herbon, in press).

The existence of significant rate differences in cpDNA evolution within the Asteraceae means that a phenetic (distance) analysis may produce a tree that conflicts substantially with the true phylogeny, particularly if the proper algorithm is not used (Nei, 1987). Many lineages within the Asteroideae are phenetically more closely related to members of the Cichorioideae than to other members of the Asteroideae. Such a relationship is also apparent upon a phenetic analysis of the limited *rbc*L sequences (only three) for the Asteraceae (Fig. 3), which shows *Helianthus* (Asteroideae) as an outlier with respect to *Lactuca* (Cichorioideae) and *Senecio* (Asteroideae). This phenetic analysis of sequence data (Fig. 3) is at odds with cladistic analyses of both the same data (H. Michaels, R. Jansen, J. Palmer, unpublished) and also restriction site data (Fig. 8; note the high confidence interval, 86%, of the Asteroideae lineage).

Orchidaceae. The focus of our molecular studies in the Orchidaceae has been the neotropical orchid subtribe Oncidiinae. This large subtribe (1,500 species; 75 genera) is one of the most diverse orchid subtribes in terms of floral and vegetative morphology and chromosome number and has long been viewed as "natural" and isolated relative to other orchid subtribes in the New World. The taxonomic circumscriptions of the two largest genera, *Oncidium* (450 species) and *Odontoglossum* (250 species), have been considered problematic since the 1840s. We hoped that a cpDNA-based study of phylogenetic relationships among the groupings identified as natural units (genera and various subgeneric categories) would aid in taxonomic realignment. We (M. Chase & J. Palmer, unpublished) used ten restriction enzymes to analyze cpDNA variation in 99 species that represent most of the currently recognized generic and subgeneric groupings in the Oncidiinae and an additional 33 species from other subtribes in the Epidendroideae sensu lato.

One problem we hoped to address with a phylogeny reconstructed from molecular data was the evolution of chromosome number in the Oncidiinae, which ranges from $n = 5$–30 among species that are not obvious polyploids. Prior hypotheses postulated that this range results from hybridization among species of lower numbers followed by episodes of chromosome doubling (Garay, 1963; Charanasri & Kamemoto, 1975). Chase (1986) studied morphological trends and concluded that hybridization and polyploidy were not involved and that taxa with lower numbers were the results of several independent lineages experiencing reduction from primitively high numbers. The number of loci coding for soluble enzymes was found to be

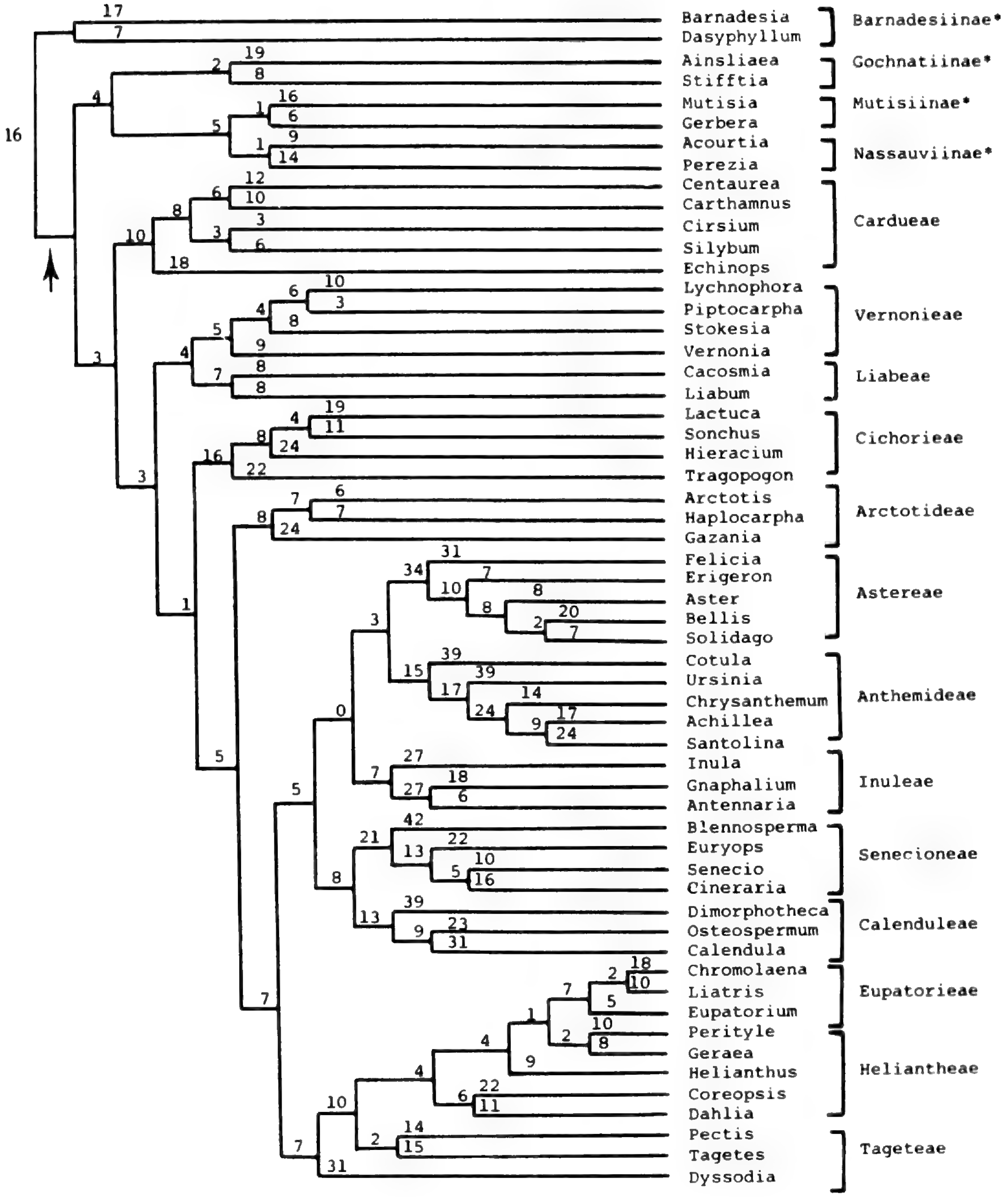


FIGURE 8. *Molecular phylogeny of the Asteraceae. Shown is a majority rule consensus tree generated by the bootstrap option of PHYLIP using 926 restriction site mutations. The numbers at each node and along each lineage indicate the number of restriction site mutations. The tree has a total of 1,318 steps and 30% homoplasy and is rooted relative to the Barnadesiinae. Brackets show the current circumscription of 13 of the tribes, while the four subtribes of the Mutisieae are indicated with asterisks. The arrow indicates the occurrence of a 22-kb cpDNA inversion (Jansen & Palmer, 1987b). Unpublished data of R. Jansen, H. Michaels, and J. Palmer.*

the same among species exhibiting the complete range of chromosome number (Chase & Olmstead, 1988), making allopolyploidy an unlikely explanation to account for these differences. The cpDNA phylogeny (M. Chase & J. Palmer, unpublished) strongly supports the idea that members of several lineages have undergone parallel reduction in chromosome number.

The traditional idea that the Oncidiinae comprise an isolated subtribe was shown by a study of seed morphology (Chase & Pippen, in press) to be fallacious (i.e., a number of other subtribes have the same seed morphology). The molecular phylogeny has identified as close relatives many of the same subtribes as did the study of seed morphology. Among these other subtribes are the Bifrenariinae, Lycastinae, Maxillariinae, Xylobiinae, and, in particular, the Lockhartiinae and Ornithocephalinae. Most systems of orchid classification have used pollinium number to place all but the Lockhartiinae in another tribe from that of the Oncidiinae. Pollinium number appears not to be a reliable indicator of relationships in these orchids (Chase & Pippen, in press; M. Chase & J. Palmer, unpublished).

The cpDNA phylogeny is concordant with the evidence from morphology that *Oncidium* and *Odontoglossum* are not monophyletic genera. *Oncidium* in particular is paraphyletic rather than a genus held together by synapomorphies. The morphologically distinct derivatives of this assemblage have been recognized as different genera. The apparent phylogenetic radiation that produced this large species complex has a strong geographic component. Members of several sections of *Oncidium* endemic to the mountains of southeastern Brazil are more closely related to genera, such as *Gomesa*, endemic to this same region, than to morphologically similar sections of *Oncidium* from other geographical areas.

We failed to find cpDNA mutations that could establish relationships among several well-defined (both by molecular and morphological data) lineages of the Oncidiinae. One explanation for this result is a slowed rate of molecular change during the period when these lineages arose. This explanation also requires a corresponding decrease in the rate of morphological change followed by increases in molecular and morphological rates during subsequent evolution in several now-separate lineages. A more likely explanation we feel is that a large number of lineages diverged in a short period of evolutionary time from a polymorphic ancestral stock. This process must have happened so rapidly that either no mutations exist at this level or the few mutations that do exist convey conflicting ideas of relationships because of homoplasy. The implications of such a phylogenetic radiation are significant in evolutionary and taxonomic terms. Radiations of this type have long been suspected to be responsible for the large numbers of closely related, taxonomically difficult species and genera found in most large families of vascular plants, but this is the first time molecular evidence documenting such a phenomenon has been uncovered (for a similar case in *Clarkia*, see symposium paper by K. Sytsma in this volume).

Fabaceae. Chloroplast DNA variation has been used to explore interspecific relationships in several legume genera (reviewed in Doyle, 1987), and studies using restriction site mapping are currently in progress to address relationships in several tribes of legumes (J. Doyle, pers. comm.). However, the high level of cpDNA sequence divergence in certain legumes (Palmer & Thompson, 1982) suggests that such efforts would be largely fruitless in these groups. Several cpDNA rearrangements have been well characterized in legumes and appear to be useful phylogenetically.

Two rearrangements, a 50-kb inversion and the loss of the *rpl*22 gene from the chloroplast genome (and its concomitant transfer to the nucleus), are shared by all members examined of the three subfamilies of legumes (Figs. 4, 5; Palmer et al., 1987; J. Palmer & J. Doyle, unpublished data). These two events may constitute legume-specific markers, as they are absent from the cpDNAs of such putatively related families as Rosaceae and Sapindaceae. However, other close relatives, such as the Connaraceae and Chrysobalanaceae, remain to be examined.

A 78-kb inversion that includes most of the large single copy region of the chloroplast genome (Palmer et al., in press) has been surveyed in 50 genera of papilionoid legumes, principally in the tribe Phaseoleae (Bruneau et al., 1988). This inversion is shared by all members examined of the subtribe Phaseolinae sensu Lackey (1981), and its distribution also helps elucidate the placement of several problematic genera. For example, *Clitoria* and *Centrosema* lack the inversion and therefore ought to be excluded from a narrowly defined Phaseolinae for which this character is a synapomorphy. In contrast, *Macrotyloma*, whose subtribal placement has been disputed, has the inversion and on this basis is best placed in the Phaseolinae.

The most intriguing legume rearrangment, both from the standpoint of cpDNA evolution and legume phylogeny, is the loss of the large cpDNA inverted repeat. This inverted duplication, which typically is on the order of 25 kb in size (Fig. 1), is a hallmark of land plant cpDNAs (reviewed in Palmer, 1985b, c). The repeat structure has been lost (one of the two repeat elements has been deleted, without the loss of genetic information) only twice among all of the nearly 1,000 species of land plants whose cpDNAs have been investigated. One of these absences characterizes at least two genera of Pinaceae (Fig. 5; Strauss et al., 1988) and the other several tribes of legumes (Palmer et al., 1987).

A total of 136 species of legumes have now been surveyed for the presence of the inverted repeat, including 124 species representing 76 genera and 24 of the 30 tribes of subfamily Papilionoideae (Lavin et al., 1988). The inverted repeat is present in most legumes, including members of all three subfamilies and a taxonomically diverse group of papilionoid tribes (Fig. 5). It is absent in all members examined from the Galegeae, Vicieae, Cicereae, Trifolieae, Carmichaelieae, and Hedysareae, a group of temperate herbaceous papilionoid tribes characterized by a combination of features, such as reduction or loss of the pulvinus and a base chromosome number of $n = 7$ or 8. In this respect our results are consistent with phylogenetic hypotheses based on traditional characters. However, two areas of apparent disagreement exist. First, *Wisteria* is the only member of the tropical tribe Milletieae that lacks the inverted repeat. *Wisteria* is also unusual within the Milletieae in its entirely temperate distribution and its base chromosome number of $n = 8$, both characters that link it with the Galegeae, which also lack the inverted repeat. Secondly, Loteae and Coronilleae, which have the inverted repeat, are commonly grouped on the basis of morphology with temperate herbaceous tribes that lack it. The distinction between these two groups of tribes is, however, also supported by some nonmolecular characters, such as root nodule morphology.

Circumstantial evidence and theoretical speculation suggest that the absence of the inverted repeat leads to an unstable chloroplast genome prone to more frequent rearrangement (Palmer & Thompson, 1982; Palmer, 1985b; Strauss et al., 1988). In some legumes, other factors, such as the presence of large dispersed repeats, also contribute to an unstable, actively rearranging chloroplast genome (Palmer et al., 1987). This acceleration in rearrangement rate can be dramatic; for example, genomes in *Pisum* and *Trifolium* differ from those of other genera in the same tribes by eight or more inversions (Fig. 5). Contrast this with the colinearity of cpDNAs of major groups of vascular plants (Fig. 1; Palmer & Stein, 1986) and with the single inversion that distinguishes cpDNAs of vascular plants and some bryophytes (Fig. 5). While interesting from the standpoint of mechanisms of molecular evolution, extensive rearrangement makes it impossible to align much or all the chloroplast chromosomes of different taxa, thus largely precluding comparative cleavage site analysis. In addition, the use of the rearrangements as characters is usually not justified owing to the enormous amount of work required to define each rearrangement as an individual, polarizable mutation.

Solanaceae. The chloroplast genomes of species in the Solanaceae are among the best known at the molecular level thanks to the complete sequencing of cpDNA from tobacco (*Nicotiana tabacum*; Shinozaki et al., 1986). A number of studies have utilized cpDNA restriction fragment variation to examine interspecific relationships in *Lycopersicon*, *Solanum*, and *Nicotiana* (Palmer & Zamir, 1982; Hosaka, 1986, and references therein), but none have addressed higher level issues in the family. The limited divergence observed in *rbc*L sequences of three disparate genera of Solanaceae bodes well for such an approach (Fig. 3; this level corresponds to that seen in the Asteraceae, where site mapping has proven successful), and we have recently initiated a comparative mapping study of 100 representative species and genera of Solanaceae.

The *rbc*L sequence data, limited as they may be, are tantalizing in placing *Nicotiana* and *Lycopersicon* closer to each other than either is to *Petunia* (Fig. 3). Although in conflict with standard schemes (D'Arcy, 1979), which place *Nicotiana* and *Petunia* in the same tribe (Nicotianeae) and *Lycopersicon* in a different subfamily (Solanoideae), this relationship is supported by sequence data for several nuclear genes (Pichersky et al., 1986) and by chromosome numbers ($n = 12$ for tobacco and tomato and $n = 7$ for petunia). It will be important to see whether the controversial relationships suggested by the phenetic treatment of *rbc*L sequence data (Fig. 3) are supported by the large-scale mapping study in progress, as well as by a cladistic analysis and a more sophisticated phenetic analysis (Nei, 1987) of the same sequence data.

Poaceae. Chloroplast DNA has been used extensively to investigate interspecific relationships in grasses (particularly in cereals), more so than in any other plant family (reviewed in Hilu, 1987). However, with few exceptions (e.g., Doebley et al., 1987), these studies have yielded limited phylogenetic insights owing to insufficient sampling of taxa and cpDNA sequences and also to nonrigorous methods of phylogenetic analysis. Similar problems exist for two studies of intergeneric and intertribal relationships of grasses (Lehvaslaiho et al., 1987; Enomoto et al., 1985). Despite these problems, a surprisingly reasonable phylogeny was derived for ten grass genera from an analysis of cpDNA restriction fragment patterns (Enomoto et al., 1985).

The *rbc*L gene has been sequenced more extensively in grasses than in any other plant family. The resulting phenogram (Fig. 3) shows good agreement with previously held concepts (Watson et al., 1985) and with a cladogram based on nuclear ribosomal RNA sequences (Hamby & Zimmer, 1988). This latter congruence is comforting, given the possibility for reticulate evolution to produce different phylogenies for maternally inherited chloroplast genes and biparentally inherited nuclear ones. The closer molecular relationship of *Triticum aestivum* to *Aegilops crassa* than to *T. urartu* (Fig. 3) is not surprising, since *Triticum* is an unnatural group with strong affinities to *Aegilops* and to several other genera in subtribe Triticinae (Kerby & Kuspira, 1987).

Several cpDNA inversions have been characterized in one or a few grasses, and at least one of these is shared by members of different subfamilies (Palmer & Thompson, 1982; Quigley & Weil, 1985; Hirai et al., 1985). These inversions are lacking in the four other families of monocots whose cpDNAs have been mapped (Fig. 1; de Heij et al., 1983; J. Palmer, unpublished). Careful exploration of the phylogenetic distribution of these inversions should, therefore, define several major branchings of grass evolution.

HIGHER-ORDER RELATIONSHIPS

The major avenue for exploring relationships among families and at higher levels is DNA sequencing. Supplementary information will also come from the rare and powerful rearrangements that lead to alterations in chloroplast genome structure and gene content.

Land plants. As discussed in the section on DNA sequencing, *rbc*L is the chloroplast gene of choice for comparative sequencing among angiosperms and gymnosperms. While the *rbc*L phenogram in Figure 3 offers little revelation concerning higher-level questions of angiosperm phylogeny, this situation will soon change owing to the coordinated *rbc*L sequencing efforts under way in several laboratories. The correspondence of the *rbc*L phenogram and also those based on more limited sampling of the genes *atp*B (Ritland & Clegg, 1987) and *psb*A (Wu et al., 1987) with generally held concepts of angiosperm phylogeny is encouraging. In contrast, a phylogenetic analysis based on sequences of the chloroplast *rpl*2 gene conflicts with generally accepted classification schemes and with other molecular data (Zurawski & Clegg, 1987). The explanation for this discrepancy appears to lie in the unusual evolutionary properties of *rpl*2, which is subject to a substantial selective constraint on third-position substitutions, perhaps owing to the presence of a gene on the strand opposite to that encoding *rpl*2 (Zurawski & Clegg, 1987). It is important to emphasize that this anomalous evolutionary behavior of *rpl*2, which makes it such a poor choice for phylogenetic study, was observed directly from consideration of the dynamics of nucleotide substitutions (Zurawski & Clegg, 1987), an observation *independent* of the realization that the gene is a poor phylogenetic marker.

Despite the lack of any systematic effort to identify and survey major rearrangements among land plant cpDNAs, several already have turned up that promise to mark dichotomies among major plant groups. The best documented is the aforementioned loss of the *rpl*2 intron (Figs. 4, 5), an event that unites the Caryophyllales (Centrospermae) in a manner consistent with the analysis of Rodman et al. (1984). Other rearrangements for which further study promises to illuminate specific branchings include the loss of the large inverted repeat in two genera of Pinaceae (Strauss et al., 1988) and a 30-kb inversion of unknown evolutionary polarity that distinguishes vascular plants from the single liverwort and moss examined thus far (Fig. 5; Ohyama et al., 1986; Calie & Hughes, 1987b).

Algae. Our knowledge of the structure and sequence of algal chloroplast genomes is quite limited compared with those of land plants. No significant comparative sequence study or data base yet exists for algal chloroplast genes, although several laboratories are now engaged in sequencing chloroplast ribosomal RNA genes in major algal groups (pers. comm. from S. Giovannoni & K. Field, R. Chapman & E. Zimmer, R. Cattolico, and J. Manhart & J. Palmer). Rates of structural rearrangement and size change in cpDNA appear to be substantially higher in algae, particularly green algae, than in land plants (e.g., Lemieux & Lemieux, 1985; reviewed in Palmer, 1987). These high rates probably preclude the use of inversions as phylogenetic characters at higher levels among algae, although they may be useful within genera. Other organizational features, in particular the content of genes and introns, hold promise for defining major events of algal evolution. The use of two such markers for defining the green algal origins of land plants is described in the next two paragraphs.

The gene *tuf*A, encoding the chloroplast protein synthesis factor EF-Tu, has previously been shown to be encoded by cpDNA in the phytoflagellate *Euglena gracilis* (Montandon & Stutz, 1983) and suggested to be cpDNA-encoded in the green alga *Chlamydomonas reinhardtii* (Watson & Surzycki, 1982). However, this gene is absent from the cpDNAs of an angiosperm and a bryophyte, as demonstrated by complete sequencing of the two genomes (Ohyama et al., 1986; Shinozaki et al., 1986). Recent studies (Fig. 5; J. Manhart, S. Baldauf & J. Palmer, unpublished data) reveal that *tuf*A is indeed encoded by cpDNA in *Chlamydomonas* and all other green algae examined, with the possible exception of *Coleochaete*, the presumed closest relative to land plants (Graham, 1985). In contrast, we find *tuf*A to be a nuclear gene in land plants. The transfer of *tuf*A from the chloroplast to the nucleus thus defines land plants as a natural, monophyletic group, with the disposition of *Coleochaete* with respect to this character in need of further study.

The chloroplast gene for tRNA-isoleucine contains a large intron in all land plants examined (Ohyama et al., 1986; reviewed in Palmer, 1985c) but lacks introns in all eukaryotic algae, including the green algae *Chlamydomonas* (Schneider & Rochaix, 1986) and *Chlorella* (Yamada & Shimaji, 1986). We find this intron to be present in *Nitella* cpDNA and are examining other charophytes and other classes of green algae (Fig. 5; J. Manhart & J. Palmer, unpublished data). This intron gain thus has the potential to define a specific lineage of charophytes as the sister group of land plants, consistent with ultrastructural and other evidence (Mattox & Stewart, 1984).

A signal accomplishment of molecular systematics is the unambiguous resolution of the longstanding controversy regarding the very origin of the chloroplasts. Findings from numerous molecular approaches, including the analysis of rRNA gene sequences (Fig. 9) and of gene organization (e.g., Cozens & Walker, 1987), have established unequivocally that chloroplasts are derived, endosymbiotic, photosynthetic bacteria (most likely cyanobacteria; reviewed in Gray, 1983). The challenges that remain for molecular systematists are to elaborate the full history of chloroplast endosymbiosis. Have different chloroplast lineages been derived from just one or from multiple independent and/or serial endosymbioses, and what are the sources of the plastid and nucleus in each of these associations (Whatley, 1983; Palmer, 1985b)? Analysis of ribosomal RNA sequences (Giovannoni et al., 1988) and consideration of chloroplast genome size and gene content (Palmer, 1985c) favor the idea of a single initiating endosymbiosis (i.e., one between a photosynthetic *prokaryote* and a nonphotosynthetic eukaryote), followed by several strictly eukaryotic symbioses.

DIRECTIONS AND PROSPECTS

Chloroplast DNA is now routinely used to investigate interspecific relationships among angiosperms and other plants. Its popularity at this level reflects both the general preoccupation of plant systematists with interspecific questions and also a set of factors that make cpDNA analysis especially appropriate at this level. These include the special utility of cpDNA for providing insights into the *directionality* of the hybridization events that are so common in plants, the relative ease of comparing cpDNA molecules at this level, the sufficiency of readily detectable mutations, and the low levels of homoplasy associated with the cladistic analysis of these mutations.

With current practices, the value of cpDNA analyses to reveal patterns of intraspecific variation and processes of speciation is marginal owing to the slow rate of cpDNA evolution. A concentrated effort is necessary to develop technical strategies that will allow the routine accumulation of sufficient numbers of cpDNA mutations to make the molecule predictably useful below the species level. In the short term such an enlargement of the cpDNA data base will involve increasing the number of restriction sites scored in a typical survey. This will mean using more retriction enzymes, particularly ones that cut frequently (100–400 times per genome), utilizing electrophoretic techniques (e.g., acrylamide gels of the type normally used for DNA sequencing) adequate to the task of resolving multiple small fragments, and hybridizing blots made from these gels repeatedly with cloned fragments spanning the genome. In the long term, it is conceivable that sufficient advances in the technology of DNA sequencing (e.g., of the type presently being sought to allow the sequencing of the three billion base pair genome of humans) will occur to permit efficient intraspecific study by this approach.

The analysis of phylogenetic relationships among genera and tribes is currently a nexus for the various approaches used to compare cpDNA molecules. Restriction site mapping, the easiest approach, is of demonstrated utility within families showing moderate levels of cpDNA divergence, such as the enormous family Asteraceae. In families of greater molecular diversity, such as the Fabaceae and Onagraceae (see symposium paper

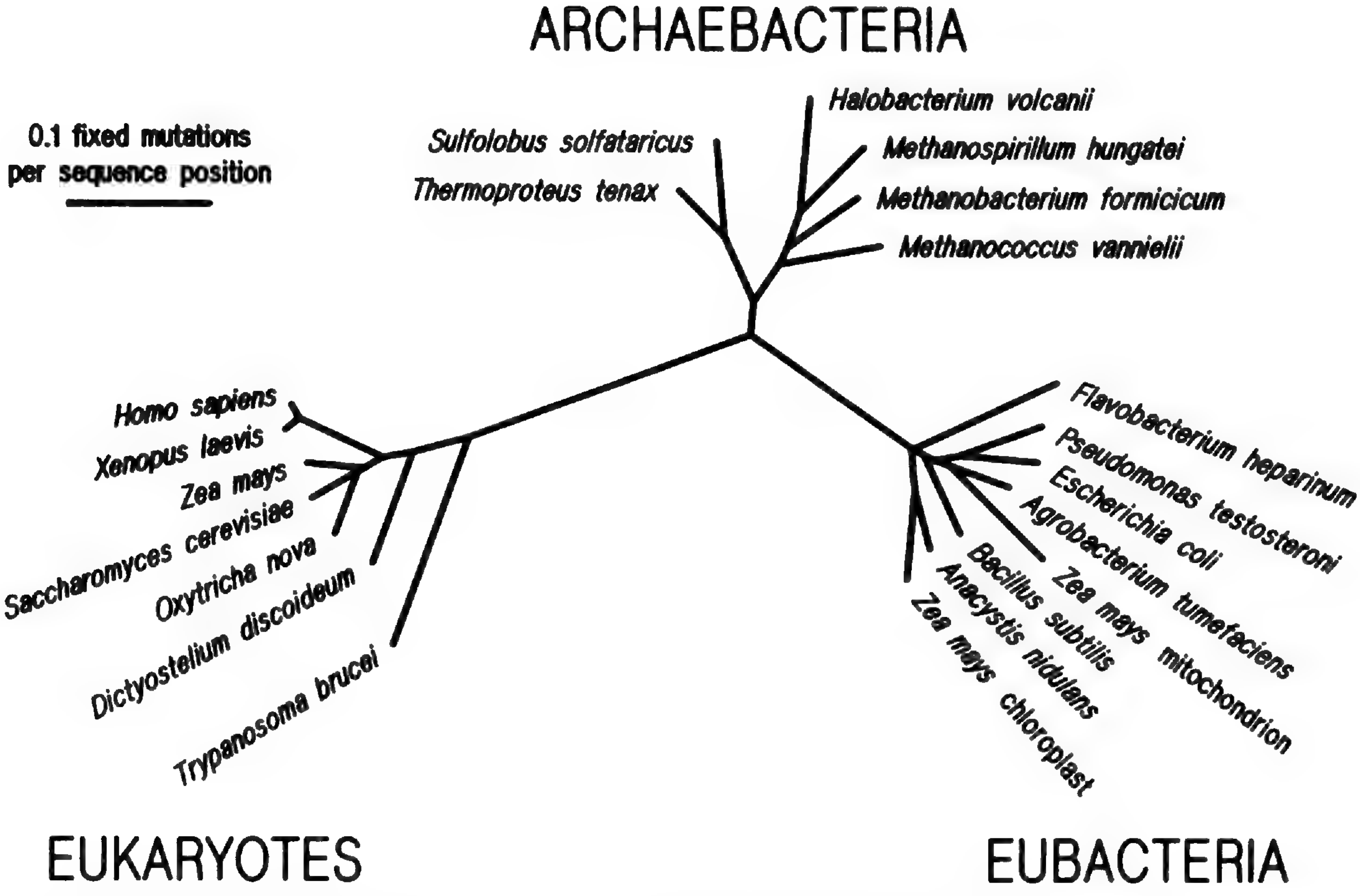


FIGURE 9. *An unrooted dendrogram based on a phenetic analysis of 16S and 18S ribosomal RNA sequences. See Pace et al. (1986) for details of tree construction and references to the primary sequence literature. Reprinted with permission from Pace et al. (1986).*

by Sytsma & Smith in this volume), direct sequencing (e.g., of *rbc*L) is a more fruitful approach. It is presently unclear, and hence unpredictable, as to why the cpDNAs of certain families are too diverse to permit comparative restriction site mapping. Factors such as the size and age (see final paragraph) of the family may in some cases be unrelated to its molecular diversity. In certain families, such as the Fabaceae, Asteraceae, and perhaps Poaceae, major rearrangements may also make significant phylogenetic contributions.

Perhaps the major accomplishment of cpDNA systematics, and molecular systematics in general, will be the resolution of the hotly debated major branchings of plant evolution, such as relationships among the families of flowering plants. DNA sequencing will be the major tool in this effort, with rearrangements serving to mark with exquisite clarity a subset of branchings. It remains to be seen whether *rbc*L will be a reliable phylogenetic indicator in all lineages. In some cases, particularly very old lineages, more conservative genes such as those encoding rRNAs may be more useful. In other cases, such as rapid radiations, sequence data from multiple genes may be necessary to provide statistically adequate phylogenetic resolution. An increasingly important component of molecular analyses as one moves back in evolutionary time will be the scope and sophistication of the computer programs that construct evolutionary trees and evaluate their statistical significance.

A frustrating but fascinating conclusion from recent cpDNA comparisons is that the rate of cpDNA sequence change may vary markedly in different, even closely related, plant lineages. These rate differences were discussed earlier in reference to the Asteraceae phylogeny shown in Figure 8 and have also been inferred from studies in the Fabaceae and Juglandaceae (J. Doyle, pers. comm.), *Populus* (K. Sytsma, pers. comm.), and *Lactuca* (E. Jandourek & J. Palmer, unpublished data). The frustrating aspect of these rate differences is the attendant inability to use molecular variation as a "clock" to date divergence times in plant evolution. The fascination stems from the fact that we presently have no satisfactory understanding of the biochemical and genetic bases of such rate heterogeneities. In conclusion, cpDNA is in general both conservative and predictable in its evolution, features which make it extremely useful for inferring phylogeny but of concomitantly lesser interest from the standpoint of molecular evolution. However, aspects of its evolution (not only differences in substitution rates, but also such remarkable mutations as the transfer of its genes to the nucleus) provide grist for the mill of the molecular evolutionist.

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RIBOSOMAL DNA VARIATION WITHIN AND AMONG PLANT POPULATIONS[1]

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ABSTRACT

The DNA sequences that code for the 17S, 5.8S, and 25S subunits of the ribosome have been useful in the study of plant evolutionary biology. The coding sequences are evolutionarily conservative and have provided information on systematic relationships among the species within a genus and have also elucidated higher level relationships. The intergenic spacer region of the sequence is highly variable, and variation occurs within populations and individuals. Analysis of intra- and interpopulation variation in rDNA has documented subdivision within populations of Clematis fremontii *and population and subspecific differentiation in* Phlox divaricata. *These studies indicate that rDNA provides a good genetic marker for the study of microevolutionary processes.*

Many of the current questions in population biology center on the levels of genetic variability within populations and on the factors that influence genetic variation. Levels of genetic variability are central to the study of population biology and evolution because the amount of variability directly influences the evolutionary potential of populations and species. Much attention has been given to the problems of measuring genetic variation for different features, such as morphology, life-history traits, chromosomes, and various types of molecules (e.g., Lewontin, 1974).

In recent years, a predominant technique for examining genetic variation has been allozyme electrophoresis. This technique has greatly expanded our understanding of the genetic processes that occur in plant species, and without it we would have information on the genetic structure of only a handful of noncultivated species. In spite of its usefulness and widespread application, there are some well-known limitations. Most frequently, only genes of a single class, those encoding soluble enzymes, are analyzed, and they often are selected on the basis of the ease of their products extraction and ability to migrate on a starch gel. Only nucleotide differences in genes that lead to changes in product amino acid composition can be detected, and then detection is usually limited to those changes in amino acid composition that result in a net change in charge of the product molecule. These genes may not be representative of the genome in general. For instance, there is evidence that many commonly studied allozymes are more variable than other categories of gene products, and that this variability may stem in part from such processes as post-translational modification (Johnson, 1979). Moreover, changes in allele migration were thought to result from single codon changes; in fact, differences may be the result of several changes in DNA structure (Sachs et al., 1986). Many of these concerns can be avoided if DNA that encodes different types of genes is analyzed.

Plant DNA is relatively simple to extract and purify, and DNA representing different portions of the genome can be studied by hybridization to cloned probes. In addition, current techniques of DNA analysis are many times more sensitive to changes in gene structure than are other macromolecular assays. Variation in fine structure can be detected at several levels: in nucleotide sequence, in sequence length, and in gene copy number. Finally, current DNA technologies are straightforward and require only small amounts of tissue. It is thus feasible to analyze the large numbers of individuals required for populational studies. The use of restriction site and sequence data offers

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the potential to reexamine once-problematic aspects of population biology. Accurate measures of genetic variation in specific portions of the genome, determination of the amount of genetic change associated with speciation, and assessment of the amount of somatic variation and its influence on population variation are examples of areas where DNA data can provide new insights.

Populational analysis offers new insights into molecular biology as well, for example, in the study of concerted evolution. Concerted evolution takes place when the members of a multigene family are more similar to each other than expected had they evolved independently from the time of the initial gene duplication that gave rise to the multigene family (Zimmer et al., 1980; Arnheim, 1983). If concerted evolution were not occurring, each individual would have a large amount of variation among the copies of a multigene family; virtually none of the copies within an individual would be the same. Early DNA hybridization studies and subsequent populational analysis indicated that this is clearly not the case for ribosomal DNA (rDNA). Most of the rDNA copies within an individual are much more similar than would be expected had they evolved independently of one another (a limited amount of variation is seen within individuals, see below, but most rDNA repeats in an individual contain very similar sequences). It is thought that gene conversion, unequal crossingover, or a combination of these are likely responsible for concerted evolution of ribosomal genes. The balance of the processes governing both concerted evolution and the turnover of multiple copy DNA families (Dover, 1982, 1987; Dover & Flavell, 1984) and their interaction with population level phenomena (e.g., gene flow, genetic drift, and organismal selection) are complex and require much additional study. The pattern of variation in specific DNA sequences within and among populations will provide information on the pattern of molecular changes among rDNA repeats.

In the following we will examine variation in DNA sequences within and among populations of plant species. Our purpose is two-fold: to quantify the type and levels of variation at specific DNA sequences and to relate levels of variation to populational features. We will concentrate on one specific DNA sequence, ribosomal DNA, that has received a great deal of attention from molecular biologists and, most recently, population biologists. Before turning our attention to ribosomal DNA variability, we will discuss the structural and functional aspects of rDNA that affect levels of variation.

STRUCTURE AND FUNCTIONAL ASPECTS OF rDNA

Ribosomal DNA is a mid-repetitive sequence with from 500 to more than 40,000 copies per genome arranged in tandem repeats (Long & Dawid, 1980; Rogers & Bendich, 1987a). Ribosomal gene repeating units are composed of a number of regions that vary in functional constraint and, consequently, in evolutionary rate (for a review see Gerbi, 1986). Figure 1 shows the segments of the rDNA that will be discussed here. Each rDNA repeat contains a transcription unit (a through f), from which the rRNA precursor (pre-rRNA) is transcribed, and a so-called nontranscribed (or intergenic) spacer (g) between the transcription units of adjacent repeats. The pre-rRNA is cleaved after transcription into the mature rRNAs: the 17S (b), 5.8S (d), and 25S (f). The sequences of the rDNA that correspond to the mature rRNAs are the coding regions. The 5′ leader sequence (a) is the external transcribed spacer (ETS). The internal transcribed spacers separate the 17S, 5.8S, and 25S RNA coding sequences (ITS-1 [c] and ITS-2 [e], respectively). The pre-rRNA is transcribed and processed into the various rRNAs. Ribosome subunits are assembled from these gene products along with the 5S rRNA and the ribosomal proteins.

The different evolutionary rates observed for the various regions of rDNA is a likely reflection of the differences in the functional constraints that govern these regions. Portions of the coding regions have a high degree of evolutionary conservation, being invariant in all organisms examined to date. The nontranscribed spacer (NTS), on the other hand, diverges among closely related taxa. Other regions of the repeat show a range of intermediate rates. The rates of divergence determine a specific sequence's utility for studying the variation among populations or higher taxonomic levels. We will review the functions of the various coding and noncoding regions and then discuss the sorts of variation seen for portions of the rDNA repeats in plants.

CODING REGIONS

The coding regions, segments of the rDNA repeat ultimately incorporated into the cytoplasmic ribosomes, are expected to vary the least. Although this is true as a rule, limited variability is possible because of a range of functional constraints. Selection appears to act to conserve functionally important secondary structure (Wheeler & Honeycutt, 1988). Higher amounts of variation at the sequence level are seen among closely related taxa

FIGURE 1. *rDNA repeat unit organization. The line corresponds to the nontranscribed spacer region (g), while boxes (hatched or filled) represent the transcribed portion of the gene. Filled boxes represent the coding regions for the 17S (b), 5.8S (d), and 25S (f) rRNAs. Hatched boxes symbolize the transcribed spacers, the external (ETS, a) and internal (ITS-1, c, and ITS-2, e). The repeating structure of these genes is represented by the adjacent ETS (a') and 17S region.*

for the portions of the rRNAs constituting the helical 'stem' portions of the molecule. Changes may occur by compensating substitutions, in which base-paired nucleotides in opposite strands of the helix change 'in response' to one another. A degree of mismatch is apparently tolerated. Presumably occasional mismatches may slow down the rate of formation of stem and loop structures without preventing the formation of the helix. In addition to guanine-cytosine and adenine-uracil pairing, pairing between guanine and uracil is possible and does not inhibit helix formation. Furthermore, even short stretches of one or a few nucleotides of mismatch do not prevent formation of helical structure as long as they are flanked by regions of base complementarity. The most conserved sequences are in single-stranded regions (Wheeler & Honeycutt, 1988). These sequences either act enzymatically or bind to proteins (either ribosomal proteins or protein translational cofactors) or other RNAs (tRNAs and mRNAs).

Some stretches of rRNA sequence do not vary in any organism for which the sequence is known. At the other extreme, portions of the large ribosomal RNA are either variable within an individual (Gonzalez et al., 1985) or present in some species of a genus but are lacking in others (Chan et al., 1983; Hadjiolov et al., 1984). Although the evolutionary dynamics of these changes is not understood, obviously there is polymorphism within populations for rRNA coding region variants. Most studies of rDNA variation analyze restriction endonuclease sites, and little variation has been reported for sites within coding regions. Sequence analysis would be much more sensitive for detecting variation, but with the exception of Gonzalez et al. (1985), most rDNA sequences are known for only a single gene copy of each species. The expected level of variation is too low to justify such a currently expensive and labor-intensive survey.

TRANSCRIBED SPACER REGIONS

The transcribed spacer regions are the portions of the rRNA transcription unit that are not seen as mature rRNAs. They show intermediate levels of variability in interspecific studies (Appels & Dvorak, 1982b; Sytsma & Schaal, 1985; Hillis & Davis, 1986; Davis, 1986), an observation consistent with the intermediate degree of functional constraint on these sequences. While some portions of the transcribed spacers may act merely as spacer DNA with the length of the sequence being more important than its information content, analysis of ITS sequences shows substantial conservation among moderately closely related species. Presumably this reflects the presence of processing signals, for which a degree of conservation is expected. Sequence conservation is also seen for portions of the ETS, again presumably due to processing signals in this region. In addition, it has been postulated that the intermediate level of conservation in transcribed spacer regions may reflect RNA-mediated gene conversion; Appels & Dvorak (1982b) suggested that the conservation seen for rDNA may be due in part to 'correction' from the rRNA transcript of differences among ribosomal gene copies within the same nucleolus.

NONTRANSCRIBED SPACERS

This region between adjacent transcription units is in fact transcribed to a degree, so it is becoming apparent that this term is a misnomer. Transcription proceeds from the 5′ transcription unit, through the spacer, to the initiation site of the adjacent repeat; these transcripts are rapidly processed to the rRNA precursor and the ephemeral nature of NTS transcripts led to this region being so-named. The NTS is the most rapidly evolving portion of the rDNA. Since it shows the greatest amount of variation within and among plant populations, it is the region most useful as a genetic marker for analyzing microevolutionary processes. The dynamics of molecular evolution in the nontranscribed spacers in plants have begun to be elucidated recently. From sequencing studies (Appels & Dvorak, 1982a; Yakura et al., 1984; Lassner & Dvorak, 1986; McMullen et al., 1986; Toloczyki & Feix, 1986) and other fine-scale genetic analyses (Appels & Dvorak, 1982b; Rogers et al., 1986), it appears that the NTS consists of at least three regions that may differ in function and may evolve at different rates.

A series of subrepeating elements in the nontranscribed spacers is seen in all higher eukaryotes for which the sequence is known. In addition, the presence of subrepeats in a number of plant species is inferred from length variability in the NTS (e.g., Cluster et al., 1984, reviewed by Rogers & Bendich, 1987a). A degree of sequence similarity has been demonstrated between NTS subrepeats of wheat (Appels & Dvorak, 1982a) and maize (McMullen et al., 1986; Toloczyki & Feix, 1986). This presumed conservation has been interpreted as evidence that the subrepeats have a function. It has been demonstrated that one class of subrepeating elements acts as enhancers of transcription in *Xenopus* (Reeder et al., 1983; Reeder, 1984), and evidence suggests that some types of subrepeats function similarly in plants (Flavell & O'Dell, 1979; Martini et al., 1982; Flavell, 1986).

No function has been demonstrated for the region of the NTS 5′ to the presumed enhancer subrepeats. This sequence is 144 base pairs in maize (Toloczyki & Feix, 1986) and at least 241 bp in wheat (Lassner & Dvorak, 1986) but may be considerably longer in other plant taxa. The region 3′ to the enhancer subrepeats is 135 to 240 bp in maize (McMullen et al., 1986; Toloczyki & Feix, 1986); in wheat it is considerably less than 960 bp (Lassner & Dvorak, 1986). This region is assumed to contain the promoter for transcription of the pre-rRNA. Although the NTS is presumed to code for no gene products, there is good evidence for functional constraints, and the NTS is therefore potentially subject to selectional forces. It is not clear how strongly these constraints govern the evolution of the NTS region of the rDNA multigene family, but they clearly differ from those governing evolution of the coding regions (see Jorgensen, this volume, for further discussion).

VARIATION AMONG INDIVIDUALS OF A POPULATION

Because of these differences in the levels and kinds of functional constraints, variation of rDNA is very different for the transcription unit versus the so-called nontranscribed spacer. In general, within a species there appears to be only little variation in the coding regions. Such variation appears to be predominantly developmental variation due to methylation (see Jorgensen & Cluster, this volume). We will concern ourselves here with variation in the nontranscribed spacer region. When the individual plants within a population show some type of rDNA variation, it is within this region. Length variation is most common and is due to a series of repetitive elements in the nontranscribed spacer region. In *Triticum* spp. and *Vicia faba*, length heterogeneity is due to copy number differences of a series of 135-bp or 325-bp elements, respectively (Appels & Dvorak, 1982a; Yakura et al., 1984). A variable number of copies of the same or highly similar DNA sequence gives rise to the different length classes.

Because rDNA is a repetitive DNA sequence within the genome, individuals can contain several different length variants. A single *V. faba* plant can have up to 20 different length variants of rDNA (Rogers et al., 1986). Native populations of *Lupinus texensis* contain plants with up to 11 length variants, although most commonly there are three or four variants per plant (D. Baum, pers. comm.). In *Phlox divaricata*, the mean number of repeats per plant is 1.98 (Schaal et al., 1987). *Clematis fremontii* has an average of 2.65 variants per individual (Learn & Schaal, 1987), whereas *Hordeum spontaneum* contains on average 2.28 variants per plant (Saghai-Maroof et al., 1984).

Such length variation is not ubiquitous. *Solidago altissima* is highly variable in the nontranscribed spacer region but this variability is limited almost exclusively to restriction site variation (Schaal et al., in prep.). Length variation is restricted to a 300-bp insertion present in low frequency within some populations. Table 1 shows the variation in restriction sites of *S. altissima*. Variation of rDNA occurs often within individual plants. Plants are most commonly polymorphic for rDNA variants that have different restriction sites. Another feature of *S. altissima* rDNA is the genetic differentiation among portions of a clone. Several plants showed variation in rDNA types within a clone for variants based on different *Eco*RI or *Eco*RV restriction sites. Such within-clone differences may occur via somatic mutation or rapid increase of a rare variant. The occurrence of variation within plants adds a level of analysis not previously possible in populational studies.

Other species show no rDNA variability. *Rudbeckia missouriensis*, an endemic of isolated rocky habitats in Missouri and Arkansas, shows no length heterogeneity nor does it show restriction site variation in a survey of six populations of glade habitats (L. King, pers. comm.). *Gaura demareei*, a hybrid-derivative species with a narrow range, contains two length variants of 10.5 and 11.3 kb. Each plant examined in a survey throughout its range was identical for the two length variants (Schaal & Raven, in prep.). Moreover, there was no restriction site variation. Similarly, species of the

Lisianthius skinneri complex show little restriction site variation or length heterogeneity (Sytsma & Schaal, 1985).

At this time no clear correlations emerge between levels of rDNA length variability and characteristics of the population biology of various species. In the three cases where no variation is observed, the species are narrowly endemic. The *R. missouriensis* populations are isolated, although population size can be in the thousands. *Gaura demareei* has a highly restricted species range, occurring predominantly within a single Arkansas county in populations often fewer than 50 individuals. Likewise, *Lisianthius* species have a very narrow range and often consist of few populations with low plant numbers. On theoretical grounds one expects that narrowly endemic species would have little variation, due to genetic bottlenecks. Variation would be expected to be lost due to sampling, in these cases either by small population size, by founder events due to repeated colonizations, or by a recent species origin after hybridization. The generation of length heterogeneity may not occur very rapidly in these species since none of them have accumulated variation; even *R. missouriensis*, where number of individuals per population is high, remains depauperate for rDNA length variation.

In marked contrast to the results obtained for *R. missouriensis* are the levels of variation detected in *Clematis fremontii*. Populations of *Clematis fremontii*, like the *Rudbeckia*, occur on islandlike glades in Missouri. These populations are predominantly limited to two counties and are often much smaller in population number than *R. missouriensis*. On theoretical grounds one would expect *C. fremontii* to show less variation than *R. missouriensis*, but this is not the case. The *Clematis* plants contain up to four length variants, and the length variation shows spatial differentiation (see below). Thus, there is no consistent pattern here between ribosomal DNA variation and population size or species range (but see Flavell et al., 1986). Since the two species with the greatest observed length heterogeneity are both legumes (*Vicia faba* and *Lupinus texensis*, see above), one might suspect that something in the ancestry or in the biology of legume species leads to such high numbers of rDNA length variants, but length heterogeneity is not great in some other legume species (soybean and its relatives, Doyle & Beachy, 1985; other *Vicia* species, Rogers & Bendich, 1987b). Clearly, much more research is necessary before associations between levels of rDNA length variation and populational characteristics, such as gene flow, population size, breeding system, or founder events can be established.

A further aspect of rDNA variation within populations is apportionment and distribution in space. One feature that distinguishes many plant populations from most animal populations is the frequent occurrence of genetic population substructure in the former. Plant populations often show significant local genetic differentiation, many times on a microgeographic scale. Such local differentiation can result from selection on a very local scale. Local differentiation may also occur via genetic drift. Such drift can be the consequence merely of nonrandom mating due to restricted pollinator behavior or to limited seed dispersal—spatially restricted gene flow causes the population to become effectively subdivided. Random genetic drift occurs among the subdivisions, thus leading to significant local genetic heterogeneity (Turner et al., 1982). Local differentiation within plant populations has been documented for genes that cause heavy metal tolerance (Jain & Bradshaw, 1966), that result in different flowering times (McNeilly & Antonovics, 1968), that cause morphological differences (Linhart, 1974), and that encode different allozymes (Schaal, 1975).

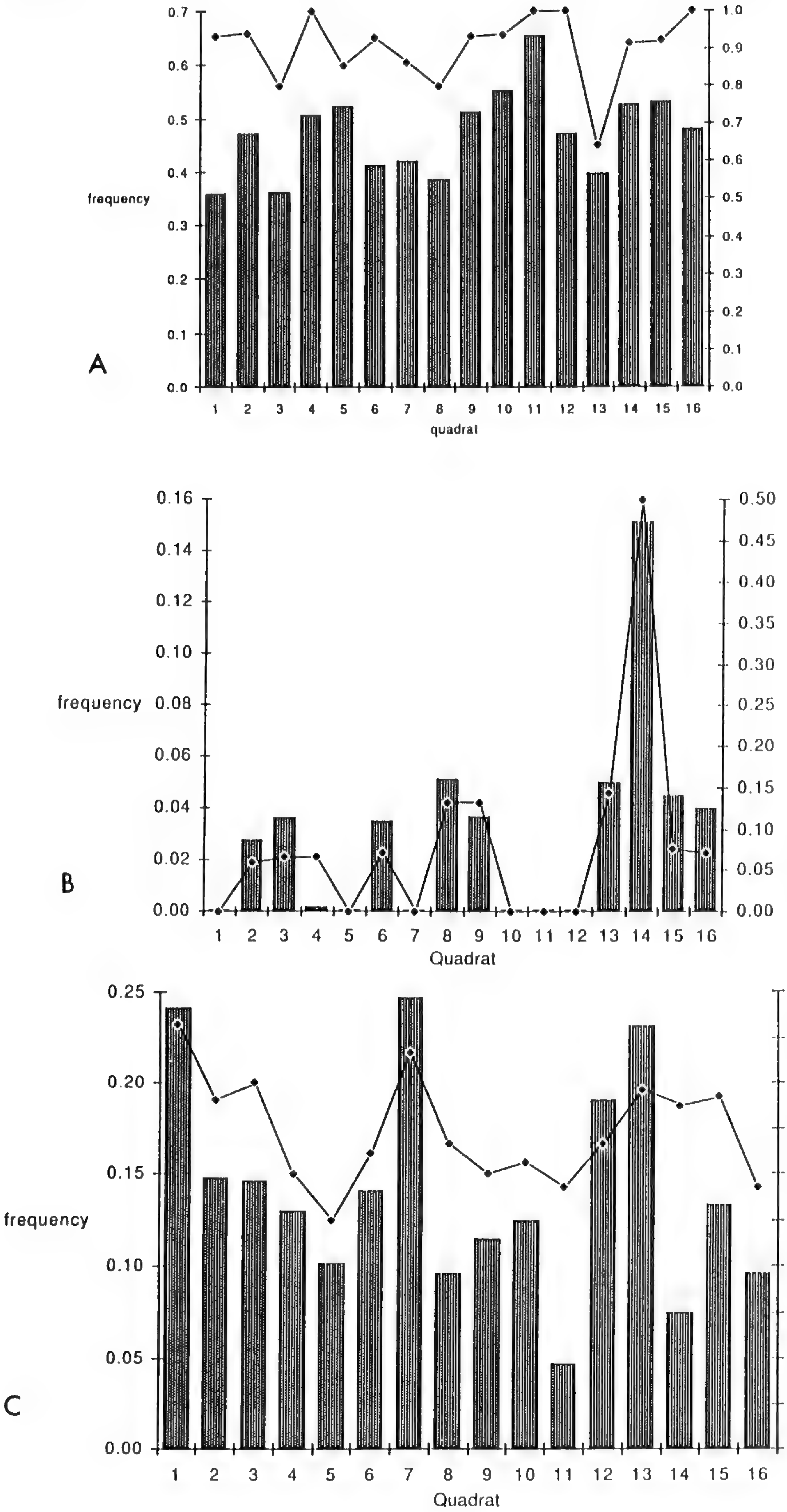
Our study of *Clematis fremontii* has documented nonrandom geographical distribution of ribosomal DNA variants within populations. A single population of *Clematis fremontii* has been analyzed for spatial variation in the frequency of rDNA-length variants. Many of the length variants that

TABLE 1. *Variation of rDNA in* Solidago altissima.

Site	Within Individuals[1]	Within Clones[2]	Between Individuals	Between Populations
*Sst*I	+	−	−	−
*Bgl*I	+	−	−	−
*Bgl*I	+	−	−	+
*Xmn*I	+	−	+	−
*Hinc*II	+	−	−	−
*Xho*I	+	−	−	−
*Bam*HI	+	−	−	−
*Eco*RI	+	+	−	−
*Eco*RV	+	+	+	−
*Xmn*I	+	−	+	+
*Hind*III	+	−	−	+
Insert	+	−	+	+

[1] Genome contains more than one rDNA variant.

[2] Differences in rDNA type occur among the parts of a clone.


A
frequency
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
quadrat
B
frequency
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
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0.20
0.25
0.30
0.35
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0.45
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1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
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frequency
0.00
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0.15
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0.6
0.7
0.8
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Quadrat

occurred in high frequency showed no significant spatial differentiation (Fig. 2A). However, two of the variants showed statistically significant microgeographic differentiation; the variants do not tend to be distributed randomly in space within the population, but rather are confined to specific areas within it (Figs. 2B, C). Such local differentiation of rDNA variants is consistent with population subdivision due to restricted gene flow, or perhaps it may be a consequence of a recent origin or dispersal of an rDNA variant into a population.

VARIATION AMONG POPULATIONS

Few studies have examined the pattern and apportionment of rDNA variants among the populations of a species. Most of the work to date has centered on cultivated species and is reviewed in Appels & Honeycutt (1986). Here we look at levels of variation in natural, noncultivated plant species. Levels of differentiation for rDNA variants vary among populations of a species. Some plant species show no significant heterogeneity within or among populations. Those species having low levels of rDNA variation within populations show little or no differentiation among populations. No significant genetic differences in rDNA types were detected among populations of *Gaura demareei*, *Rudbeckia missouriensis*, or members of the *Lisianthius skinneri* complex. Judging from their ranges and/or other determinations of genetic variability, it is likely that these species have undergone genetic bottlenecks and variation has been lost within and between populations. In the few highly variable examined species, significant genetic heterogeneity is detected among populations.

The best-studied example to date is the widespread woodland perennial *Phlox divaricata* (Schaal et al., 1987), in which there is clear differentiation of rDNA variants. Populations often contain unique rDNA variants and may be distinguished by the number of variants (2–6) they contain (Schaal et al., 1987). There is clear differentiation between population systems. *Phlox divaricata* subsp. *laphamii* shows less rDNA diversity than subsp. *divaricata*. The subspecies differ in the numbers and types of variants they contain, and in the overall genetic diversity (Table 2).

The variation in *Phlox divaricata* provides corroborative information on the origin of the subspecies. Based on morphological criteria, subsp. *laphamii* is considered derived from subsp. *divaricata*. This hypothesis appears to be supported by the apportionment of rDNA variation; rDNA variability in subsp. *laphamii* is a subset of the variability seen in the other, more widespread subspecies.

Variation among populations also has been analyzed in the old-field perennial *Solidago altissima* (Schaal et al., in prep.). Differentiation in this species occurs for a 200-bp sequence which is fixed in one population and is present in low frequencies in other populations. Populations are also differentiated for restriction sites. As with intrapopulation variation, too few species have been analyzed to draw conclusions about levels of rDNA variation and such populational characteristics as size, gene flow, or bottlenecks. Clearly, populations are differentiated for levels and kinds of rDNA variation. Whether the differentiation is related to selection, genetic drift, gene flow, or any other population-level genetic process remains to be determined. Although the mechanisms responsible for generating rDNA length variation obviously require further study, such variants can and have been used to reconstruct aspects of the evolutionary history of plants (see also Sytsma & Schaal, 1985; Doyle et al., 1984, 1985).

CONCLUSIONS AND PROSPECTS

The use of DNA sequences in studies of population biology is in its infancy and holds a great deal of potential for understanding processes and answering persistently elusive questions. The ability to assess variation in a wide diversity of DNA sequences is a major technical advance. Virtually any segment of DNA can be studied, whether it is a coding or noncoding sequence, or is single copy,

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FIGURE 2. *Frequencies of some rDNA repeat length variants in* Clematis fremontii. *Individuals were sampled from a 160-m transect at Victoria Glade, Jefferson County, Missouri (see Learn & Schaal (1987) for details). Variants A (Fig. 2B) and E (Fig. 2C) show statistically significant local differentiation along the transect.—A. Variant C, 11.3 kilobase pairs (kb). Numbers along the abscissa refer to quadrat position along the transect. The left ordinate and the histogram bars are mean frequency of variant within individuals in a quadrat. The right ordinate and the line are proportion of the individuals within a quadrat bearing a variant C. Variant C is the most common variant in the population and does not show significant local differentiation.—B. Variant A (10.2 kb). Axes as in Figure 2A.—C. Variant E (11.9 kb). Axes as in Figure 2A.*

TABLE 2. *Population variation in rDNA repeat-type frequency of* Phlox divaricata.

Subspecies and Population	Repeat-Type Frequency							
	V-1	V-2	V-3	V-4	V-5	V-6	V-7	V-8
Subspecies *laphamii*								
CC			0.19			0.50	0.31	
T			0.09	0.27		0.55		
WH				0.18		0.55		
F				0.42	0.25			0.08
Results for subspecies overall			0.08	0.38	0.04	0.24	0.10	0.02
Subspecies *divaricata*								
TC				0.29	0.14	0.21		
PH		0.50		0.20	0.30			
B	0.19			0.19	0.10		0.19	
M	0.21	0.08		0.13	0.12		0.17	
Results for subspecies overall	0.11	0.13		0.16	0.19	0.06	0.10	
Results for all populations	0.070	0.078	0.031	0.239	0.141	0.132	0.10	0.003

mid-repetitive, or highly repetitive DNA. In fact, one strategy of population analysis is to clone random portions of the genome, and study variation of restriction sites in these random sequences (e.g., Hofker et al., 1986).

From the studies discussed above, some DNA sequences, specifically segments of rDNA, vary at the appropriate levels for studies of population processes. This is in contrast to other sequences, such as chloroplast DNA, where variation is usually seen at the interspecific or intergeneric level, and is most informative for phylogenetic studies. There are clear differences among individuals and populations in rDNA. An added dimension to studying variation occurs with the use of mid-repetitive sequences, since single individuals contain many copies of a sequence and thus can themselves be polymorphic. Studies of ribosomal DNA provide an additional level of analysis, that of the individual; the apportionment of variation can be examined at the within-plant as well as the between-plant levels.

Another potentially important aspect of rDNA studies is the ability to detect somatic mutations. There currently is much speculation in the literature on the role of somatic mutation in plant population biology (Whitam & Slobodchikoff, 1981; Gill & Halverson, 1984; Walbot, 1985; Walbot & Cullis, 1985). Several workers suggest that somatic mutation and subsequent variation leads to differences in ecological parameters, such as susceptibility to insect predation. It is argued that somatic variation in DNA sequences may have an adaptive function. These ideas are contested, in part because the frequency of somatic variation is not known. With current methods of analyzing DNA sequences, it is possible to document unequivocally the occurrence and frequency of somatic variation.

A final new area where DNA analysis is potentially important for population biology is rapid genomic change. Many organisms alter their DNA in response to stress, as in the case of gene amplification in response to toxic agents (Schimke, 1983). McClintock (1984) suggested that genome change is a way in which plants routinely deal with stress. Walbot & Cullis (1985) suggested that flexibility is an important feature of the plant genome. Genome flexibility has been demonstrated in flax, where heritable variation in rDNA cistron number is induced by environmental changes (Cullis, 1986). Such heritable changes in genome size have profound implications for population biology. Alteration of genomes in response to environmental variation may contribute to the genetic adaptation of a plant species. Such a process can alter the genetic characteristics of populations and, on a practical level, can confound such experiments as reciprocal transplants. There is much future work on the interface between plant molecular biology, population genetics, and ecology; blending among these disciplines promises to add greatly to our understanding of plant evolution.

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TABLE 2. *Continued.*

Repeat-Type Frequency				Mean Number of Repeats/ Plant
V-9	V-10	V-11	V-12	
				2.0
0.09				1.2
0.18			0.09	1.2
0.25				1.5
0.12			0.02	1.5
	0.15		0.21	2.3
				2.0
		0.04	0.30	2.6
		0.12	0.17	3.0
	0.03	0.05	0.17	2.5
0.051	0.016	0.031	0.108	1.98

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DNA AND MORPHOLOGY: COMPARISONS IN THE ONAGRACEAE[1]

Kenneth J. Sytsma and James F. Smith[2]

ABSTRACT

Comparisons of systematic information generated from both classical systematic approaches and from DNA analysis at a number of taxonomic levels in the Onagraceae are presented. Phylogenetic results from chloroplast DNA restriction fragment analysis in Clarkia *sect.* Sympherica *(=* Peripetasma*) are not entirely congruent with results from morphology, but are congruent with distribution of duplications of isozyme-coding loci. Chloroplast DNA and nuclear rDNA evidence for the origin of the monotypic genus* Heterogaura *from within the genus* Clarkia *is discussed with respect to morphological divergence between the two genera. Detailed chloroplast DNA restriction site mapping within the seven diploid sections of* Clarkia *and subsequent preliminary intersectional phylogenetic analysis are presented. These DNA-based relationships are compared with a morphological and cytological model of relationships, and to various gene duplication-based models. Section* Godetia *is implicated as the sister group to the rest of* Clarkia, *a result concordant with preliminary cladistic analysis of morphological and isozymic characters. The monophyletic nature of sections encompassing the PGI gene duplication is not rejected or supported by this cpDNA restriction site analysis. Preliminary DNA restriction fragment analysis for the nine previously described sections of* Fuchsia *and one new section is presented and then compared with published biogeographical, fossil, morphological, and cytological results. The preliminary chloroplast DNA analysis in* Fuchsia *indicates that the disjunct Old World sect.* Skinnera *was the first lineage to diverge, followed by the monotypic Central American sect.* Jimenezia. *The phylogenetic relationships of the other sections of* Fuchsia *remain unclear. Comparisons of systematic results using cpDNA restriction site variability and morphological, cytological, and isozymic variability are reviewed for the Onagraceae and other angiosperms.*

Phylogenetic analysis of plants using molecular techniques is increasingly providing detailed and often unexpected evidence of phylogenetic relationships among populations, species, sections, genera, and tribes (Gottlieb, 1977a, b; Gottlieb & Weeden, 1979; Odrzykoski & Gottlieb, 1984; Sytsma & Schaal, 1985a; Sytsma & Gottlieb, 1986a, b; Jansen & Palmer, 1987, 1988; Rieseberg et al., 1988; Soltis et al., in press). A major strength of many of these new molecular techniques—e.g., chloroplast DNA (cpDNA) restriction fragment analysis—is that they provide numerous independent characters that can be used as historical markers to define more rigorously the phylogenetic relationships of the plants (see Sytsma & Gottlieb, 1986b, and Jansen & Palmer, 1988, for examples). Those molecular techniques that provide but a single piece of information, such as analysis of cpDNA inversions or duplications of isozyme encoding genes, are still powerful, since the underlying genetic or structural bases can be clearly demonstrated and the essentially neutral character changes can be argued to be strictly homologous and rare (see Jansen & Palmer, 1987, and Gottlieb & Weeden, 1979, for examples, respectively).

The Onagraceae provide unique opportunities for the application of these "modern" molecular and genetic techniques, especially those involving proteins and nucleic acids. The Onagraceae are a well-defined family of seven tribes, 16 genera, and approximately 650 species (Raven, 1988). An abundant and detailed information base for the family has been generated already using morphology, anatomy, chromosomal features, and flavonoid chemistry. Ongoing systematic studies using proteins, nucleic acids, and formal cladistic analyses that complement the information already available are making the Onagraceae the best-studied plant family of their size (Raven, 1979, 1988).

Given the large information base generated from the more "classical" systematic approaches on Onagraceae, phylogenetic analyses using proteins and/or nucleic acids are especially applicable to the

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study of relationships among Onagraceae. First, detailed genotype-based phylogenies can be constructed for taxa within Onagraceae. Second, phylogenies resulting from morphology, anatomy, and other phenotypic characters can be compared with molecular phylogenies to determine which studies are providing similar or congruent phylogenies. This will permit identification of consistently monophyletic lineages in these independent studies. Additionally, certain kinds of characters *might* be viewed with suspicion if they suggest relationships at odds with those provided by other types of characters. Third, incongruencies found among these independently derived phylogenies can point to further research along either of two lines: (1) a reexamination of specific data sets or the techniques themselves to identify possible reasons for the incongruencies (e.g., nonhomologous characters, high levels of homoplasy, rapid or uneven rates of character divergence among lineages, and hybridization/introgression); and (2) reassessment of relationships not previously supported or even suspected with other available information.

The classic series of studies by Gottlieb and his associates using the distribution of isozyme-encoding gene duplications within Onagraceae (Gottlieb, 1977b; Gottlieb & Weeden, 1979; Odrzykoski & Gottlieb, 1984; Soltis et al., 1987) illustrate well how molecular techniques can be used in this fashion. These studies have generated phylogenetic hypotheses, made comparisons with morphologically and cytologically based phylogenies with which they often differ substantially, questioned several models of phylogenetic relationships previously supported by classical studies, and lastly initiated several new and rewarding lines of research (e.g., genetic studies of duplications and subsequent silencings, effects of different isozyme number and activity in plants, and verification of progenitor/derivative species relationships).

In this paper, we use evidence from cpDNA restriction fragment analysis and site mapping to produce phylogenies within Onagraceae, compare these with other molecular and morphological phylogenetic hypotheses, reexamine a number of lineages that are either not supported by molecular evidence or not supported by morphological evidence, and finally raise questions that these cpDNA studies now permit us to ask. Previous cpDNA phylogenetic studies in *Clarkia* sect. *Sympherica* (= *Peripetasma*) and the genus *Heterogaura* (Sytsma & Gottlieb, 1986a, b) will be reviewed and additional nuclear rDNA evidence introduced. Preliminary cpDNA phylogenetic analysis of sectional relationships within *Clarkia* will be described and compared with relationships based largely on morphology, chromosome number, and crossing relationships (Lewis & Lewis, 1955), and to relationships based on gene duplications (Gottlieb & Weeden, 1979; Soltis et al., 1987). Preliminary cpDNA phylogenetic analysis of sectional relationships within *Fuchsia* will be then presented and compared with those described by Berry (1982) and Raven (1979, 1988). Lastly, systematic results of DNA versus morphology will be reviewed in the Onagraceae and other angiosperms.

PHYLOGENETIC ANALYSIS OF *HETEROGAURA* AND *CLARKIA* SECT. *SYMPHERICA*

INTRODUCTION

Clarkia is composed of approximately 44 species, most of which are restricted to California, but with *C. pulchella* Pursh, the type species, confined to the northwest U.S. outside California. The *C. tenella* polyploid complex exhibits a disjunct distribution in California and Argentina and Chile. The largest section of *Clarkia* recognized by Lewis & Lewis (1955) is sect. *Sympherica*, the valid name for the former sect. *Peripetasma* (Holsinger & Lewis, 1986). Section *Sympherica* is comprised of three morphologically well-defined diploid subsections and the tetraploid subsect. *Prognatae*, the latter comprising only *C. similis* Lewis & Ernst, which is believed to be an allopolyploid derived from hybridization between subsects. *Lautiflorae* and *Micranthae* (Lewis & Lewis, 1955).

Relationships within sect. *Sympherica* based on morphology and crossing experiments (Lewis & Lewis, 1955; Davis, 1970) are illustrated in Figure 1. Subsection *Micranthae* consists of one strictly self-pollinating species with small, inconspicuous, and white flowers, whereas subsects. *Sympherica* (three species) and *Lautiflorae* (four species) consist of primarily outcrossing species with large, showy, and colorful flowers. Petals of subsect. *Lautiflorae* are more or less uniform in color with some flecking, whereas petals of subsect. *Sympherica* have distinct areas of color. In addition, subsect. *Lautiflorae* has terete or grooved immature capsules, whereas subsect. *Sympherica* has deeply eight-ribbed immature capsules.

Isozyme analysis challenged certain relationships within sect. *Sympherica*. Odrzykoski & Gottlieb (1984) found that the distribution of gene duplications and subsequent silencings for isozymes of 6-phosphogluconate dehydrogenase (6PGD) indicated that the plastid isozymes are coded by two loci in all diploid species examined except for two

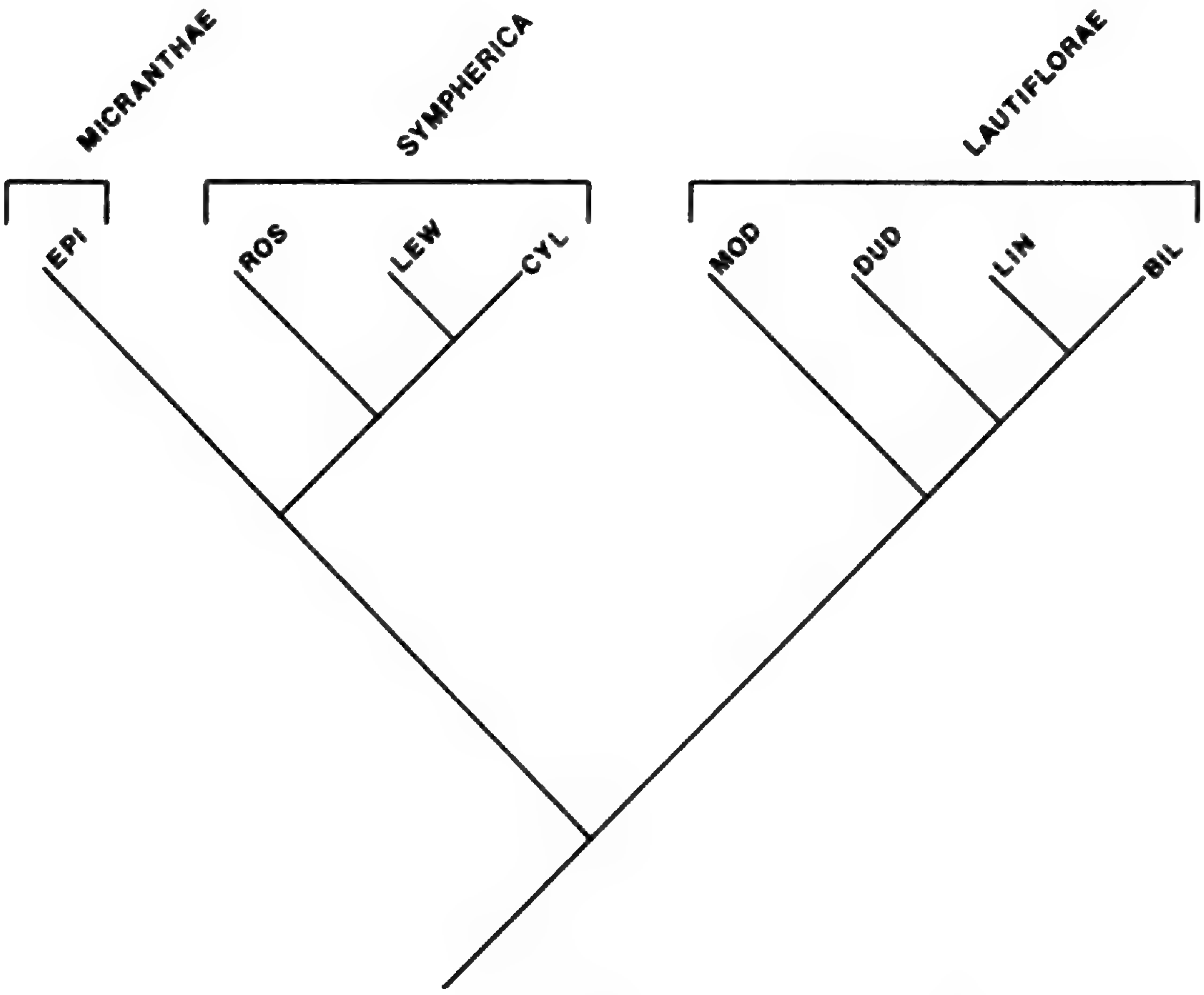

FIGURE 1. *Relationships within* Clarkia *sect.* Sympherica *based on morphological and crossing studies of Lewis & Lewis (1955) and modified after Davis (1970). Subsections are indicated above the species abbreviations.*

species in sect. *Sympherica, C. epilobioides* (Nutt.) Nels. & Macbr. (subsect. *Micranthae*), and *C. rostrata* Davis (subsect. *Sympherica*), which have a single locus coding for the plastid isozymes. In addition, all species of *Clarkia* have a single locus coding for the cytosolic isozyme of 6PGD except for four species of sect. *Sympherica*—*C. epilobioides, C. rostrata,* and the other two species of subsect. *Sympherica, C. cylindrica* (Jeps.) Lewis & Lewis, and *C. lewisii* Raven & Parnell (formerly *C. bottae* (Spach) Lewis & Lewis).

The most parsimonious explanation for the distribution of these character states as suggested by Odrzykoski & Gottlieb (1984) is illustrated in Figure 2. The duplications of the two genes coding the plastid and cytosolic 6PGD isozymes are ancestral in *Clarkia* and retained in the four species of sect. *Sympherica* subsect. *Lautiflorae: C. biloba* (Dur.) Nels. & Macbr., *C. lingulata* Lewis & Lewis, *C. modesta* Jeps., and *C. dudleyana* (Abrams) Macbr. The loss of one of the duplicated cytosolic 6PGDs occurred in the common ancestor of the four species of subsects. *Micranthae* and *Sympherica.* This cytosolic 6PGD loss was then followed by the loss of one of the duplicated plastid 6PGDs in the common ancestor of *C. epilobioides* and *C. rostrata.* Thus, subsect. *Sympherica* is paraphyletic with one species sharing a more recent common ancestor with a species from another subsection than it does with species in its own subsection. This isozyme-based phylogeny clearly contradicts the morphological model in Figure 1 in that *C. rostrata* is placed as the sister species to the distinctive selfer *C. epilobioides* rather than with *C. cylindrica* and *C. lewisii,* species it closely resembles and with which it can experimentally produce fertile hybrids.

A more dramatic difference in results between the classical and molecular techniques was seen when *Heterogaura heterandra* (Torr.) Cov. was used as the outgroup in preliminary cpDNA analysis of sectional relationships in *Clarkia* (see Phylogenetic Analysis of Intersectional Relationships within *Clarkia*). *Heterogaura* is a monotypic genus closely related to *Clarkia,* based on floral morphology, stigma surface, seed coat structure, anther anatomy, and flavonoids (Raven, 1979, 1988; Tobe & Raven, 1985, 1986; Averett et al., 1982). *Heterogaura heterandra* is a strictly self-pollinating annual limited to the slopes of the Sierra Nevada in California and Oregon. It differs markedly from *Clarkia* in having only four fertile anthers (four are sterile), an unlobed stigma, and a round nutlike indehiscent fruit with one or two seeds. In contrast, members of *Clarkia* generally have eight fertile anthers, four-lobed stigmas (although self-pollinat-

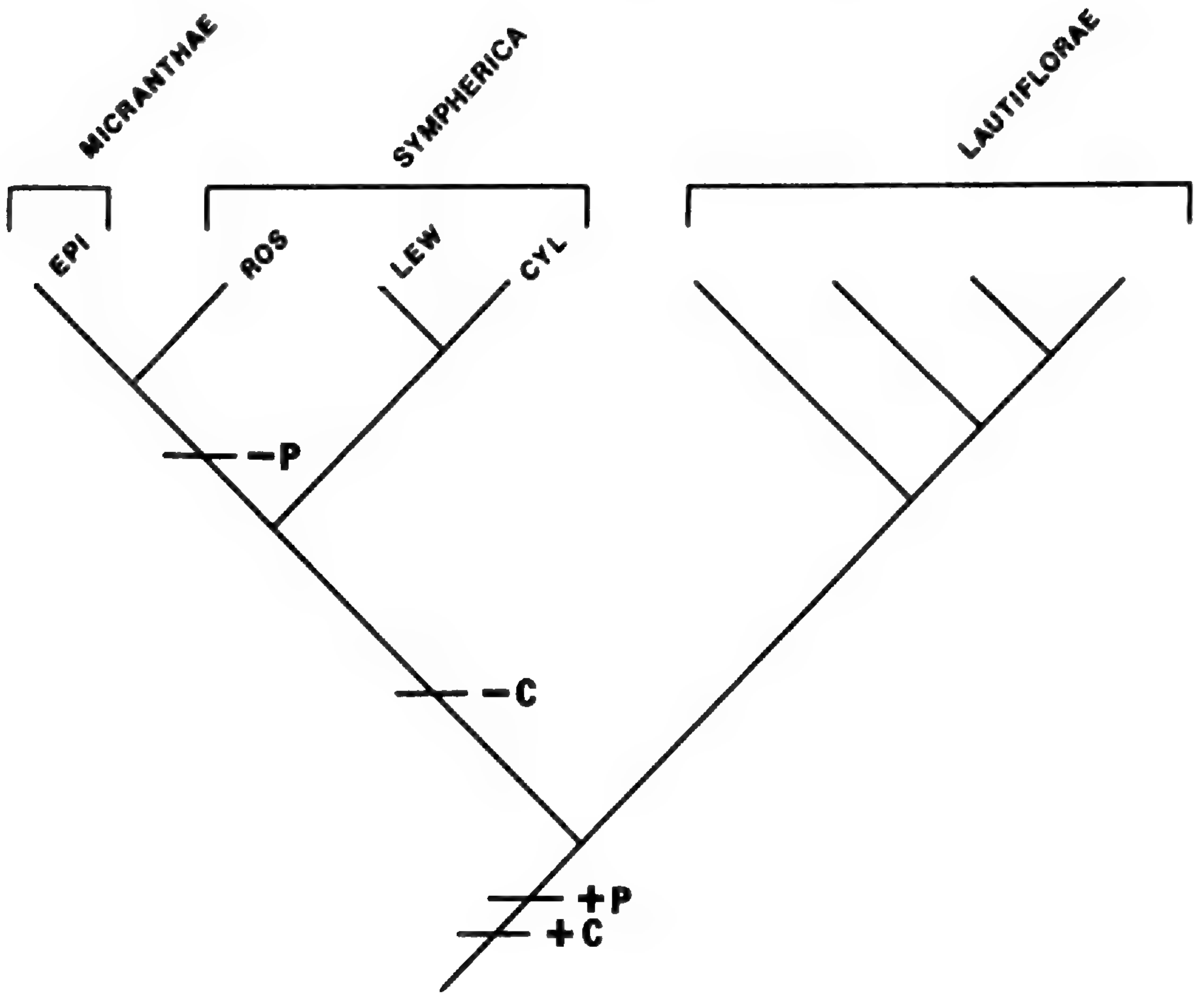

FIGURE 2. *Relationships within* Clarkia *sect.* Sympherica *based on gene number for 6-phosphogluconate dehydrogenase (Odrzykoski & Gottlieb, 1984). Plastid (P) and cytosolic (C) duplications and losses are indicated by + and −, respectively. Subsections are indicated above the species abbreviations. Note that relationships within subsect.* Lautiflorae *are not resolved with the isozyme data.*

ing species have short lobes), and elongated, many-seeded capsules that dehisce along four septa. The floral and fruit differences between the two genera are so distinctive that they have been maintained as separate genera since 1866, when *H. heterandra* was first named.

The long-standing idea that *Heterogaura* is the sister group to *Clarkia* was questioned when it became apparent that restriction fragment analysis of cpDNA indicated that *Heterogaura* was not aligning itself as a basal clade to all of *Clarkia*. Instead, *Heterogaura* exhibited synapomorphies with certain lineages within section *Sympherica* (Sytsma & Gottlieb, 1986a). Section *Sympherica* is relatively advanced in *Clarkia* based on morphology (Lewis & Lewis, 1955) and on the presence of a PGI (phosphogluco isomerase) duplication (Gottlieb & Weeden, 1979). Thus, cpDNA analysis suggested that *Heterogaura* was not an appropriate outgroup for *Clarkia* and, more importantly, indicated that the genus might be derived more recently from within *Clarkia*.

An extensive restriction fragment and site analysis of cpDNA in *Clarkia* sect. *Sympherica* and *Heterogaura heterandra* was initiated to address these discrepancies between the classical results and the results from both isozyme gene duplication and cpDNA restriction fragment analysis (Sytsma & Gottlieb, 1986a, b).

MATERIALS AND METHODS

Seeds of *Heterogaura heterandra* and the eight species of *Clarkia* sect. *Sympherica* were germinated, grown for four to seven weeks, and total DNA extracted using the protocol of Zimmer et al. (1981). Two populations each of *C. biloba*, *C. epilobioides*, *C. lewisii*, *C. modesta*, and *H. heterandra* were assayed; one population was examined for all other species. Only one site difference was seen within a species (*C. biloba*), and this character state was autapomorphic to this one population. *Clarkia xantiana* Gray (sect. *Phaeostoma*) and *C. amoena* (Lehm.) Nels. & Macbr. (sect. *Rhodanthos*) were used as outgroups.

DNAs were digested with 29 restriction enzymes, electrophoresed in agarose gels, and Southern blotted to reusable nylon membrane. The entire clone bank of the *Petunia* (Solanaceae) cpDNA genome was used successively to probe the nylon membranes for homologous cpDNA fragments. Detailed protocols of prehybridization, nick-translation, hybridization, and washes are provided in Sytsma & Schaal (1985a).

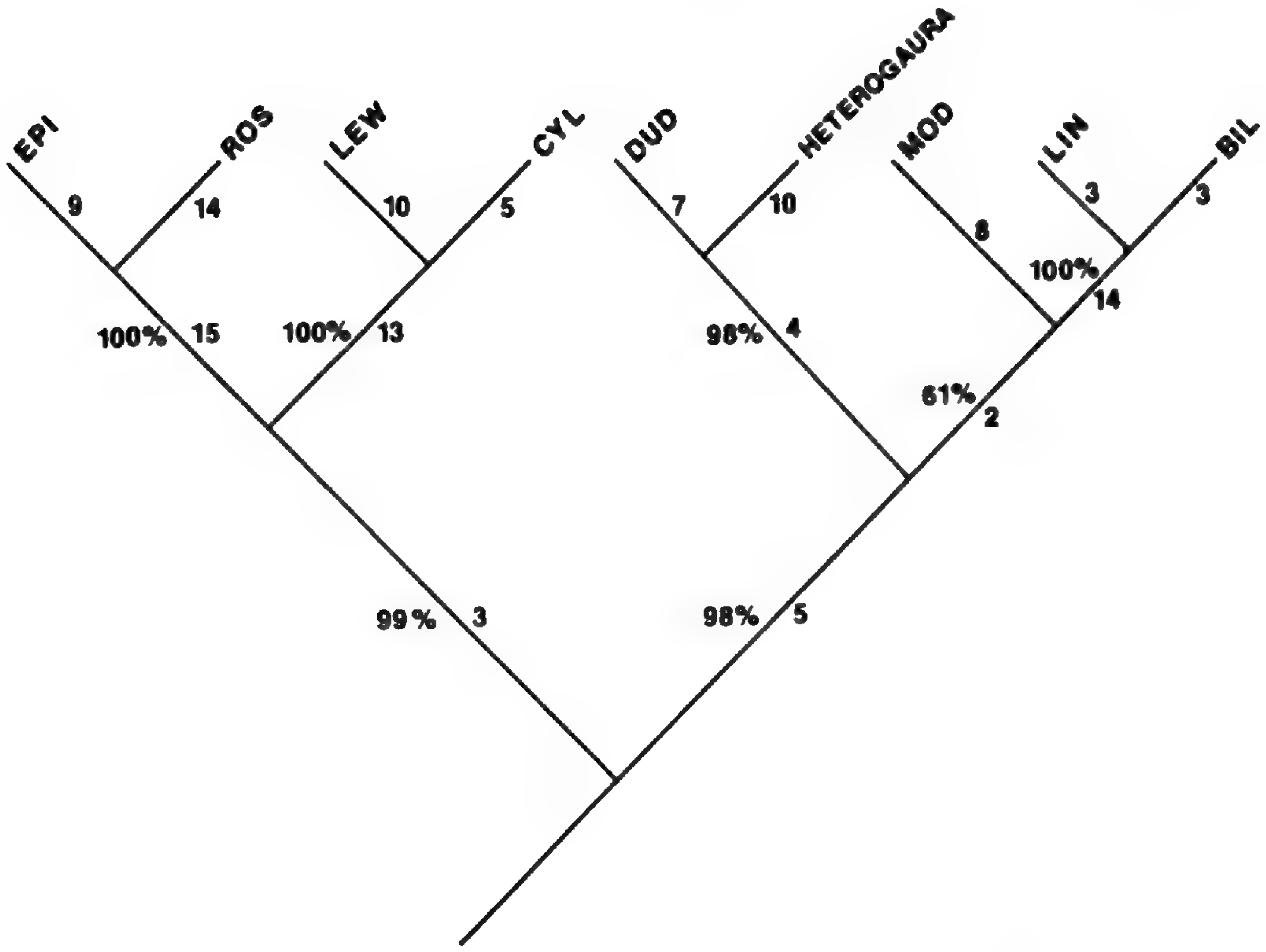

FIGURE 3. *Most parsimonious (Wagner) tree of* Clarkia *sect.* Sympherica *and* Heterogaura heterandra *generated by the "branch-and-bound" option of PAUP. The tree was rooted with* Clarkia xantiana *and* C. amoena. *The tree is 125 steps long and includes two parallel gains, three parallel losses, and one gain/loss. Numbers indicate numbers of restriction site mutations along each lineage. Percentages along branches reflect the number of times that the monophyletic group defined by that branch occurred in 100 bootstrap samples. Based on Sytsma & Gottlieb (1986b).*

Methods of phylogenetic analysis, explained in detail elsewhere (Sytsma & Gottlieb, 1986a, b), included Wagner parsimony (Farris, 1970) (PAUP version 2.4.0, Swofford, 1985), Dollo parsimony (Farris, 1977) (PHYLIP version 3.0, Felsenstein, 1985), and the Fitch & Margoliash (1967) phenetic approach using p values of Nei & Li (1979). Felsenstein's (1985) bootstrap method (in PHYLIP) was utilized to place confidence intervals on resulting phylogenies. A majority-rule consensus Wagner parsimony tree was used to construct a phylogeny indicating all inferred monophyletic lineages determined by bootstrap analysis.

PHYLOGENETIC ANALYSIS AND DISCUSSION

The 29 restriction enzymes used to digest the DNAs recognize approximately 605 restriction sites in each of the cpDNAs. Because all 29 enzymes recognize six base pair sequences, about 3,630 nucleotide base pairs were sampled in each of the species. A total of 119 site changes were documented within *Clarkia* sect. *Sympherica* and *Heterogaura* (these restriction site mutations are listed as table 3 in Sytsma & Gottlieb, 1986b), and 55 of these mutations are shared by at least two but not all members of the ingroup (including *Heterogaura*) and were used as the data matrix in the phylogenetic analyses (Table 1). The PAUP (BANDB option) and PHYLIP (MIX option) programs found a single most parsimonious (Wagner) tree of 125 steps (Fig. 3). This tree requires an additional six steps beyond the 119 site changes to account for the observed variation. The most parsimonious Dollo tree is exactly congruent to the Wagner tree but is four steps longer. The unrooted Fitch & Margoliash network based on nucleotide sequence divergences is topologically congruent to the shortest Wagner tree (see fig. 4 in Sytsma & Gottlieb, 1986b).

The shortest cpDNA phylogenetic tree provides unambiguous evidence for relationships within *Clarkia* sect. *Sympherica*. The cpDNA analysis substantiates Odrzykoski & Gottlieb's (1984) suggestion that *C. rostrata* is indeed phylogenetically closer to *C. epilobioides* than to its morphologically related species, *C. cylindrica* and *C. lewisii*. These results are the first alternative genetic confirmation of phylogenetic relationships based on gene duplication data, and they greatly strengthen the utility of the latter approach in systematics.

Lewis & Lewis (1955) first considered the populations now recognized as *C. rostrata* to be unusual northern members of *C. cylindrica*, but Davis (1970) later separated out *C. rostrata* and indicated that it was more similar to *C. lewisii* than

TABLE 1. *Data matrix of 55 restriction site characters for* Heterogaura heterandra *and the eight species of* Clarkia *sect.* Sympherica. *Outgroup states were determined from examination of* C. amoena *and* C. xantiana. *No autapomorphies are listed. The character state "0" indicates absence of a restriction site and "1" indicates presence of a site. Details concerning each character are presented in Sytsma & Gottlieb (1986b).*

Outgroup	1100010110110100010110001001101000100011000100101100100
Clarkia epilobioides (subsect. *Micranthae*)	01000101110000000000000100101111000110001001110101000110
C. rostrata (subsect. *Sympherica*)	01000101110000000000000100101111000110001001110101000110
C. lewisii (subsect. *Sympherica*)	0110010100111011001110011000101011100011100000100100110
C. cylindrica (subsect. *Sympherica*)	0110010100101011011110011000101011100011100000100100110
C. dudleyana (subsect. *Lautiflorae*)	1100000110100100010111001001101100000001001010000111101
Heterogaura heterandra	1100000110110100010111001001101100000001000010000111101
C. modesta (subsect. *Lautiflorae*)	1000010010110100010111001001101100100011000100101111101
C. lingulata (subsect. *Lautiflorae*)	1001111010110100110110001011000100101111010101111111001
C. biloba (subsect. *Lautiflorae*)	1001111010110100110110001011010100101111010101111111001

to *C. cylindrica*. Moreover, *C. rostrata* can be crossed successfully with the former but not the latter (Davis, 1970). Davis concluded that the close morphological similarity among these three species of subsect. *Sympherica* suggested a common origin or even the derivation of one species from another. *Clarkia rostrata* is found the farthest north in foothills of the Sierra Nevada in Stanislaus, Merced, and Mariposa counties; *C. lewisii* is found only in the Coast Ranges in Monterey and San Benito counties; and *C. cylindrica* is found farther south and in more xeric habitats along the foothills of the southern Sierra Nevada and Tehachapi Mountains (subsp. *clavicarpa*) and in the southern Coast Ranges (subsp. *cylindrica*) (see Fig. 4). All of the progenitor-derivative species pairs examined in *Clarkia* have indicated that the direction of evolution is from north to south or from mesic to more xeric habitats (Lewis, 1962; Lewis & Roberts, 1956; Lewis & Raven, 1958; Vasek, 1958; Gottlieb, 1974). Because of the northern distribution and wide separation of *C. rostrata* and *C. lewisii* and because of the continuous and more southern distribution of the two subspecies of *C. cylindrica*, Davis (1970) suggested that the former two species may have become restricted in their distribution and perhaps preceded *C. cylindrica* or have been involved in its origin.

The gene duplication and the cpDNA data indicate that the evolutionary events within section *Sympherica* are more complex than data based on morphological similarity and crossing relationships indicate. The similarity between *Clarkia rostrata* and the lineage encompassing *C. cylindrica* and *C. lewisii* strongly suggests that the common ancestor of the lineage comprising these three species plus *C. epilobioides* almost certainly resembled the former three species. Alternatively, strong phenetic convergence in *C. rostrata* towards *C. lewisii* and *C. cylindrica* would have to be invoked. *Clarkia epilobioides* is clearly closely related to *C. rostrata* and exemplifies a lineage that has undergone a tremendous amount of morphological divergence relative to other species. *Clarkia epilobioides* ranges from San Francisco to Baja California and has a disjunct range in Arizona (Fig. 4). Because of its exclusively inbreeding mode of reproduction, but despite its northern (and southern) distribution, it is almost certain that *C. epilobioides* has been derived from an outcrossing taxon and does not represent an ancient lineage as might *C. rostrata* and *C. lewisii*.

CpDNA restriction fragment and site analysis have demonstrated clear phylogenetic relationships among the four extant species of subsects. *Micranthae* and *Sympherica* (Fig. 3). Further studies

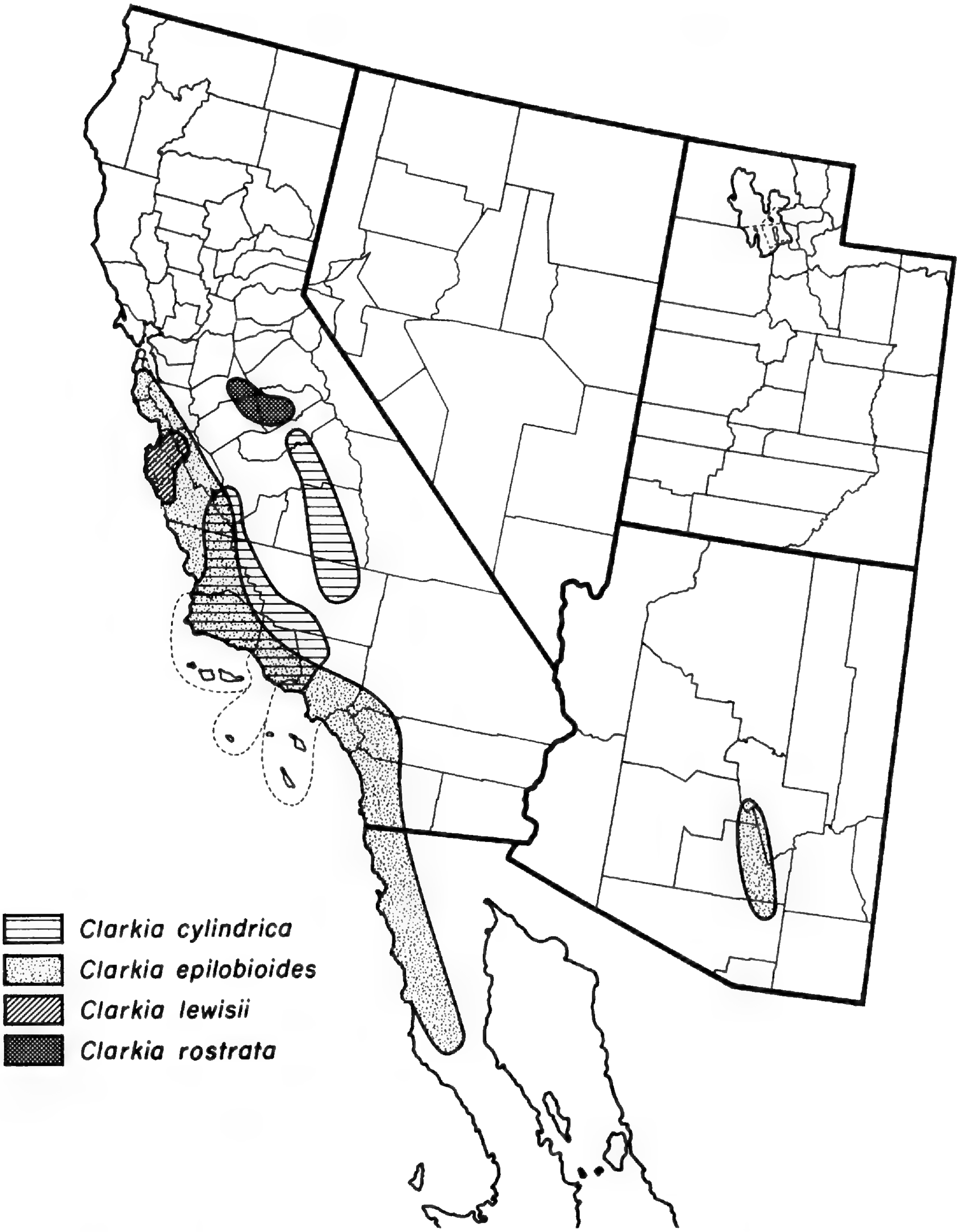

FIGURE 4. *Distribution range of the four species in* Clarkia *sect.* Sympherica *subsects.* Sympherica *and* Micranthae. *Ranges in California, Arizona, and Baja California are provided for* C. cylindrica, C. rostrata, C. lewisii, *and* C. epilobioides. *Adapted from Lewis & Lewis (1955) and Davis (1970).*

involving additional populations from throughout the ranges of these four species and involving biparentally inherited DNA (nuclear genome) are needed to clarify how these species evolved. Questions remaining include: Are *C. rostrata* and *C. lewisii* ancestral in this lineage? Did *C. epilobioides* and *C. cylindrica* diverge independently (or together) from that lineage? What evolutionary forces permitted the rapid morphological divergence in *C. epilobioides?* Can *C. epilobioides* be crossed with three species currently placed in subsect. *Sympherica*, especially *C. rostrata?*

The most parsimonious tree (Fig. 3) also clarifies the relationships within subsect. *Lautiflorae* and the relationship of *Heterogaura heterandra* to *Clarkia*. The cpDNA analysis verifies the close relationship of the proposed progenitor-derivative species pair of *C. biloba* and *C. lingulata* (Lewis & Roberts, 1956; Gottlieb, 1974). Only six mutations separate the two species. The placement of *C. modesta* is the only portion of the phylogenetic tree that is not statistically documented using the bootstrap analysis. The cpDNA analysis conclusively places it within subsect. *Lautiflorae*, but its exact position in the subsection is not certain. The position of *C. modesta* as shown in Figure 3, however, is supported by chromosome numbers. This most parsimonious tree indicates that only one aneuploid decrease from the more widespread $n = 9$ of the section to $n = 8$ (only *C. biloba* and *C. modesta*) has to be invoked. The subsequent reversal to $n = 9$ in *C. lingulata* has been amply demonstrated.

The most striking conclusion of this phylogenetic analysis is the documentation that the genus *Heterogaura* is actually derived within *Clarkia* (Sytsma & Gottlieb, 1986a). Indeed, *H. heterandra* is placed firmly within subsect. *Lautiflorae* with *C. dudleyana* as its sister species. The two species share nine cpDNA synapomorphies despite the extensive morphological divergence between the two. The derivation of *H. heterandra* from a common ancestor with *C. dudleyana* is supported by the next three most parsimonious trees as well. The extreme floral and fruit reduction in *Heterogaura* relative to *Clarkia* have masked the close phylogenetic relationship of *Heterogaura* to an advanced subsection within *Clarkia*.

Flavonoid analysis of *Heterogaura heterandra* and five species of *Clarkia* indicates that the four compounds present in the *Heterogaura* flavonoid profile are also found in the few species of *Clarkia* examined (Averett et al., 1982). Besides cpDNA and nrDNA analyses, therefore, the only evidence that supports a relationship of *Heterogaura* to specific lineages within *Clarkia* is chromosome number. Raven (1979) speculated that *Heterogaura*, with $n = 9$ (found elsewhere only in some *Clarkia* and *Boisduvalia*), "might have been derived from a species of *Clarkia* with the same chromosome number." Morphological or cytological evidence, however, could not place *Heterogaura* near any particular *Clarkia* species because their morphological divergence had completely obscured the relationships.

This study raises additional questions that can or should be addressed in the future: What are the evolutionary forces that permit such rapid morphological divergence as seen in *Heterogaura?* Is the morphological divergence seen in *Heterogaura* (and also *C. epilobioides*) common and thus indicative of what might occur frequently in plants? Can *H. heterandra* be crossed with *C. dudleyana*? How many genes were necessary to get expression of the extreme fruit and floral reduction in *Heterogaura*? Should additional mono- and ditypic genera be suspected as similar derivations from *within* related and more speciose genera instead of as sister genera to these genera (the monotypic *Stenosiphon* and closely related *Oenothera*, for example)? Is the relationship of *Heterogaura* to *Clarkia* actually more complex, involving hybridization and/or introgression, and thus the cpDNA results described here incomplete by not also using biparentally inherited nuclear DNA?

The last question is particularly important because other cpDNA studies have yielded unusual results that suggest hybridization followed by introgression (Palmer et al., 1983, 1985). In these instances, results from cpDNA analysis can be quite different from results from nuclear DNA analysis. For these reasons, restriction site mapping of nuclear ribosomal DNA (rDNA) has been initiated within *Clarkia* and *Heterogaura* to determine if nuclear DNA analysis provides phylogenetic results similar to cpDNA analysis. Methodology for rDNA analysis follows that described in Sytsma & Schaal (1985a). One preliminary piece of information directly concerns the issue of the relationship of *Heterogaura* to *Clarkia*. A partial *Sst I* restriction site map for rDNA in *Clarkia* is shown in Figure 5. *Sst I* fragments *b* and *c* are conserved across the four genera of Onagraceae examined. Fragment *a*, however, is found only in species of *Clarkia* sects. *Sympherica* (*C. biloba*, *C. lingulata*, *C. lewisii*), *Phaeostoma* (*C. xantiana*), *Fibula* (*C. bottae*), and *Heterogaura heterandra*. The *Sst I* site in the 18S gene that delineates fragment *a* is absent in other sections of *Clarkia* and in *Oenothera* and *Lopezia*. These *Clarkia* and other genera thus lack fragment *a* and instead have a large *Sst I* fragment that encompasses fragment *a*, the 18S gene, and an undetermined portion of the nontranscribed spacer region (NTS region in Fig. 5). Outgroup analysis (using *Oenothera* and *Lopezia*) would indicate that the absence of the *Sst I* site in the 18S gene (and thus absence of fragment *a*) is the plesiomorphic condition. This preliminary

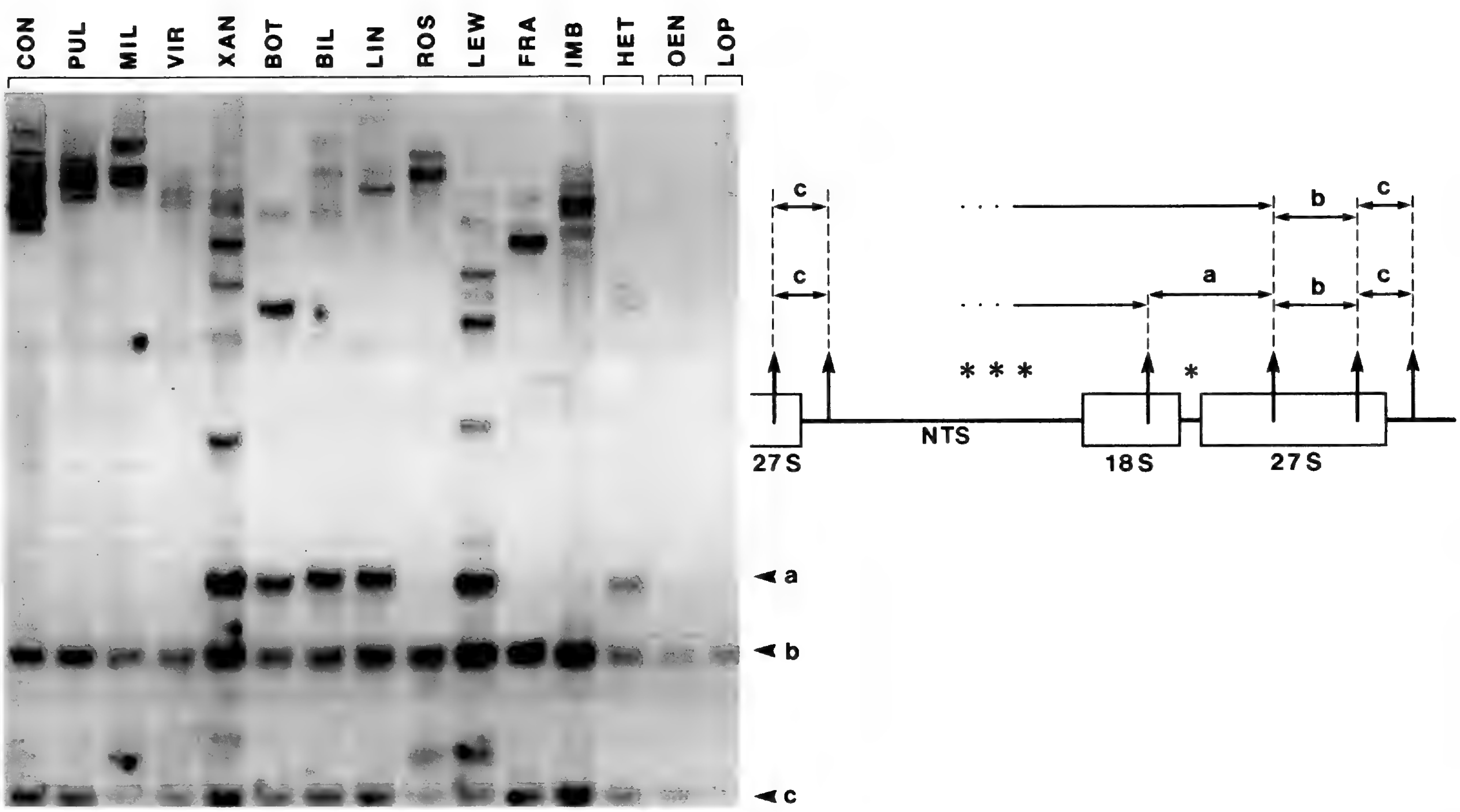

FIGURE 5. *Autoradiogram of* Sst I *restriction fragment patterns and restriction site map for nuclear rDNA in species of* Clarkia, Heterogaura, Oenothera, *and* Lopezia. *Autoradiogram resulted from probing total DNAs (each DNA represents a pooling of several to numerous individuals per population) with a* Glycine *rDNA repeat clone. Ladderlike pattern of higher molecular weight fragments is due to spacer-length variation in fragments spanning portions of the nontranscribed spacer region.*

nuclear rDNA evidence confirms that *Heterogaura* is indeed derived from within the genus *Clarkia* because the former shares a synapomorphy with sections *Sympherica*, *Phaeostoma*, and *Fibula*, sections of *Clarkia* now believed to be related based on gene duplication data (Gottlieb & Weeden, 1979) and cpDNA restriction site mapping data (see Phylogenetic Analysis of Intersectional Relationships within *Clarkia*).

A word of caution should be noted here concerning the phylogenetic use of a single molecular character as done here with rDNA. One could argue that nuclear rDNA evidence for the placement of *Heterogaura* within *Clarkia* is based solely on a single restriction site character that exhibits homoplasy. *Clarkia rostrata* has lost the *Sst I* site that is found in other members of sect. *Sympherica*, even though the weight of morphology (Davis, 1970), isozyme gene duplications (Odrzykoski & Gottlieb, 1984), and cpDNA analysis (Sytsma & Gottlieb, 1986b) fully supports its inclusion in sect. *Sympherica*. Thus, *C. rostrata* has lost the *Sst I* site secondarily. Does this homoplasy involving *C. rostrata* cast doubt on the relationship of *Heterogaura* to *Clarkia* using nuclear rDNA? No, because the loss of the *Sst I* site in *C. rostrata* (thus producing the plesiomorphic character state) is a statistically likely gain/loss type of convergence (Templeton, 1983). On the other hand, there is little such support that the gain of the *Sst I* site in *Heterogaura* is also due to convergence rather than to shared common ancestry with certain lineages within *Clarkia*. Such a convergent restriction site gain is an order of magnitude less likely to occur than a convergent loss or a gain/loss (Templeton, 1983).

PHYLOGENETIC ANALYSIS OF INTERSECTIONAL RELATIONSHIPS WITHIN *CLARKIA*

INTRODUCTION

The monograph of *Clarkia* by Lewis & Lewis (1955) was a landmark study in classical biosystematics. Prior to their work, *Clarkia* was divided into a number of distinct genera (*Clarkia*, *Godetia*, *Phaeostoma*, and *Eucharidium*). Using extensive population collections in which they examined floral and vegetative morphology, chromosome number, and crossing relationships, Lewis & Lewis were able to define convincingly 11 natural sections in the inclusive generic concept of *Clarkia*. The naturalness of *Clarkia* has been commented on by subsequent researchers (Raven, 1979, 1988) and demonstrated on molecular grounds (Pichersky & Gottlieb, 1983).

Relationships among the seven predominantly diploid sections, as viewed by Lewis & Lewis (1955), are depicted in Figure 6. Ancestral clarkias were viewed as having relatively large, lavender-pink, bowl-shaped (godetia-type) flowers with petal markings, being self-compatible but outcrossed, possessing the chromosome number $n = 7$, and having a northern distribution (Lewis, 1980). Evolution in *Clarkia* has occurred primarily from north to south and involved development of floral tubes (sects. *Eucharidium* and *Clarkia*), extensive repatterning of the chromosomes with subsequent aneuploid increases and decreases from the primitive haploid number 7 or polyploidy (all sections), and formation of autogamous breeding systems (many sections). The large classical information base for *Clarkia* and the spectacular evolutionary changes that are seen in the genus have made it a model system for subsequent evolutionary studies (Lewis, 1980; Raven, 1988).

Recent isozyme analysis, however, has challenged certain aspects of the phylogeny proposed on morphology, chromosomes, and crossing studies. Gottlieb & Weeden (1979) provided evidence that a duplication of the cytosolic gene for PGI (phosphogluco isomerase) defines four diploid sections (*Sympherica*, *Phaeostoma*, *Fibula*, and *Eucharidium*), previously not placed together by Lewis & Lewis (1955), as a monophyletic lineage. Indeed, sect. *Eucharidium*, with its distinctive stamen reduction, elongated floral tube, pollen features (Small et al., 1971), and lepidopteran pollination syndrome, represents the greatest morphological divergence from putative ancestral clarkias (Lewis, 1980). Section *Eucharidium* originally was retained within *Clarkia* only because it was strongly suspected of being involved in the intersectional derivation of the polyploid *C. pulchella* (Lewis & Lewis, 1955). The weight of this molecular evidence led Lewis (1980) to accept the argument of Gottlieb & Weeden (1979) and to propose the phylogeny illustrated in Figure 7. An analysis was initiated using restriction site mapping of cpDNA from representatives of the diploid sections to test these alternative models of sectional relationships in *Clarkia*. Presented here are preliminary phylogenetic results from this analysis; a more detailed phylogenetic analysis on an expanded data set is in progress (Sytsma et al., in prep.).

MATERIALS AND METHODS

Total DNAs of two species of each of the seven diploid sections (one species in the monotypic *Fibula*) were obtained as described above. These rep-

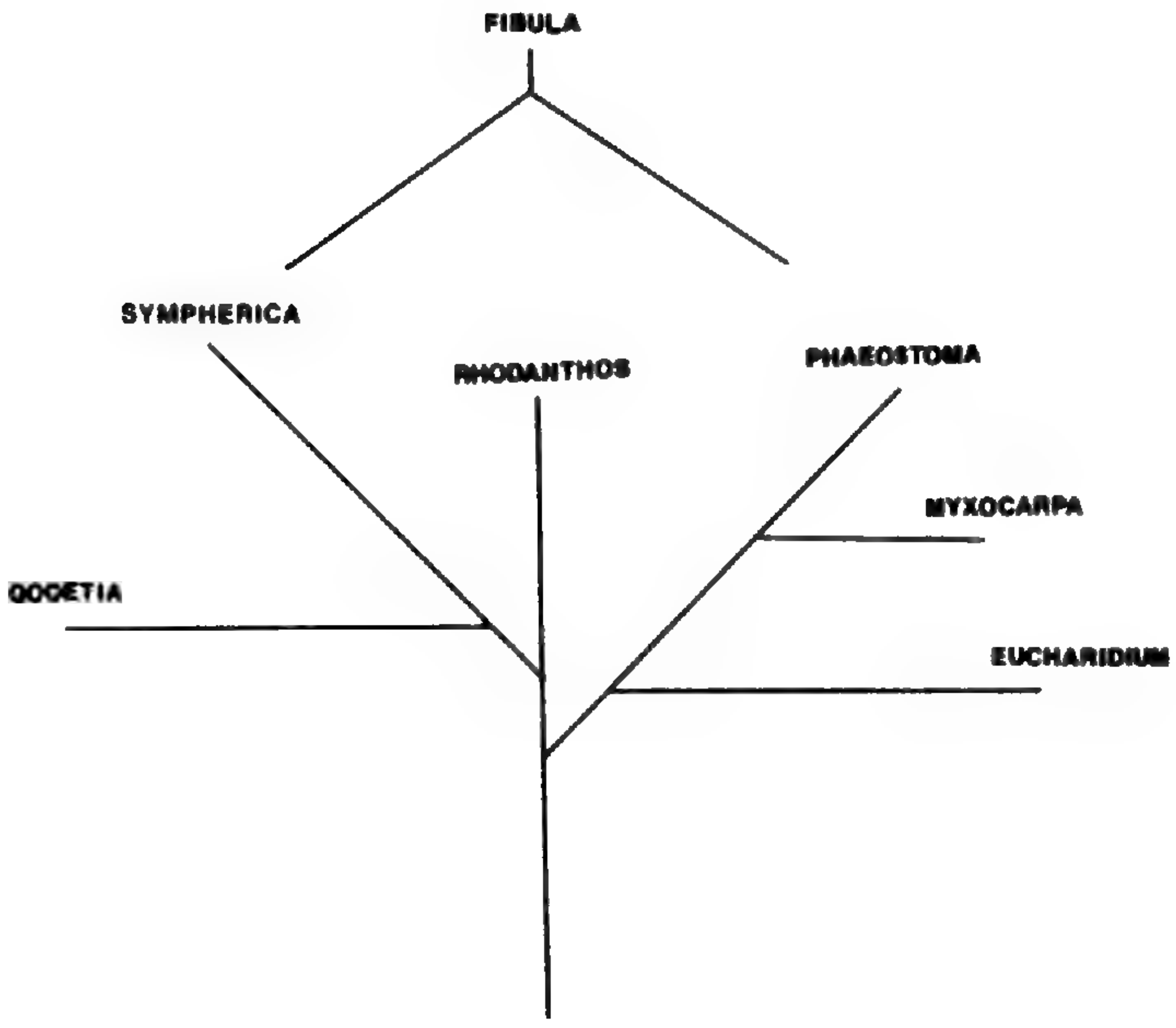

FIGURE 6. *Relationships among the seven diploid sections of* Clarkia *based on morphology, chromosome numbers and features, and crossing relationships. Phylogeny modified after Lewis & Lewis (1955). (*Rhodanthos *is the former* Primigenia, *and* Sympherica *is the former* Peripetasma.*)*

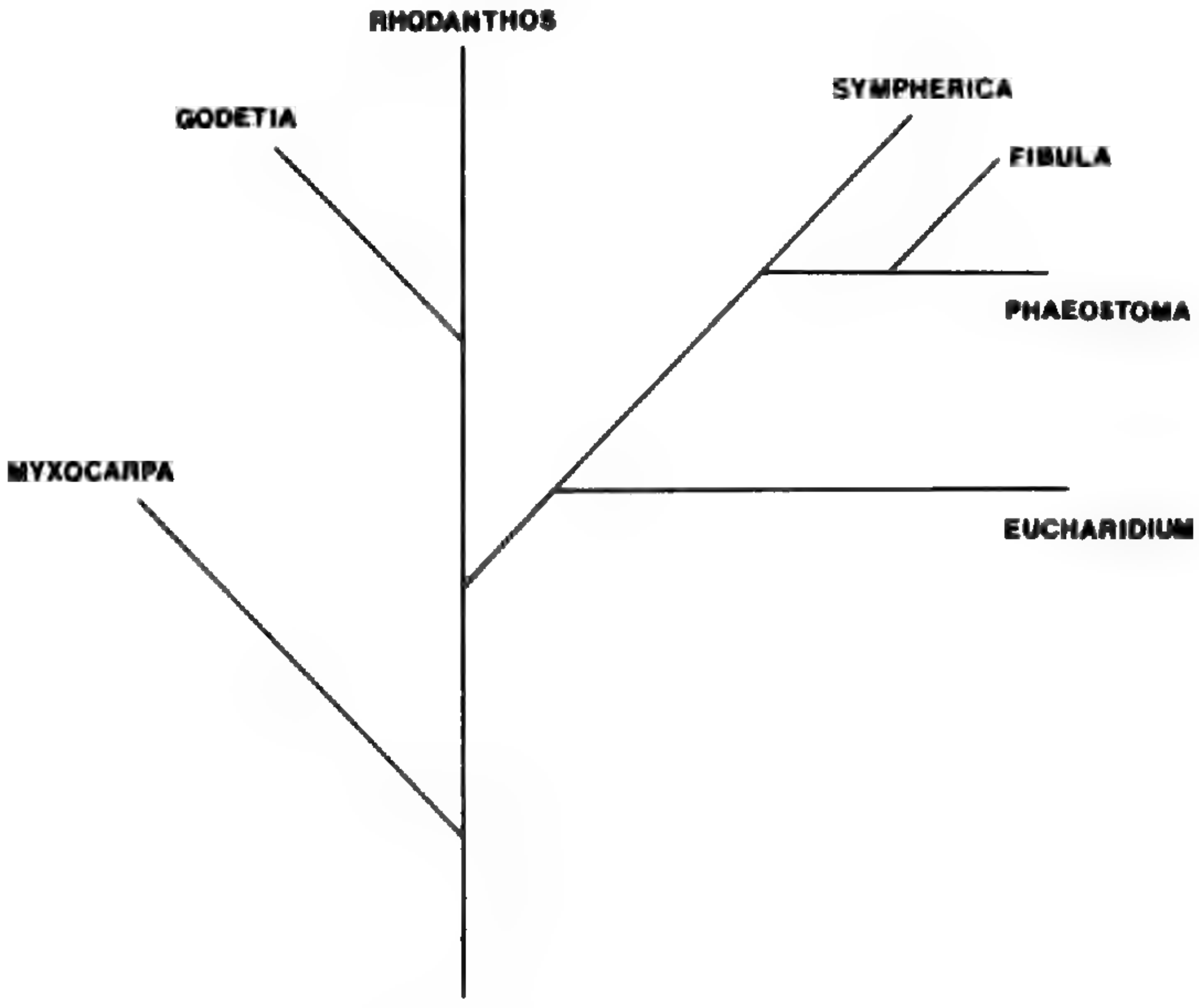

FIGURE 7. *Relationships among sections of* Clarkia *based on the inclusion of the distribution of the duplicated PGI gene with morphology, chromosome numbers and features, and crossing relationships. Phylogeny modified after Lewis (1980).*

resentative species were *Clarkia amoena* and *C. lassenensis* (Eastw.) Lewis & Lewis (sect. *Rhodanthos*), *C. imbricata* Lewis & Lewis and *C. williamsonii* (Dur. & Hilg.) Lewis & Lewis (sect. *Godetia*), *C. mildrediae* (Heller) Lewis & Lewis, and *C. virgata* Greene (sect. *Myxocarpa*), *C. breweri* (Gray) Greene and *C. concinna* (Fisch. & Mey.) Greene (sect. *Eucharidium*), *C. xantiana* and *C. unguiculata* Lindl. (sect. *Phaeostoma*), *C. bottae* (sect. *Fibula*), and *C. biloba* and *C. rostrata* (sect. *Sympherica*).

Preliminary surveys of restriction fragment variation using methods described above indicated that substantial amounts of site mutations and length mutations are evident at the intersectional level in *Clarkia*. The amount of both types of variation was so high that even the small portions of the chloroplast genome examined with individual probes often exhibited fragment patterns too complex to interpret accurately. Numerous insertions and deletions made it difficult to decide what were homologous fragments. The increased frequency of multiple mutations in a given fragment often generated complex fragment patterns. For these reasons, restriction site mapping using only seven enzymes, rather than restriction fragment comparisons of numerous enzymes, was selected as the method to examine the phylogenetic relationships among sections in *Clarkia*. This method involves reciprocal double digests to map exactly an enzyme's restriction sites relative to sites of other enzymes. Although this method is more laborious and less productive in terms of numbers of mutations screened, the method produces precise cpDNA maps for groups in which variation is often too great and interpretation of homology too difficult for simple fragment pattern analysis. The restriction enzymes *Pst I*, *Sal I*, *Sma I*, *Kpn I*, *Pvu II*, *Xho I*, and *Nru I* were used to digest total DNAs alone and in double digests with at least two other enzymes. Replicate filters were successively probed with the entire *Petunia* clone bank (courtesy of J. Palmer & E. Clark), portions of the *Lactuca* clone bank (courtesy of R. Jansen), and *rbcL* and B subunit *atpase* gene clones (courtesy of G. Zurawski). Map positions for these probes are illustrated elsewhere (Sytsma & Gottlieb, 1986b, fig. 1). Alignment of the maps was facilitated by the conservative nature of the chloroplast genome (Palmer, 1985a, b, 1986a, b; Palmer & Stein, 1986) and of specific restriction sites, especially sites of *Pst I* within the *rbcL* gene and *Pvu II* and *Sma I* within the rRNA genes of the inverted repeat (Sytsma & Gottlieb, 1986b, and J. Palmer, pers. comm.).

Phylogenetic analysis utilized Wagner parsimony (PAUP) to derive the most parsimonious trees. Because *Heterogaura* is no longer an appropriate outgroup to *Clarkia*, *Oenothera* (tribe Onagreae) and *Epilobium* (tribe Epilobieae) were examined. *Oenothera biennis*, currently mapped (Sytsma & Smith, unpubl. data), is not an appropriate outgroup even though it is placed within the same tribe as *Clarkia*, because it contains a large inversion in the large single copy region of the chloroplast genome. *Epilobium brachycarpum* Presl (=*E. paniculatum* Nutt. ex Torr. & A. Gray), although placed in a separate tribe, was used as

TABLE 2. *Data matrix of 23 restriction site characters for representatives of the seven diploid sections of* Clarkia *(13 species) and one outgroup (*Epilobium*). No autapomorphies are listed. The character state "0" indicates absence of a restriction site and "1" indicates presence of a site. Details concerning each character will be presented elsewhere (Sytsma & Gottlieb, in prep.).*

Epilobium brachycarpum	11111001000010000001110
Clarkia biloba (*Sympherica*)	00111001000010000000000
C. rostrata (sect. *Sympherica*)	00111001000010000000000
C. xantiana (sect. *Phaeostoma*)	10110001000011100100000
C. unguiculata (sect. *Phaeostoma*)	00111001000010000000000
C. bottae (sect. *Fibula*)	00010001001011000100000
C. concinna (sect. *Eucharidium*)	01100000011010010010000
C. brewerii (sect. *Eucharidium*)	01100001011011110010000
C. imbricata (sect. *Godetia*)	00100001000010011001111
C. williamsonii (sect. *Godetia*)	00100001000010011001111
C. amoena (sect. *Rhodanthos*)	00110001000000000000000
C. lassenensis (sect. *Rhodanthos*)	00110001000000000000000
C. virgata (sect. *Myxocarpa*)	00110111100110000000000
C. mildrediae (sect. *Myxocarpa*)	00110110100110000000000

the outgroup for *Clarkia*. The PAUP option BANDB (Hendy & Penny, 1982) was run to find most parsimonious trees. These trees were used to construct a strict consensus tree using the PAUP option CONTREE.

PHYLOGENETIC ANALYSIS AND DISCUSSION

Restriction site maps of cpDNAs from the seven sections of *Clarkia* and from *Epilobium brachycarpum* are presented elsewhere (Sytsma et al., in prep.). The seven restriction enzymes mapped to date recognize ± 100 sites on average in each cpDNA. This represents 0.4% of the total nucleotide sequence of each cpDNA. A total of 51 restriction site mutations were found among the 13 *Clarkia* species examined. An additional 14 site mutations were found in *Epilobium* relative to all *Clarkia*, but these are not further analyzed here because they do not provide additional information concerning relationships among *Clarkia* sections; they are being used in a family-wide phylogenetic analysis (Sytsma & Smith, in prep.). Of the 51 restriction site mutations documented, 23 are phylogenetically informative; that is, they are shared by at least two but not all of the OTUs. The data matrix for these 23 restriction site characters in the seven sections examined makes up Table 2. No autapomorphies were included in the PAUP analysis. To simplify the phylogenetic analysis further, *C. rostrata* and *C. imbricata* were removed from the phylogenetic analysis because for these 23 characters they are identical in character states to *C. biloba* and *C. williamsonii*, respectively. These species pairs are identical for the phylogenetically informative characters examined here, although a number of autapomorphies were seen for individual species.

The Wagner analysis using option BANDB found 201 most parsimonious trees of length 32. With the autapomorphies included, these trees have a total length of 60 steps and a consistency index (Kluge & Farris, 1969) of 0.850. The strict consensus tree derived from 100 of these most parsimonious trees is illustrated in Figure 8A. The high level (15%) of homoplasy in the *Clarkia* data set, which is similar to that found within the entire Asteraceae (Jansen & Palmer, 1988, pers. comm.) could be due in part to (1) multiple changes between the outgroup *Epilobium* and the ingroup *Clarkia*, (2) the more rapid divergence of cpDNA in the strictly annual *Clarkia*, and/or (3) the greater age of *Clarkia* relative to the Asteraceae. The first situation would give rise to trees where errors are made in the determination of the plesiomorphic character state. Two additional PAUP analyses were thus performed: (1) scoring the plesiomorphic state of characters involved in multiple changes from outgroup to ingroup as unknown (characters 1 and 2 scored as missing in the outgroup in this instance) and (2) removal of the outgroup taxon and use of midpoint rooting. Midpoint rooting can clearly only be justified if rates of character change throughout lineages are nearly equal. Clocklike evolution of chloroplast DNA could not be statistically rejected for *Clarkia* sect. *Sympherica* (Sytsma & Gottlieb, 1986b), thus lending support to the use of midpoint rooting within *Clarkia*. Scoring the outgroup state of characters 1 and 2 as missing and allowing PAUP to determine the plesiomorphic states resulted in the same 201 most parsimonious trees, but homoplasy was reduced by two convergences in each tree (58 total steps including autapomorphies, C.I. = 0.879, 12% rate of homoplasy). Removal of *Epilobium* completely and resorting to midpoint rooting resulted in 15 most parsimonious trees, each five steps shorter than trees generated with *Epilobium* present (55 total steps including autapomorphies, C.I. = 0.927, 7% rate of homoplasy). The strict consensus tree of these 15 trees is depicted in Figure 8B.

Phylogenetic relationships among sections of *Clarkia* as depicted in the consensus tree of Figure 8A suggest that sect. *Godetia* is monophyletic and the sister group to the rest of *Clarkia*. The early divergence of sect. *Godetia* is also seen when *Epilobium* is removed as an outgroup and midpoint rooting is performed (Fig. 8B). Section *Godetia* consists of diploid and polyploid species similar in many respects to sect. *Rhodanthos* and, according to Lewis & Lewis (1955), almost certainly derived from the "primitive" *Rhodanthos* and not clearly related to any other section. Several morphological features constant in sect. *Godetia*, notably the erect buds and rachis and the conspicuously eight-ribbed ovary, are found in portions of sect. *Rhodanthos* (Lewis & Lewis, 1955). Derivation of sect. *Godetia* from elements within sect. *Rhodanthos* is consistent with respect to chromosome number, since all diploid species of sect. *Godetia* apparently have evolved with increase in chromosome number from $n = 7$ (found in sect. *Rhodanthos*) to both $n = 8$ and $n = 9$ (found in sect. *Godetia*). Further support for this early split of sect. *Godetia* comes from a preliminary cladistic analysis of 38 characters encompassing morphology and isozyme gene duplications, which places sect. *Godetia* as the sister group to the rest of *Clarkia* (K. Holsinger, pers. comm.). It is possible that sect. *Godetia* was indeed the first lineage splitting off from ancestral clarkias, but it also appears that this ancestral group, perhaps now encompassing sect. *Rhodanthos*, continued to evolve and subsequently split off the other sections. A larger survey of species within sect. *Rhodanthos* would be needed to detect the possibility that this section is paraphyletic, with different elements giving rise independently to *Godetia* and to the other sections. This scenario is implicitly suggested by the phylogenetic model of Lewis & Lewis (1955; also see Fig. 6) and by the distribution of phosphoglucomutase (PGM) gene duplications (Soltis et al., 1987).

Relationships within the second lineage comprising the other six diploid sections is not clear, as all sections split at a polychotomous node (Fig. 8A). Of these six sections, all but sect. *Phaeostoma* are monophyletic lineages. *Clarkia xantiana* and *C. unguiculata* (sect. *Phaeostoma*) consistently do not form a monophyletic clade in most of the 100 most parsimonious trees examined in detail (data not shown). Indeed, *C. xantiana* often is aligned with *C. bottae* of sect. *Fibula*, whereas *C. unguiculata* often is aligned with *C. biloba* and *C. rostrata* of sect. *Sympherica*. These relationships are seen in the consensus tree when the outgroup is omitted (Fig. 8B). Lewis & Lewis (1955) postulated that *C. bottae* (formerly *C. deflexa*), the only species of sect. *Fibula*, represented a diploid hybrid between sects. *Sympherica* and *Phaeostoma*. If this is true, the maternal genome of *C. bottae* most likely came from a species similar to *C. xantiana* of sect. *Phaeostoma* and not *C. unguiculata* as postulated by Lewis & Lewis (1955).

The proposed monophyletic nature of sects. *Eucharidium*, *Sympherica*, *Phaeostoma*, and *Fibula* based on the presence of the PGI duplication (Gottlieb & Weeden, 1979) cannot be rejected or supported with the results of cpDNA restriction site

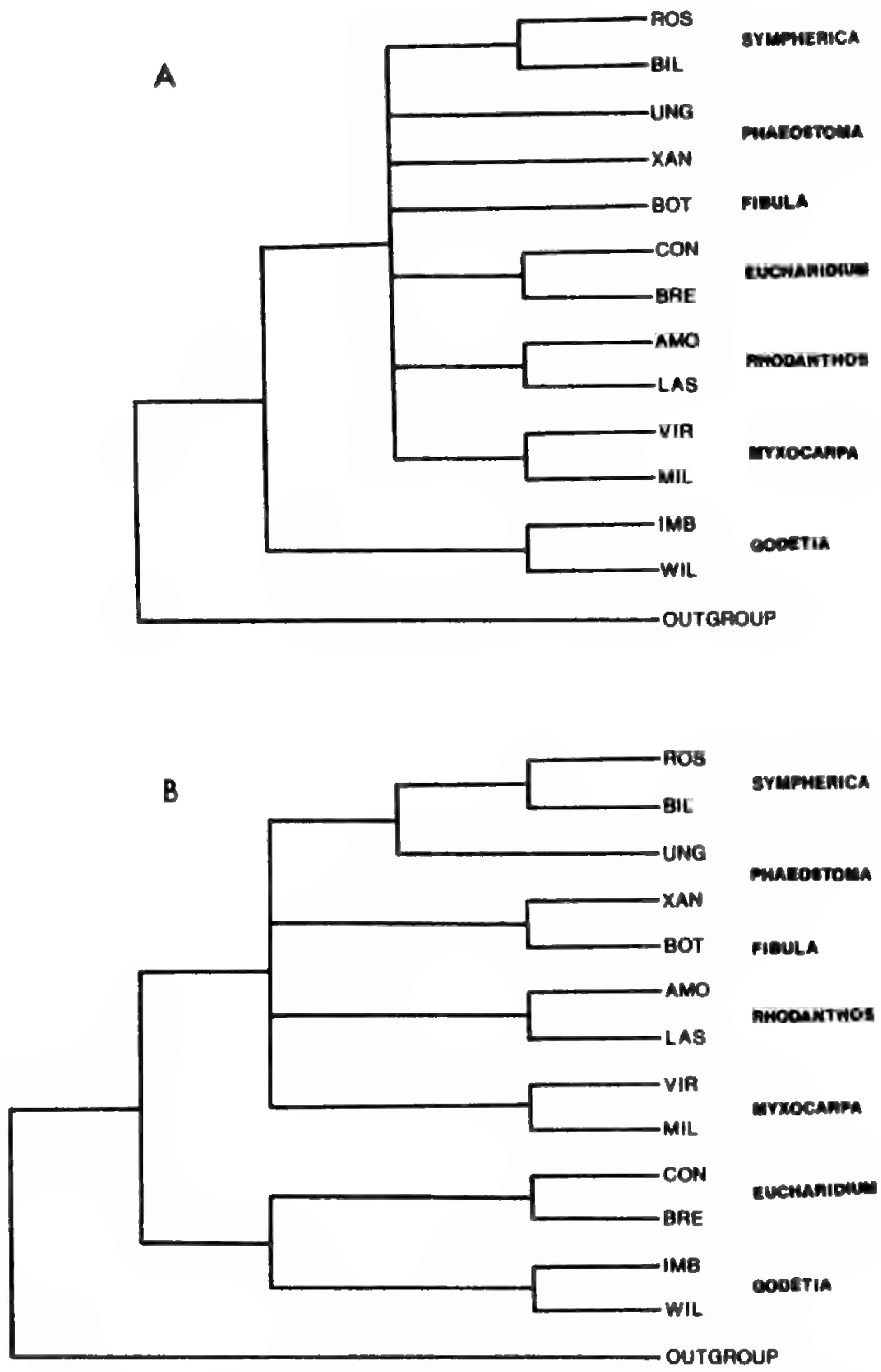

FIGURE 8. *Strict consensus trees of relationships among sections in* Clarkia *based on chloroplast DNA restriction site mapping.—A. This phylogenetic tree is rooted with* Epilobium *and is derived from PAUP analyses using 100 most parsimonious trees.—B. This phylogenetic tree is based on the full data set minus* Epilobium, *rooted using the MIDPOINT option in PAUP, and using 15 most parsimonious trees. See text for discussion.*

mapping when using *Epilobium* as an outgroup, since all four sections, along with sects. *Rhodanthos* and *Myxocarpa*, split from a polychotomous node (Fig. 8A). However, when *Epilobium* is removed as an outgroup and midpoint rooting is used, sect. *Eucharidium* is placed in a lineage with sect. *Godetia* and is separate from the other three sections with the PGI gene duplication (Fig. 8B).

Preliminary nuclear rDNA evidence supports the separation of sect. *Eucharidium* from sects. *Sympherica*, *Phaeostoma*, and *Fibula*. As detailed earlier, sects. *Sympherica*, *Phaeostoma*, and *Fibula* share a synapomorphic gain of an *Sst I* site in the 18S gene of nrDNA (Fig. 5). Section *Eucharidium* retains the plesiomorphic condition also found in sects. *Myxocarpa*, *Godetia*, and *Rhodanthos* and in *Oenothera* and *Lopezia*. This rDNA site mutation could also be argued as arising within a monophyletic lineage of the four sections but *after* the split of sect. *Eucharidium*.

An obvious problem that is apparent with the *Clarkia* cpDNA data set is the low number of synapomorphic characters shared by two or more sections. A rapid and early divergence of most of the sections within *Clarkia* could account for the relatively low numbers of phylogenetically informative site changes encountered *among* sections. The slowly evolving chloroplast genome would not be expected to exhibit numerous changes in the short time intervals when the sections shared common ancestors. Conversely, most cpDNA sequence changes would be expected in the long time periods *after* most sections had already diverged. Additional restriction enzymes that recognize low numbers of sites in cpDNA (*Bgl I*, *Sst I*, for example; see Palmer, 1986a) are now being examined for variation within *Clarkia*. Additional analyses are also under way to examine individually the sets of most parsimonious cpDNA-derived trees for the number in each tree of unlikely convergent gains and loss/gains relative to the more likely convergent losses and gain/losses (Templeton, 1983). A subset of more likely trees (i.e., with fewer convergent gains or loss/gains) might then be found to demonstrate more rigorously phylogenetic relationships within *Clarkia*.

PHYLOGENETIC RELATIONSHIPS AND DIVERGENCE WITHIN *FUCHSIA*

INTRODUCTION

Fuchsia is a genus of 102 species belonging to ten sections (Berry, 1982; Raven, 1988; Berry et al., 1988). Most species of this genus of outcrossing shrubs and some trees occur in South America, including 60 species of sect. *Fuchsia* (two in Hispaniola), 14 species of sect. *Hemsleyella*, 8 species of sect. *Quelusia*, the monotypic sect. *Kierschlegeria*, and an undescribed monotypic section from northern Peru. Twelve species of sects. *Ellobium*, *Encliandra*, *Jimenezia*, and *Schufia* occur in Mexico and Central America. The four species of sect. *Skinnera* are found in New Zealand (3) and Tahiti (1).

Most lines of evidence point to an origin of *Fuchsia* in austral temperate forests of South America in Paleogene times (Berry, 1982; Raven, 1988). The species of the large South American sect. *Quelusia*, restricted to the mountains of southeastern Brazil, with one species in Chile, possess the largest suite of generalized characters in the genus and may represent the extant section most similar to ancestral fuchsias. These characters include shrubby habit, bisexual flowers, well-developed petals, bird-pollination, numerous seeds, and segmented-beaded viscin pollen threads (Skvarla et al., 1978; Berry, 1982; Nowicke et al., 1984; Averett et al., 1986; Raven, 1988). Raven (1988) postulated that *F. lycioides* Andr. (sect. *Kierschlegeria*) is related to sect. *Quelusia*, based on their polyploidy and temperate South American distribution. But *F. lycioides* has a number of derived characters, including its dry coastal scrub habitat, summer deciduousness, functional dioecy, small flowers, few seeds, and smooth viscin pollen threads.

The first offshoot in *Fuchsia* probably involved the lineage that dispersed to New Zealand and subsequently Tahiti (Fig. 9). This lineage, now comprising four species in sect. *Skinnera*, separated from the rest of *Fuchsia* at least 25 million years ago since fossil pollen has been recorded in late Oligocene and early Miocene deposits from New Zealand (Mildenhall, 1980; Daghlian et al., 1985) and eastern Australia (P. Berry, pers. comm.). *Skinnera* is the most distinctive section in the genus, with the advanced conditions of male sterility (Godley, 1955), reduced petals, and varying life forms that include a tree, a scandent shrub, and an almost herbaceous creeper.

Other early dispersal events probably included the ancestor to the morphologically related sections *Encliandra*, *Jimenezia*, and *Schufia* of Mexico and Central America (Fig. 9). These sections share unusual characters of small flowers, smooth viscin pollen threads, male sterility, and lobed adnate nectaries (Breedlove et al., 1982; Berry, 1982). These three sections are so distinctive that it is difficult to relate them to their South American relatives (Raven, 1988). The two most speciose

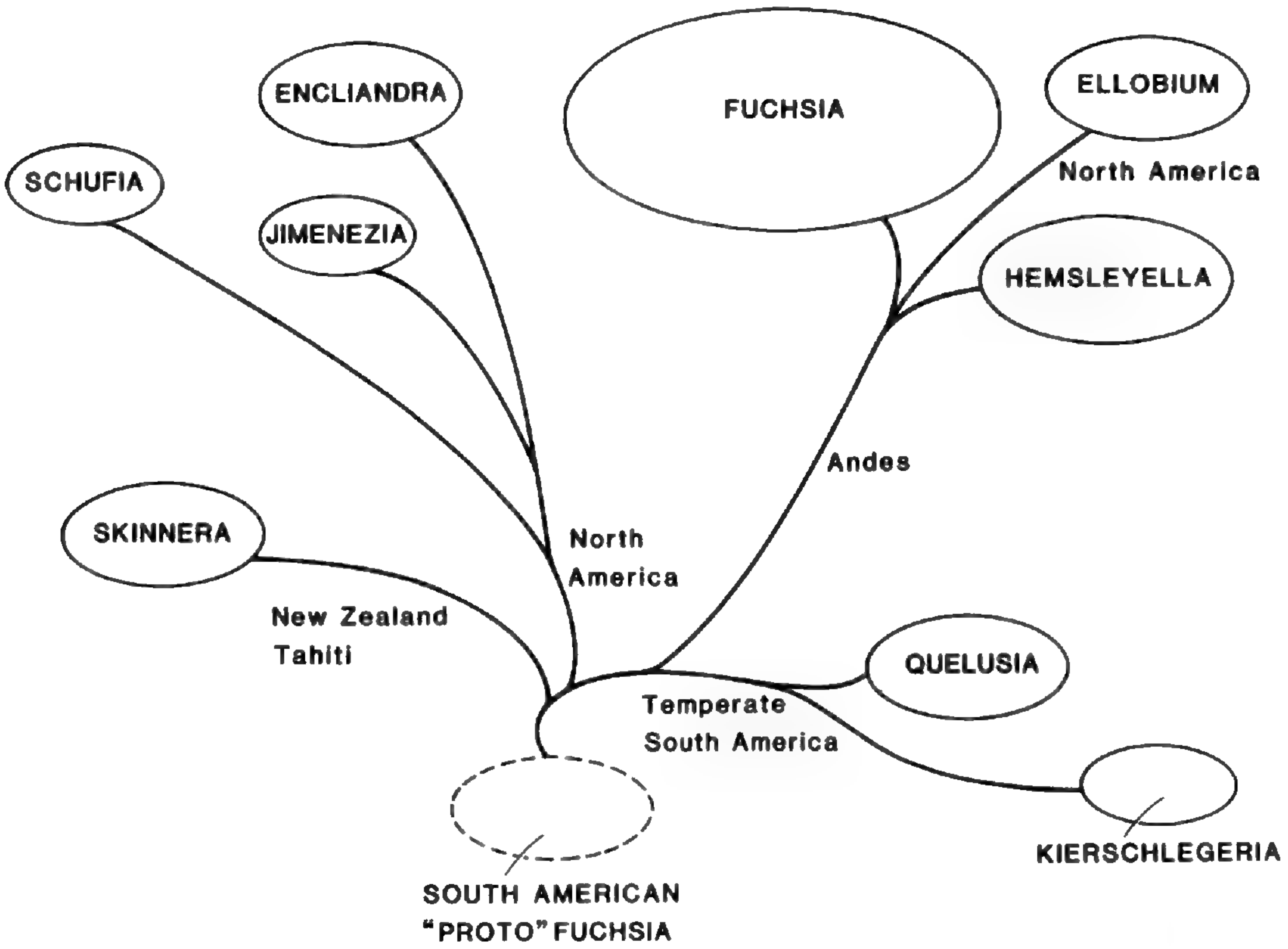

FIGURE 9. *Schematic diagram illustrating probable dispersal events in the genus* Fuchsia *(based almost entirely on ideas presented in Berry, 1982; Breedlove et al., 1982; and Raven, 1988). No extant section is depicted as ancestral to the genus. Section* Quelusia, *however, is depicted as retaining the greatest number of character states that such an ancestral fuchsia would probably have had. See text for discussion.*

sections, *Fuchsia* and *Hemsleyella*, occurring mostly on moist slopes of the tropical Andes, most certainly evolved rapidly as the Andes uplifted to their present height over the past few million years (Berry, 1982; Raven, 1988). The fourth Mexican and Central American section, *Ellobium*, is related to these two Andean sections and represents an additional and probably Neogene dispersal event of *Fuchsia* northward (Fig. 9).

Flavonoid analyses of many *Fuchsia* species have provided useful information concerning evolution within the genus (Williams et al., 1983; Averett & Raven, 1984; Averett et al., 1986). Flavones, otherwise rare in the Myrtales (Gornall et al., 1979), are found in Onagraceae only in *Circaea* and *Fuchsia*. The presence of flavones is presumed to be ancestral in *Fuchsia*, since they are found in all species of sect. *Skinnera*, in the primitive *F. splendens* of sect. *Ellobium*, in the primitive *F. magellanica* Lam. of sect. *Quelusia*, in sect. *Kierschlegeria*, and in two species of sect. *Fuchsia* (Averett et al., 1986). The presence of sulfated flavones only in sect. *Skinnera* again emphasizes the distinctiveness of the section within *Fuchsia* (Williams et al., 1983).

A chloroplast DNA restriction fragment and site analysis was begun in *Fuchsia* to look at a number of systematic and evolutionary questions in the genus. Can sect. *Skinnera* be shown to have diverged first in the genus? Do cpDNA divergence data indicate large genetic differences among the four species of the Old World which exhibit extremes in plant form? Are sects. *Quelusia* and *Kierschlegeria*, which are polyploid and inhabit putative ancestral biogeographic habitats, closely related? Does cpDNA analysis support the monophyletic origin of sects. *Encliandra*, *Schufia*, and *Jimenezia* from an early dispersal event? Does the Central American section *Ellobium* relate to the Andean sects. *Fuchsia* and *Hemsleyella* in a phylogenetic sense? What are the closest relatives of the recently discovered monotypic and tuber-bearing section from western Peru? Initial surveys of cpDNA restriction fragment variation in representatives of all sections, tentative phylogenetic interpretation, and answers to some of these questions are presented here.

MATERIALS AND METHODS

Total DNA from 16 taxa of *Fuchsia* was extracted from leaf tissue as described above. Representative species from the sections in *Fuchsia* included *F. excorticata* L. f. (sect. *Skinnera*), *F. jimenezii* Breedlove, Berry & Raven (sect. *Jimenezia*), *F. arborescens* Sims and *F. paniculata* Lindley (sect. *Schufia*), *F. thymifolia* H.B.K. (sect. *Encliandra*), *F. splendens* Zucc. (sect. *Ellobium*), *F. lycioides* Andr. (sect. *Kierschlegeria*), *F. magellanica* and *F. regia* (Vand. ex Vell.) Munz (sect.

TABLE 3. *Data matrix of 46 restriction site characters for representatives of the nine described sections of* Fuchsia *and* F. pachyrrhiza *of the new monotypic section from western Peru. Outgroup character states were derived from both* Clarkia *and* Epilobium. *Autapomorphies are listed. The character state "0" indicates absence of a restriction site and "1" indicates presence of a site.*

Outgroup	0010001000000101100000101000110000000110011010
Fuchsia splendens (sect. *Ellobium*)	0010001001000001100000001000110000000110010010
F. thymifolia (sect. *Encliandra*)	0000011000000001100000001000100000000010010010
F. boliviana (sect. *Fuchsia*)	0010001100000001100000001010110000000110010010
F. nigricans (sect. *Fuchsia*)	0010001000000000100000001000110000100110010110
F. verrucosa (sect. *Fuchsia*)	0010001000000001100000001000110000000110010010
F. tillettiana (sect. *Hemsleyella*)	0010001000000000100000001000110000010111010010
F. jimenezii (sect. *Jimenezia*)	0011101000100111110111101001111100011100101001
F. lycioides (sect. *Kierschlegeria*)	0010001000011001100000001100010010010110010010
F. magellanica (sect. *Quelusia*)	0010001000001001101000001100010000010110010000
F. regia (sect. *Quelusia*)	0010001000001001100000001100010000010110010010
F. arborescens (sect. *Schufia*)	0010000000000001100000001000110001000110010010
F. paniculata (sect. *Schufia*)	0010001000000001100000001000110001000110010010
F. excorticata (sect. *Skinnera*)	1110001010000101000000110000110000000110011010
F. pachyrrhiza (sect. *Pachyrrhiza*)	0010001000000001100000001000110000000110010010

Quelusia), *F. tillettiana* Munz (sect. *Hemsleyella*), *F. boliviana* Carrière, *F. nigricans*, and *F. verrucosa* Hartweg (sect. *Fuchsia*), and *F. pachyrrhiza* Berry & Stein (sect. *Pachyrrhiza*).

Eleven restriction enzymes were utilized (*Sst I*, *Hind III*, *Eco RV*, *Pvu II*, *Bgl I*, *Kpn I*, *Pst I*, *Sma I*, *Sal I*, *Bst EII*, and *Sph I*). Filters were sequentially probed with *Petunia* probes that cover only the large single copy region. Phylogenetic analysis followed procedures described above for the analysis of cpDNA variation within *Clarkia* sect. *Sympherica*. Polarity of restriction site changes was determined from cpDNA maps of *Clarkia* and *Epilobium* in which most of the sites for these eleven restriction enzymes have been determined (see above). Restriction fragment patterns were examined in these outgroup genera for restriction enzymes not completely mapped. Wagner analysis (PAUP) was used to determine most parsimonious trees and the CONTREE program utilized to generate a strict consensus tree.

RESULTS AND DISCUSSION

Approximately 100 restriction sites were examined in each taxon with the combination of probes and restriction enzymes. Forty-six restriction site mutations were seen among the 16 ingroup taxa surveyed. Only nine of these mutations are shared by at least two but not all species of *Fuchsia* examined and thus are phylogenetically informative (Table 3). Nucleotide divergence within *Fuchsia* is high, with p values ranging up to 4.8%. *Fuchsia jimenezii* (sect. *Jimenezia*) exhibited the most site divergence, followed by *F. excorticata* (sect. *Skinnera*). PAUP analysis generated over

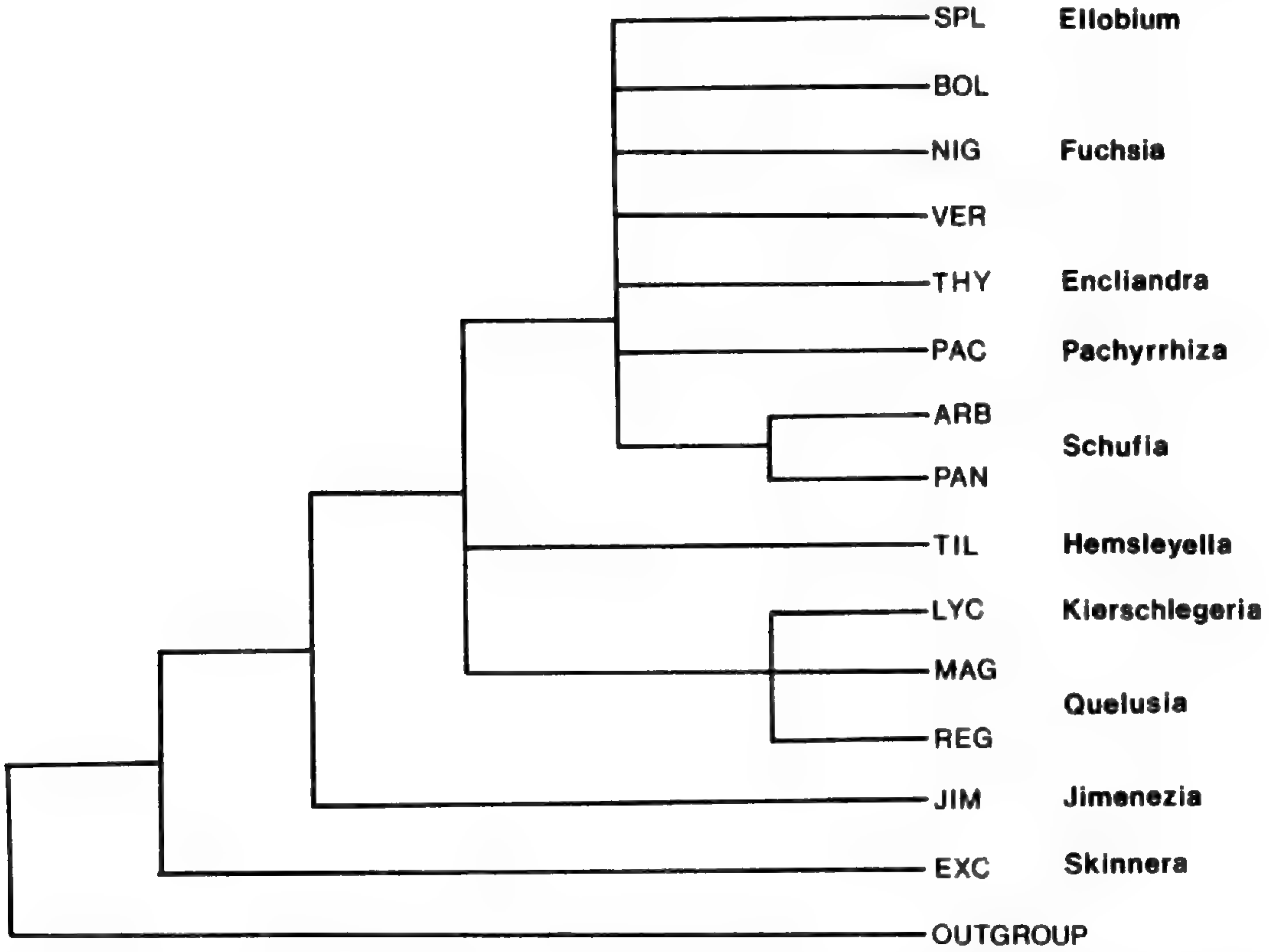

FIGURE 10. *Strict consensus tree depicting relationships among the sections of* Fuchsia *based on cpDNA restriction site mutations. The tree was generated from a subset of most parsimonious trees that lacked an unlikely convergent gain. Species are listed by abbreviation (see Table 3).*

100 most parsimonious trees of 49 steps (C.I. = 0.94). Inspection of the 100 trees retained in memory by PAUP showed that three lineages were implicated as the sister group to the rest of *Fuchsia*: (1) sect. *Skinnera*, (2) sect. *Skinnera* with sect. *Jimenezia*, and (3) sect. *Jimenezia*. Inspection of all 100 trees by the CHGLIST option in PAUP further indicated that all trees in categories (2) and (3) above required an additional unlikely convergent gain or loss/gain (see Templeton, 1983). This unlikely convergence is not found in trees in category (1). A consensus tree was obtained for all the trees not requiring this unlikely convergence and is depicted in Figure 10. This preliminary cpDNA restriction fragment analysis indicates that most mutations encountered (39 out of 49) are autapomorphies. Relationships among sections based on the available phylogenetically informative cpDNA data are thus tentative and subject to change as additional restriction site mutations are found in the ongoing phylogenetic analysis of *Fuchsia*.

The consensus tree indicates that the Old World sect. *Skinnera* and the monotypic Central American sect. *Jimenezia* are the first lineages to split off from the presumed ancestral *Fuchsia* stock in temperate South America. The consensus tree places sect. *Skinnera* as the sister group to all other *Fuchsia* sections, including *Jimenezia*. This placement, however, is based on a single and homoplasious restriction site synapomorphy for all sections excluding *Skinnera*. As indicated above, the ancient split and long evolutionary divergence of sect. *Skinnera* is supported by the presence of 30-million-year-old fossil *Fuchsia* pollen, the spectacular morphological divergence within the section, and the presence of sulfated flavones.

The large cpDNA divergence evident in the monotypic sect. *Jimenezia* relative to all sections is surprising and merits further research. Based on floral structure and reproductive characters, *Fuchsia jimenezii* has been suggested to occupy an intermediate position between the Central American sections *Encliandra* and *Schufia* (Berry, 1982). The large cpDNA divergence between sect. *Jimenezia* and sects. *Encliandra* and *Schufia* is thus contrary to results from floral characters. Berry (pers. comm.) indicates, however, that many such floral characters appear to have evolved several times independently in the genus *Fuchsia* based on preliminary cladistic analysis of floral and vegetative morphology. The distant relationship of sect. *Jimenezia* to these two other sections, as suggested by the cpDNA cladistic analysis, indicates that substantial morphological convergence is indeed present in *Fuchsia*. Again, additional cpDNA data are needed to determine more firmly the position of *F. jimenezii* within *Fuchsia*.

The remaining eight sections of *Fuchsia* share three synapomorphies, but relationships among these sections are not clear based on the preliminary cpDNA consensus tree in Figure 10. Three distinct lines diverge early: (1) a lineage comprising sects. *Kierschlegeria* and *Quelusia*, which is defined by three synapomorphies; (2) sect. *Hemsleyella*, defined by two autapomorphies; and (3) an unresolved lineage comprising five sections (*Schufia*, *Encliandra*, *Fuchsia*, *Ellobium*, and *Pachyrrhiza*), defined by one homoplasious site mutation. The lack of substantial numbers of cpDNA site synapomorphies linking any of these sections (except for *Kierschlegeria* and *Quelusia*) is very suggestive that the genus *Fuchsia* diverged rapidly and profusely following the early separation of sect. *Skinnera* into the Old World and sect. *Jimenezia* into Central America. Indeed the three species examined from sect. *Fuchsia* do not even form a monophyletic lineage within the strict consensus tree depicted in Figure 10.

The close phylogenetic relationship of the temperate South American sects. *Kierschlegeria* and *Quelusia* is supported by cpDNA restriction fragment analysis. These two sections have already been suggested to be closely related (Raven, 1988), despite the unusual derived vegetative and floral characters of *F. lycioides* of sect. *Kierschlegeria*. The lack of resolution among other sections of *Fuchsia* in this cpDNA restriction site analysis does not provide much evidence for or against the prevailing phylogeny. The phylogenetic relationships of the new sect. *Pachyrrhiza* from Peru to other *Fuchsia* sections also are not resolved. These and additional representatives of *Fuchsia* are currently being surveyed with larger numbers of restriction enzymes and with an entire cpDNA clone bank to maximize the numbers of site mutations for phylogenetic analysis. However, if most sections of *Fuchsia* did indeed diverge quickly and at about the same time, as suggested by this study, there may not be substantial and thus statistically useful numbers of cpDNA synapomorphies. A preliminary cladistic analysis of morphological and cytological characters in *Fuchsia* likewise demonstrated the early divergence of sect. *Skinnera* and also failed to resolve relationships among the remaining New World sections (P. Berry and J. Crisci, pers. comm.).

DNA VERSUS MORPHOLOGY: A REVIEW

Chloroplast DNA restriction site comparisons in the Onagraceae have substantiated many relationships based on morphology, cytology, and experimental crosses. Most relationships in *Clarkia* sect. *Sympherica* are congruent with the earlier results of Lewis & Lewis (1955) and Davis (1970). For example, subsect. *Lautiflorae* is shown to be a natural lineage, with *C. lingulata* and *C. biloba* as a close sister species pair, supporting morphological and cytological evidence (Lewis & Roberts, 1956) and isozymic evidence (Gottlieb, 1974). Large chloroplast DNA differences among sections of *Clarkia* are consistent with the results of early work, suggesting that the genus, although natural, is composed of at least several evolutionarily distinctive sections (Lewis & Lewis, 1955). Likewise, the preliminary cpDNA analysis in *Fuchsia* provides evidence in support of the early divergence of the Old World sect. *Skinnera*, an event also suggested by morphological and phytochemical studies.

However, each of these separate cpDNA studies in the Onagraceae also provides strong evidence that DNA and morphology can result in different phylogenetic conclusions. The DNA results place *Clarkia rostrata* with the morphologically dissimilar *C. epilobioides* rather than with *C. lewisii* and *C. cylindrica*, species with which *C. rostrata* is barely distinguished morphologically, an unexpected result supported by isozyme evidence (Odrzykoski & Gottlieb, 1984). Even more unexpected is the discovery that cpDNA characters, as well as nuclear rDNA characters, provide compelling evidence that the monotypic *Heterogaura* is actually derived within *Clarkia* and has *C. dudleyana* as its closest relative. This relationship is clearly at odds with the great morphological differences between the two genera involving taxonomically important floral and fruit characters. The cpDNA analysis of *Fuchsia* indicates that *F. jimenezii* is one of the most ancient lineages within the genus but provides no evidence for a relationship of *F. jimenezii* to sects. *Schufia* and *Encliandra*, sections with which it shares several derived characters.

A survey of published phylogenetic studies using chloroplast DNA in angiosperms is presented in Table 4. Although a number of these studies encountered no incongruity between the relationships generated with cpDNA and morphology, crossing studies, or isozymes, many of the studies have found at least some instances of incongruity. Various explanations for these discrepancies are provided in these studies: (1) morphology or reproductive isolation may not be good measures of phylogenetic relatedness; (2) reliance on phenetic rather than cladistic studies of morphological variation; (3) unequal rates of morphological or genomic divergence; (4) unknown levels of molecular variation *within* ancestral species; and (5) cytoplasmic exchange through introgressive or secondary hybridization. The last explanation has been used in addressing incongruities in cpDNA studies of *Brassica* and *Pisum* (see Table 4). Cytoplasmic

TABLE 4. *Comparison of chloroplast DNA restriction data versus morphological, cytological, and/or isozymic data in phylogenetic studies within angiosperms.*

I. Studies indicating congruence
   A. *Citrus* (Green et al., 1986)
   B. *Coffea* (Berthou et al., 1983)
   C. *Cucumis* (Perl-Treves & Galun, 1985; Perl-Treves et al., 1985)
   D. *Linum* (Coates & Cullis, 1987)
   E. *Nicotiana* (Kung et al., 1982)
   F. *Solanum* (Hosaka et al., 1984; Hosaka, 1986)
   G. *Triticum* (Bowman et al., 1983; Tsunewaki & Ogihara, 1983)
   H. *Zea* (Doebley, 1987; Doebley et al., 1987)

II. Studies indicating incongruencies or unexpected relationships
   A. Asteraceae subtribe Barnadesiinae (Jansen & Palmer, 1987, 1988)
   B. *Clarkia rostrata* and *C. epilobioides* (Sytsma & Gottlieb, 1986b)
   C. *Daucus capillifolius* and *D. carota* subsp. *sativus* (DeBonte et al., 1984)
   D. *Helianthus annuus* and *H. bolanderi* (Rieseberg et al., 1988)
   E. *Heterogaura heterandra* and *Clarkia dudleyana* (Sytsma & Gottlieb, 1986a)
   F. *Heuchera micrantha* (Soltis et al., in press)
   G. *Lisianthius* (Sytsma & Schaal, 1985a, b)
   H. *Nicotiana debneyi* and *N. repanda* (Salts et al., 1984)
   I. *Populus nigra* and *P. alba* (Smith & Sytsma, in prep.)

III. Studies indicating introgression or secondary hybridization
   A. *Brassica napus* (Palmer et al., 1983)
   B. *Lycopersicon chmielewskii* (Palmer & Zamir, 1982)
   C. *Pisum sativum* (Palmer et al., 1985)

exchange via hybridization and introgression, giving rise to different and sometimes unexpected organeller- and nuclear-based phylogenies, is probably common in angiosperms. Clearly, a molecular phylogenetic study would be more thorough (and also more willingly accepted by the systematic community) if both the biparentally inherited nuclear genome and a predominantly uniparentally inherited organeller genome are examined and compared.

Doyle (1987), in a perceptive review of the promises and pitfalls of plant systematics at the DNA level, stated that the available DNA studies (both nuclear and organeller) suggest that "sweeping statements that a particular molecular phylogeny is 'right' and that more traditional approaches, such as morphology, are 'wrong' when the two do not happen to agree are unwarranted *without further investigations*" [italics added]. If, however, further investigations using alternative genetic or molecular methods consistently provide results contrary to the traditional approaches, it is then time to reexamine these traditional approaches.

The examples presented here of *Clarkia epilobioides/C. rostrata* and *C. dudleyana/Heterogaura heterandra* might well be some of the most definitive examples of where molecular phylogeny could be considered 'right' and the traditional approach 'wrong.' In these two cases, data from chloroplast DNA, nuclear rDNA, and isozymes provide independent and congruent phylogenies, contrary to phylogenies using morphology. Doyle (1987) further stated that "it is just such instances of incongruence that are likely to lead to major revelations about the evolution of the taxa being studied—or of the molecules being used in the analysis." Thus, disparity between DNA and morphology (1) is expected to occur in some or many systematic studies, (2) should be the basis for including additional systematic procedures to examine the disparity, (3) will provide insight into relative rates of molecular and morphological divergence, (4) should provide insight into what characters (morphological or molecular) in a given group are particularly prone to convergence or parallelism and thus less phylogenetically useful, and (5) will undoubtedly permit new or previously nontraditional questions to be asked and answered.

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MODES AND TEMPOS IN THE EVOLUTION OF NUCLEAR RIBOSOMAL DNA: NEW CHARACTERS FOR EVOLUTIONARY STUDIES AND NEW MARKERS FOR GENETIC AND POPULATION STUDIES[1]

Richard A. Jorgensen[2,3] *and*
Paul D. Cluster[2]

ABSTRACT

The tempo of evolutionary change determines in what manner any class of characters is informative in evolutionary studies and at which taxonomic levels. Here we describe and summarize some fundamental features of the evolution of the DNA sequences that encode ribosomal RNA genes in the nuclear genome of higher plants. By analyzing a sample of angiosperm species having known phylogenetic relationships at five different taxonomic levels ranging from the intraspecific to the interfamilial, we show that plant ribosomal DNA determines at least eleven classes of characters that can be distinguished by comparisons at the DNA level. These classes are temporal and physical subsets of three basic modes of variation: length variation, single base pair substitution, and DNA modification. We also discuss the impact of length variants on population genetic studies and the implications of these studies for understanding the molecular mechanisms of rDNA evolution.

Because DNA is the richest and most unambiguous source of genetic variability, information on its evolution is fundamentally important to evolutionary biology. Research into the evolution of DNA is still in its infancy, and workers studying DNA variation are still faced with (1) cataloging both the classes of DNA sequences (characters) that are found in the genomes of various organisms and the ways (modes) in which these characters vary among organisms, and (2) measuring the approximate rate (tempo) of change in the different character classes. From this fundamental information it is possible to begin to ascertain at which phylogenetic level a particular character is useful in reconstructing phylogeny. Here we examine modes and tempos of evolution in nuclear-encoded ribosomal DNA. The available technology allows us to estimate the tempo of evolution in three basic modes: length variation, base pair substitution, and nucleotide modification.

PHYSICAL AND GENETIC DESCRIPTION OF rDNA

Ribosomal DNA, or rDNA, is the set of DNA sequences that directs the synthesis of ribosomal RNA. Each haploid nuclear genome of a higher plant cell typically contains 1,000 to 10,000 copies of ribosomal DNA (Ingle et al., 1975), a range roughly twenty-fold higher than in animal genomes. Copies of rDNA exist in long tandem arrays at one or a few chromosomal locations. Within a species, the number of copies of rDNA varies by as much as four-fold (Cullis & Davies, 1975; Long & Dawid, 1980). Unequal crossing-over is one likely mech-

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[1] *Editor's note: This and the following article by H. J. Price are based upon the authors' presentations at the 1982 A.I.B.S. meetings as part of a symposium originally planned for publication in the* Annals of the Missouri Botanical Garden. *After the manuscripts were prepared, plans were changed, and the symposium was never published. Publication here of the 1987 Missouri Botanical Garden Annual Systematics Symposium, dealing with the same subject matter, provides an opportunity to present these updated papers as complements to the more recent symposium.*

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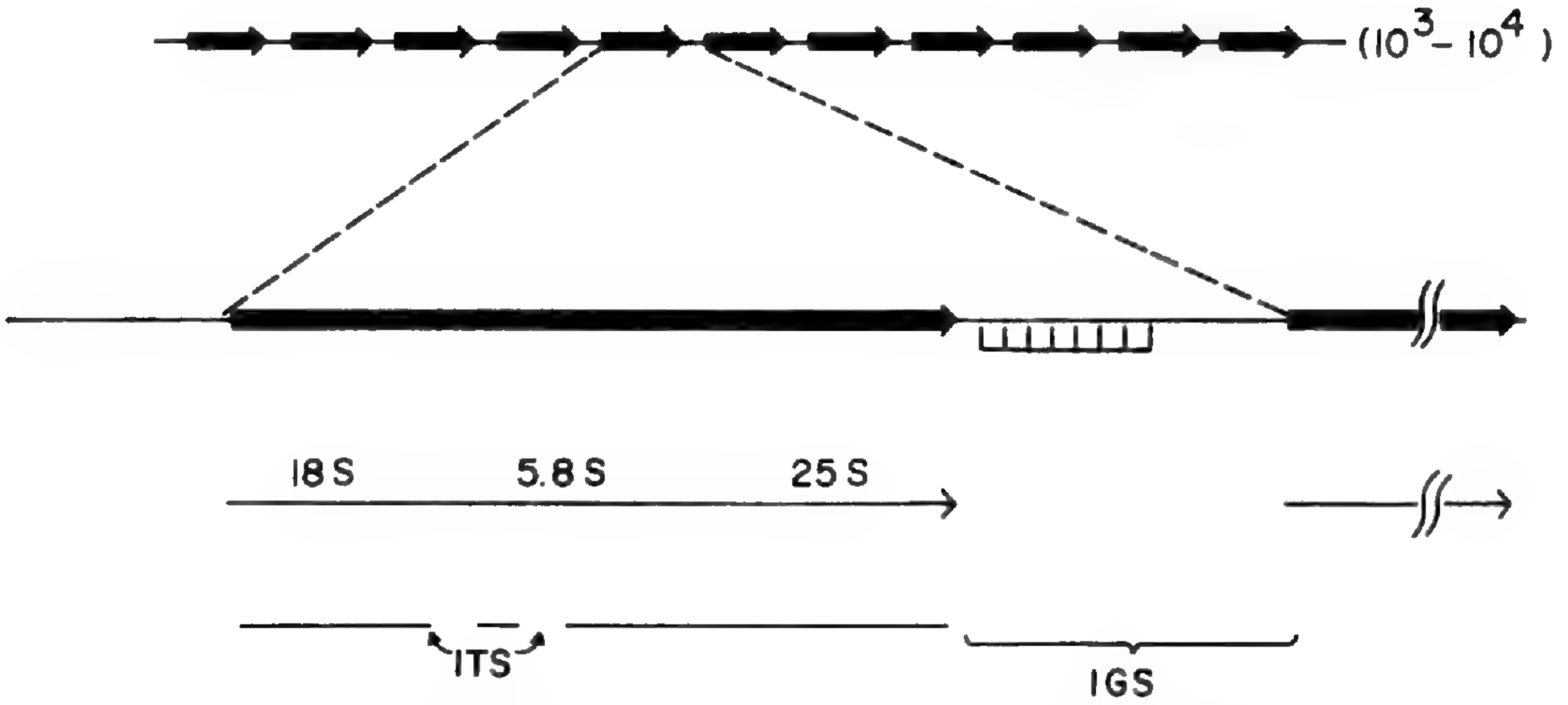

FIGURE 1. *Schematic representation of rDNA repeat structure. 18S, 5.8S, and 25S refer to ribosomal RNAs. ITS and IGS refer to internal transcribed spacer and intergenic spacer, respectively.*

anism responsible for variations in copy number (Szostak & Wu, 1980). Although there is some heterogeneity among copies of rDNA within individuals (see below), the rDNA repeat units of an individual plant are highly homogeneous. That is, while several types of rDNA repeat unit may be found in a single plant, many hundreds of repeat units are identical as assayed by Southern blot analysis. This homogeneity was first observed in comparisons within species contrasted with comparisons between species and is presumably the result of concerted evolution of rDNA repeat units, as explained by Arnheim et al. (1980). Similarly, in species where rDNA is found to reside at two or more genetic loci, repeat units are found to be quite homogeneous within each locus. Thus, loci can usually be distinguished by their repeat types, and homogeneity is greater within loci than between loci (Dvorak & Appels, 1982; Saghai-Maroof et al., 1984).

The physical structure of higher plant ribosomal DNA (Fig. 1) is similar to that in other higher eucaryotes (Long & Dawid, 1980, for review). The three ribosomal RNA coding regions lie in the order 5′, 18S, 5.8S, 25S, 3′, and are transcribed as a single large precursor, which is processed subsequently to the mature rRNA forms. Several hundred base pairs of DNA separate the 18S cistron from the 5.8S cistron and the 5.8S cistron from the 25S cistron. These two intercistronic regions are referred to as internal transcribed spacers (ITS). The region separating the transcription units of adjacent rDNA repeats is called the intergenic spacer (IGS, formerly NTS or nontranscribed spacer; Dover et al., 1982) and in most plants ranges in length from one to eight kilobase pairs (kb). A tandemly repeating sequence comprises part of the IGS region. This sequence varies interspecifically in length, ranging generally from 100 to 200 bp, while within species its length varies only slightly. The length of this subrepeat has been shown to be 130 bp in wheat, 180 bp in peas, 325 bp (comprised of two copies of a 155-bp sequence and one 14-bp sequence) in broad bean, 115 bp in both barley and oats, and 200 bp in maize (Appels & Dvorak, 1982; Jorgensen et al., 1982; Yakura et al., 1984; Saghai-Maroof et al., 1984; Cluster et al., in prep.; and McMullen et al., 1986, respectively). The number of these elements within a given rDNA repeat unit is variable, and thus the overall length of the IGS is variable, within and between populations. This variability in length of the IGS is discussed in detail below.

An individual plant's rDNA array is often heterogeneous with respect to the three basic modes of variation: length, nucleotide sequence, and base modification (e.g., Siegel & Kolacz, 1983; Appels & Dvorak, 1982; Waldron et al., 1983; Jorgensen et al., 1982, 1987). It should be noted that a fourth mode of rDNA variation occurs, namely variation in the copy number of rDNA per haploid genome; because it is a quantitative character it is rarely measured. rDNA copy number is unlikely to be informative taxonomically because it is extremely variable within species, although in genetic analyses it may have some utility. In Figure 2 the three principal modes of variation are illustrated for a single individual of the garden pea (Jorgensen et al., 1987). This individual carries a minimum of three types of rDNA repeat units, and each of the three is distinguished by the three modes. First, each type of repeat has a different overall length due to variation in the number of 185-bp subrepeats in the IGS. Second, nucleotide substitutions are evident in several regions of the rDNA repeat unit. Type "L" repeats (see Fig. 2) carry EcoRI sites in two of their nine subrepeats that are not present in types "S" or "C," and in the nonsubre-

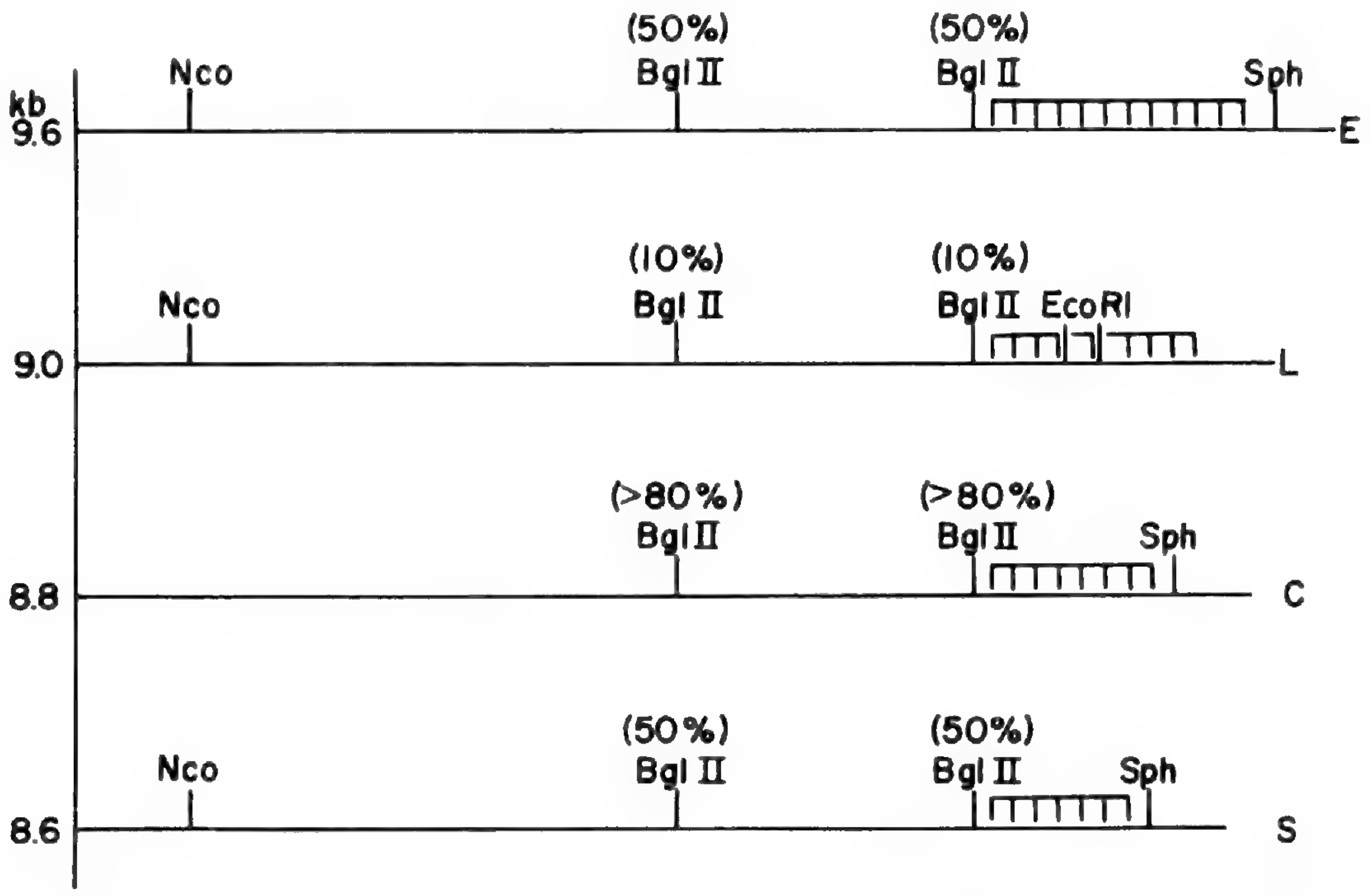

FIGURE 2. *Maps of four pea rDNA repeat units. L, C, and S refer to distinct repeat types found in a single pea plant. E refers to another repeat type found in* Pisum elatius. *Nco and Sph refer to NcoI and SphI.*

peat region of the IGS types "C" and "S" carry an SphI site not found in type "L." Within the rRNA coding sequence, an NcoI site in the 18S gene is present in both type "L"and "S," but absent in the cloned type "C" repeat. Third, the BglII cleavage sites of types "L"and "S" differ in their degree of apparent base modification such that only 10% of the BglII sites of "L" repeats are cleaved, while 50% of the BglII sites of "S" repeats are cleaved.

TEMPORAL ANALYSIS OF PLANT rDNA VARIATION

For a given mode of sequence evolution, the taxonomic level at which any segment of DNA is useful for making phylogenetic determinations is determined by the tempo at which that segment of DNA varies. Tempo can be estimated by analyzing DNA variation in species from several levels within an accepted taxonomic hierarchy. We have chosen nine legume genera for study: three (*Vicia, Pisum,* and *Lathyrus*) are from the tribe Vicieae and the rest (*Medicago, Trifolium, Lupinus, Wisteria, Cytisus,* and *Phaseolus*) are each from a different tribe. Seven genera are represented by a single species. *Vicia* is represented by five species, *Pisum* by four. For *V. sativa* and *P. sativum,* four and twenty, respectively, distinct isolates were examined. Outside the legume family we have compared the rDNA of wheat (*Triticum aestivum*) and pumpkin (*Cucurbita pepo*). Postulated phylogenetic relationships between species in this hierarchy are depicted in Figure 3.

Using the cloned rDNA repeat unit from *Pisum sativum* and detailed physical maps of both the cloned repeat and the pea nuclear genomic repeats described above, we performed nitrocellulose blot analysis (Southern, 1975) of rDNA sequences in the genomic DNA of each species. "Southern analysis" requires the use of a specific probe homologous to DNA sequences being analyzed. Different regions of the rDNA repeat unit were analyzed independently by use of seven different purified restriction fragments as probes (Fig. 4). The ITS region was analyzed by DNA sequencing because it was too small to analyze effectively by Southern analysis.

MODES AND TEMPOS OF VARIATION IN DIFFERENT rDNA REGIONS

A. Base Modifications

We have characterized in some detail two types of base modification in plant rDNA. They are distinguished both by sequence specificity and by degree of variability among taxa, as will be explained here. Most common is an evolutionarily conservative type of base modification typified by the BamHI site in the 25S gene. This site is modified in about one-half of the rDNA repeats of all the legume species in our survey, as well as in several other species (Gerlach & Bedbrook, 1979; Goldsborough et al., 1981; Jorgensen et al., 1982; Siegel & Kolacz, 1983). Siegel & Kolacz (1983) have postulated that this methylation is due to a CCG sequence of which the BamHI site (GGATCC) is a part. (That only one-half the sites are cleaved by

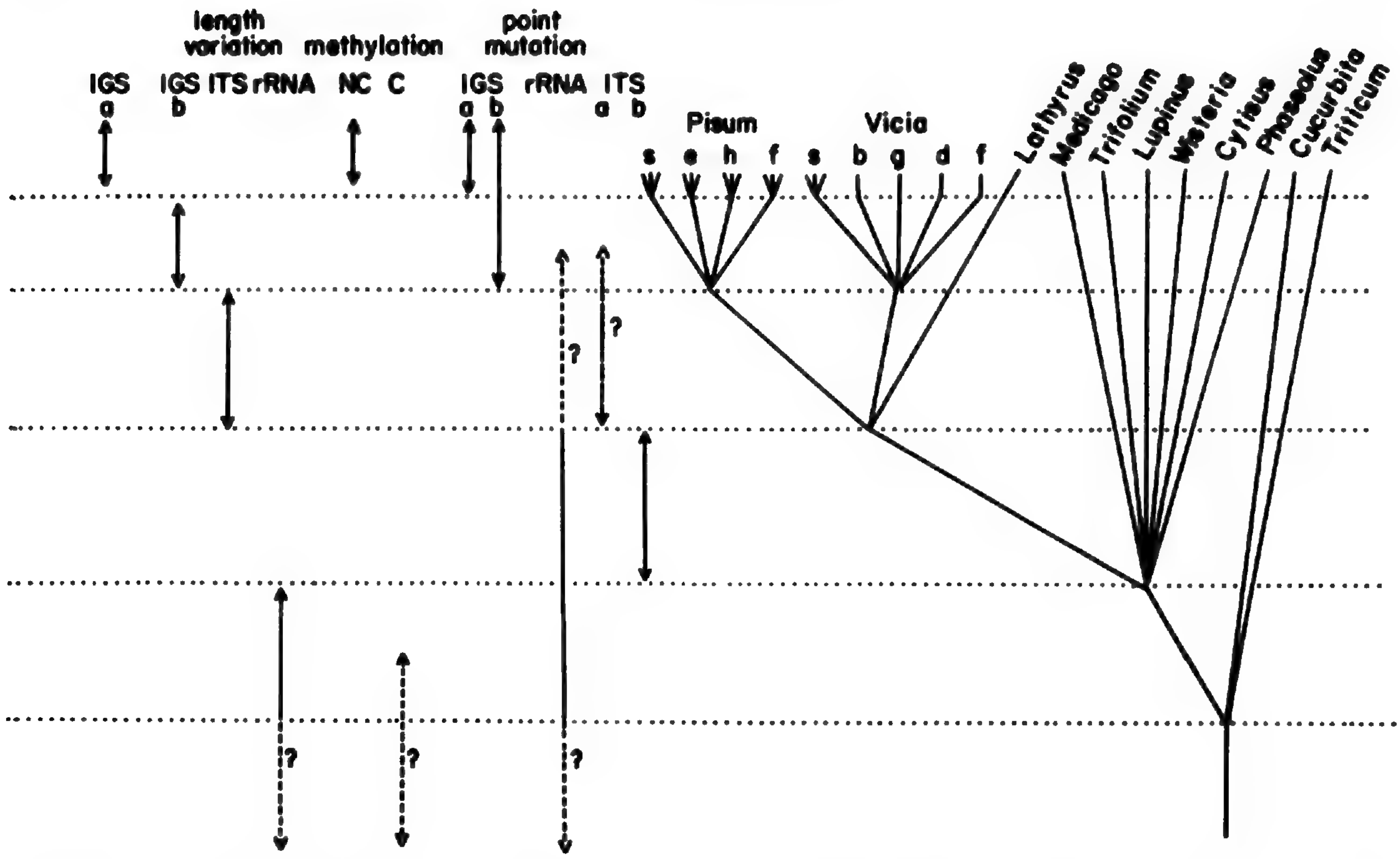

FIGURE 3. *Schematic drawing of evolutionary relationships among species analyzed and the taxonomic levels at which the eleven characters classes are proposed to be useful in reconstructing phylogeny. The taxonomic levels indicated are intraspecific [*Pisum sativum *(s)*, P. elatius *(e)*, P. humile *(h)*, P. fulvum *(f), and* Vicia sativa *(s)], intrageneric (*Vicia *and* Pisum*), intratribal (Vicieae), intrafamilial (Fabaceae), and within angiosperms. The cladogram is not meant to represent relationships but is presented only to illustrate the taxonomic levels being compared. IGS refers to intergenic spacer; ITS refers to internal transcribed spacer; NC to nonconservative; C to conservative.*

BamHI appears to be due to the fact that methylation occurs at either but not both C residues.) Methylation of CG and CXG sequences has been observed in all plants investigated to date. It is presumed that many of the other enzyme cleavage sites that contain CG or CXG sequences could be subject to evolutionarily conservative modification. However, the extreme conservatism of the 25S BamHI site modification is a specific example of the general phenomenon of plant cytosine modification, and it is unwise to generalize from this. In fact, within or near various structural genes a substantial number (and perhaps a large fraction) of CG and CXG sequences are unmethylated in a variety of plants, and the possibility of variation in plant CG, CXG modifications certainly exists.

In contrast to the BamHI modification, modification of the BglII sites in pea rDNA is apparently variable by degree among individual pea plants, just as it is variable among rDNA repeats of the same plant (Jorgensen et al., 1982, 1987). BglII sites do not contain CG or CXG sequences but could be part of CXG sequences. It is not clear whether the variable modification of BglII sites in rDNA is due to variation in (a) modification by the CG, CXG system, (b) modification by another system, or (c) sequences adjacent to the site. Adenine modification prevents cleavage by certain restriction enzymes, but these have not been analyzed for variability among plants.

B. Single Base Pair Substitutions

1. Coding Regions. The coding regions for mature rRNAs were compared in two ways: by comparing restriction maps of cloned repeats from pea, wheat, and pumpkin (Jorgensen et al., 1987) and by comparing Southern blots of legume species rDNA using probes A, B, C, and D (Fig. 4). The 18S genes of pea and wheat were found to differ at three of ten six-bp cleavage sites (at least three of 60 bp), while the genes of wheat and pumpkin differ at five of nine, and the genes of pea and pumpkin at two of eight. The 5′ end of the 25S gene shows no site conservation in comparisons of these three species, which is consistent with the fact that this is one of the last-conserved regions in comparisons among frog, yeast, and slime mold rDNA (Gerbi et al., 1982). The rest of the 25S gene shows substantial similarity among species:

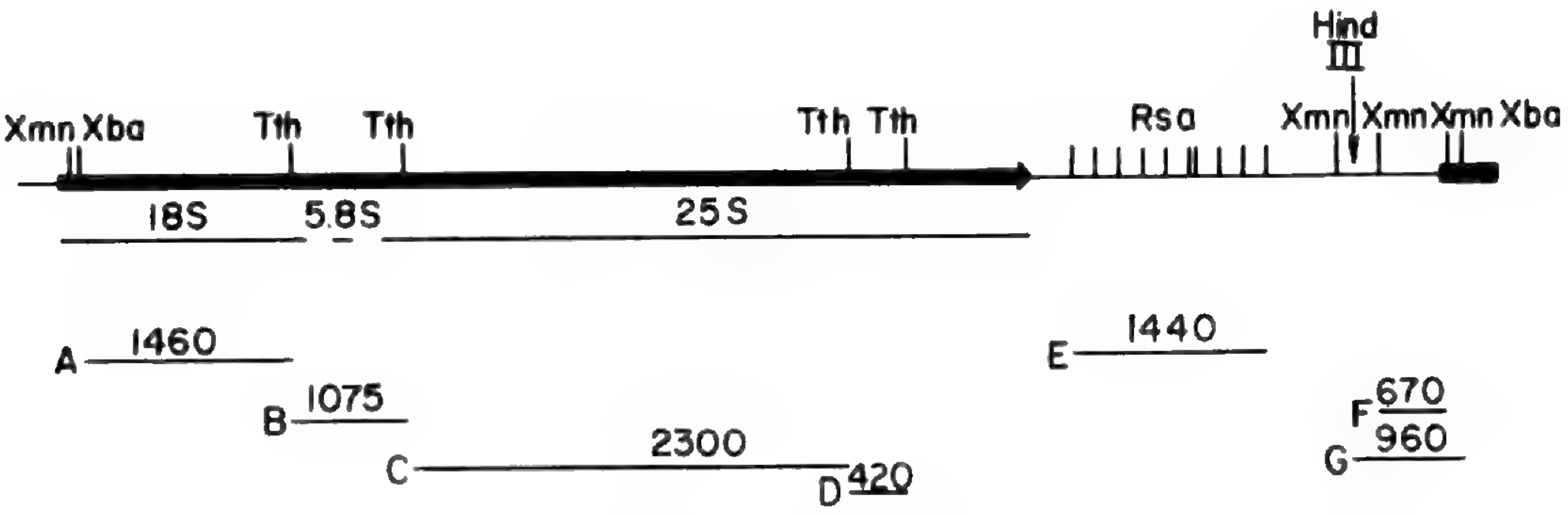

FIGURE 4. *Map indicating restriction fragments (A–G) used to study rDNA variation. Numbers indicate length of fragments in base pairs. Xmn, Xba, Rsa, and Tth refer to XmnI, XbaI, RsaI, and Tth111I.*

pea and pumpkin differ at three of ten sites, pea and wheat at eight of twelve, and wheat and pumpkin at five of ten. Although it is possible to align and compare the restriction maps of the pea, wheat, and pumpkin coding regions, a statistically significant number of mutations have not been analyzed to permit phylogenetic conclusions.

Southern analysis of different legume species reveals very little sequence divergence in the rRNA coding sequences, even after use of all available enzymes insensitive to base modification (Jorgensen et al., 1982). Figure 5 summarizes this analysis with a comparison of pea, vetch, and bean, illustrating the only two cleavage site mutations that could be detected in this survey of 19 cleavage sites (for a survey of 114 bp). The degree of sequence divergence in this rDNA region is at least several-fold less in the legume family than among peas, pumpkins, and wheat.

It is important to recognize the limitations inherent in the use of restriction enzyme analysis of plant rDNA for phylogenetic investigations. First, the choice of restriction enzymes for nuclear DNA analysis in plant genomes is more limited than for animal genomes or for plant organellar genomes due to the fact that plant nuclear DNA is methylated at most CG dinucleotides and CXG trinucleotides (Gruenbaum et al., 1981), and because many restriction enzymes that cleave sequences containing CG, CXG sequences do not cleave if these sequences are methylated. Thus, analysis of genomic rDNA by Southern blot is quite limited relative to analysis of rDNA clones using restriction enzymes with respect to the number of variants that can be detected. Cloned sequences are not necessarily a good alternative because the use of single clones from an array of thousands entails the risk of not being representative. Second, because rRNA coding sequences are only 5.5 kb long, in contrast to chloroplast DNA which amounts to about 150 kb (see Palmer et al., this volume), relatively few cleavage sites are available and relatively few variants can be detected. The obvious solution to this problem is to utilize rRNA sequencing. By doing so, Zimmer (this symposium, not published here) has shown that the conservative nature of the coding region is extremely useful in phylogenetic comparisons between distantly related genera and closely related families.

2. *ITS Region.* The ITS region, because it is small, also cannot be analyzed well with restriction enzymes. The DNA sequence of the 5.8S gene and its surrounding ITS sequences has been determined in pea and lupine (Jorgensen & Hess, unpubl.; Rafalski et al., 1983). A schematic comparison of

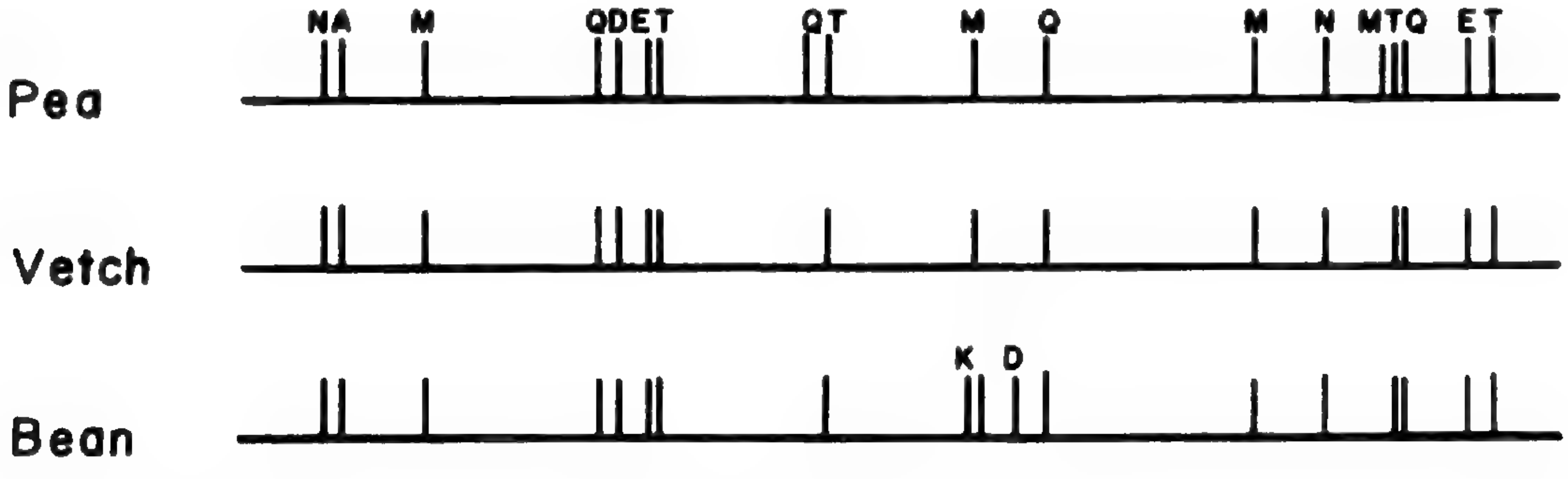

FIGURE 5. *Maps comparing coding regions of pea (*Pisum sativum*), vetch (*Vicia sativa*), and bean (*Phaseolus vulgaris*) rDNA. Symbols are coded as follows: N, XmnI; A, XbaI; M, BamHI; Q, SstI; D, BstEII; E, EcoRI; T, Tth111I; K, KpnI.*

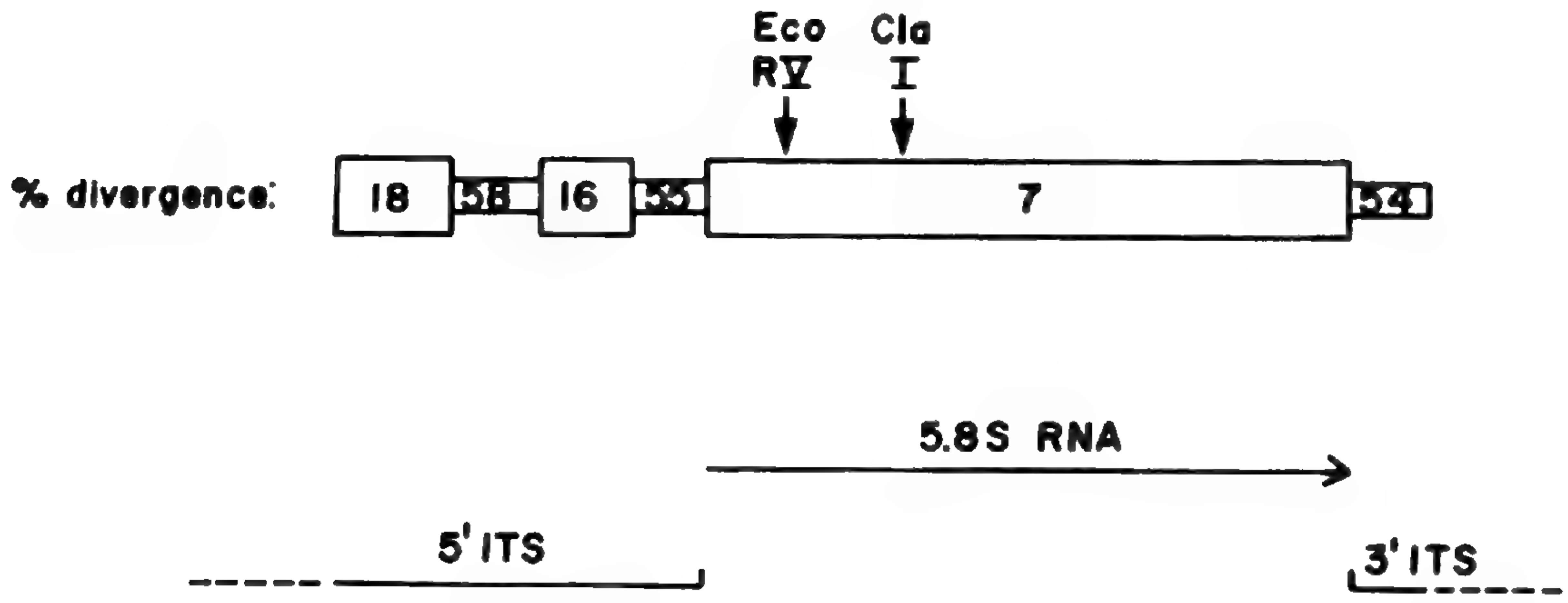

FIGURE 6. *Map of 5.8S rRNA gene and ITS regions. Numbers indicate % divergence in nucleotide sequence between* Pisum sativum *and* Lupinus luteus *rDNA clones.*

these sequences is shown in Figure 6. DNA in the ITS was observed to change at two distinct rates, both faster than that within the 5.8S gene. The 5.8S rRNA of *Vicia faba* has been sequenced (Tanaka et al., 1980) and differs from the pea 5.8S rRNA by 2%.

3. IGS Region. Restriction enzyme analysis of the nonsubrepeat segment of the IGS region reveals many cleavage site variants within legume genera (Jorgensen et al., 1982). These variants appear to have some utility in assessing phylogenetic relationships and in genetic studies of interfertile populations and species (Zimmer et al., in prep.). In the IGS subrepeats, DNA sequence and restriction pattern analyses indicate that subrepeat sequences are variable within and among individual genomes in a species (Appels & Dvorak, 1982; Jorgensen et al., 1987). This variation in single base pair substitutions in the IGS is of interest primarily within species. Because this variability is very difficult to detect with restriction analyses of total genomic DNA, it is of limited utility, except in studies of the evolution of the subrepeat itself.

C. Length Variation

1. Coding Regions. The ribosomal RNA transcription unit was surveyed for length variants by monitoring four restriction fragments (A–D) indicated in Figure 4. Fragment A, a 1,460-bp XbaI–TthI fragment, lies entirely within the 18S gene; fragments B (2,300-bp Tth fragment) and D (420-bp Tth fragment) lie entirely within the 25S gene; fragment C, the 1,075-bp TthI fragment, carries the entire ITS region and the 5.8S gene within it, as well as short portions of the 18S and 25S genes. Within the legumes, no length variations were observed (detection limit, 50 bp) in any of the three fragments that lie within the rRNA genes.

The 5.8S rRNA coding regions of pea, broad bean, and lupine have now been sequenced (Hess & Jorgensen, unpubl.; Tanaka et al., 1980; Rafalski et al., 1983). Comparison of these sequences shows that the 164-bp 5.8S gene differs in length between pea and broad bean by only one base pair and between pea and lupine by two adjacent base pairs. Length variation of this sort is very likely to be found also within the 18S and 25S genes by DNA sequence comparisons, but not by restriction fragment comparisons, as the differences are too small to detect by agarose gel electrophoresis.

2. ITS Region. Overall length variation in the ITS, as monitored by changes in the 1,075-bp TthI fragment, is much more prevalent than are length changes in the three coding sequence restriction fragments. The pea ITS 1,075-bp TthI fragment detects fragments varying in size from 1,000 to 1,200 base pairs among the nine legume genera surveyed. At least six of these size classes are distinct from all the others. Within *Pisum* and *Vicia* no length variation was observed. Thus, length variants of 50 bp or greater appear to be restricted mostly to the intergeneric level, at least in the tribe Vicieae. Whether small variants ever occur within these genera and whether observed variation results from the accumulation of many small variants or few large variants remains to be determined. For particular ITS length variants to be of practical use in studying relationships among genera, they will have to be large and rare, rather than small and common. Particular length variants in chloroplast DNA have been quite useful (in conjunction with point mutations) in developing chloroplast DNA phylogenies (Palmer et al., this volume).

3. IGS Region. By far the most variable region of the rDNA repeat unit is the subrepeat-containing region. Length variants of restriction fragments carrying this region almost always differ by a multiple of the length of the subrepeat. For example, 14 distinct fragment lengths were observed in a sample of 12 pea lines, each length differing from the others by a multiple of 180 bp. Similarly, detailed intraspecific surveys of IGS variability among hundreds of individuals have demonstrated variation produced by 15 increments of 115 bp in barley (Saghai-Maroof et al., 1984) and by 17 increments of 115 bp in wild oats (*Avena barbata*) (Cluster et al., in prep.), indicating that the subrepeat length is 115 bp in each of these species. This large number of variants results in a large number of IGS phenotypes observed within and among populations (see below). For example, 11 distinct phenotypes were observed among the 12 pea lines.

The next most length-variable region is the part of the IGS region without subrepeats. We have monitored this region in *Pisum* with a 960-bp restriction fragment (G) produced by combined cleavage with HindIII and XbaI and with two XmnI fragments (E and F) of 310 bp and 670 bp (Fig. 4). Among ten pea lines that showed extensive variation in length of IGS-a, we found only two IGS-b types. These probably resulted from a single substitution event, this resulting in several restriction site differences as well as a 100-bp length difference. This finding illustrates the need for caution in interpreting restriction patterns and consideration of the possibility that restriction site variants in the IGS-b may be the result of deletions, insertions, or substitutions rather than point mutations. Interpretation of the molecular basis of mutations in this region in the absence of direct DNA sequence information is prone to error due to the small length changes potentially involved.

D. Summary of Tempos and Modes

Based on the results described above, Figure 3 illustrates the taxonomic levels at which the 11 identified character classes may have some utility in evolutionary genetic studies. It should be noted that characters in the single base pair substitution (point mutation) mode will be best detected by sequencing of rRNA or cloned rDNA, not by restriction analysis, as is demonstrated by Zimmer (this symposium, not published here). Clearly the size of the rRNA coding region indicates that this region will provide the greatest number of characters and so will be the most informative. Further, we would expect this region to be useful at levels ranging from the intergeneric to the interfamilial. It would be interesting to test the utility of the nonrepeated IGS region for intrageneric comparisons, although length variations (i.e., additions and deletions) might preclude this possibility if they are found to occur so frequently as to obscure sequence similarities. Characters in the base modification and length modes will be best detected by restriction analyses of total genomic DNA. It appears that character classes in these two modes will be useful primarily in intraspecific genetic studies, as described in the next section.

VARIATION WITHIN AND AMONG POPULATIONS OF A SINGLE SPECIES

The rDNA spacer length (sl) phenotype of individual wild oat plants usually is comprised of 4–10 variants, out of 17 variants known in the species, often in widely varying copy numbers. From among over 500 individuals sampled, at least 40 distinct phenotypes were distinguished by scoring the most abundant sl variants (Cluster et al., in prep.). Variation of rDNA sl phenotypes among populations of wild oats in California closely tracks previously established patterns of differentiation identified by allozymes, morphological characters, and quantitative characters. Furthermore, the degree of variability suggests that it may be possible to identify and differentiate populations on the basis of rDNA variability alone nearly as accurately as with the available set of variable allozyme loci. Similarly, in 75 samples of barley, 15 distinct sl phenotypes could be distinguished (Saghai-Maroof et al., 1984). Most of these were comprised of two or three sl variants. The level of intraspecific polymorphism in the IGS is, therefore, extremely high. In the case of wild oats, the ability of sl variants to distinguish in detail among and between populations is probably the result of two genetic properties of rDNA variants in this species: (1) that these variants lie at a minimum of four independently segregating loci and (2) that each locus contains hundreds or thousands of repeat units which can be of more than one sl variant type.

Another result of genetic analysis of rDNA is the observation of nonrandom distribution of sl variants in several species, which suggests that genetic exchange occurs less frequently between than within nucleolus organizer regions. This situation occurs in barley (Saghai-Maroof et al., 1984), wheat (Dvorak & Appels, 1982), pea (Ellis et al., 1984; Polans et al., 1986), and mouse (Arnheim et al., 1982); however, random distribution has been reported in humans (Krystal et al., 1981). In wild oats the most abundant sl variants were present in nearly all isolates, including both parents of the single F2 analyzed, and so it is not possible to assess accurately whether these variants are distributed randomly or nonramdomly among loci, even though five less-abundant variants are nonrandomly distributed. In species where a degree of nonrandomness is observed, rDNA appears to be a new and useful genetic marker (Saghai-Maroof et al., 1984). However, the multilocus nature of rDNA spacer length variation may place a severe limitation on its use in population genetics because of the difficulty in determining each plant's genotype, except for those genomes possessing only a single major nucleolus organizing region (e.g., tomato and corn). Still, the great amount of phenotypic diversity will clearly be useful.

Also noteworthy is the observation that the composite frequency distribution of rDNA sl variants in California wild oats shows a nearly Poisson distribution of sl variants centered at sl variant 8. There at at least three ways to explain this distribution. First, it could be the result of classical forces in population divergence such as genetic drift and/or selection on loci at or correlated with rDNA. Second, it could be the result of stochastic molecular processes, perhaps involving DNA replication or repair. Third, it could be determined by the function of the subrepeat.

The first explanation is based on the fact that in populations that reproduce substantially by selfing, a correlational structure is imposed on all components of the genome, allowing selection at each locus to affect allelic frequencies at all other loci in the genome. Thus, sl variant frequencies at rDNA loci must reflect the selective effects of many other loci and could be determined by these forces (Saghai-Maroof et al., 1984).

The second explanation considers whether the observed distribution could be simply a consequence of the molecular mechanisms that create new spacer length variants. New variants can appear in evolutionary time by mechanisms such as unequal crossing-over, resulting in repeated cycles of amplification and contraction of arrays of both repeats and subrepeats of rDNA. Accordingly, one can hypothesize that the number of subrepeats in the intergenic spacer region would be determined by a feature(s) of these mutational mechanisms whereby very long subrepeat arrays are more likely to be shortened than lengthened and short arrays are more likely to be lengthened than shortened, resulting in a balance in wild oats, for instance, at slv-8. Since various cellular processes might affect this mechanistic optimum, it could be possible for species to differ in their optimum number of subrepeats, were such a mechanism the only one operating on the distribution.

The third explanation considers what function the IGS might have, based on recent observations on the transcriptional and structural nature of the subrepeat elements (Reeder, 1984; Flavell et al., 1987). Briefly, it is hypothesized that the IGS subrepeats function analogously to enhancer sequences, increasing the transcription of the repeat unit(s) to which they are adjacent. It has been observed that rDNA repeat units with more subrepeats are transcribed with strong preference over units with fewer subrepeats, probably due to an interaction between subrepeats and some positive transcription factor. Furthermore, loci with repeat units having more subrepeats show nucleolar dominance over loci having fewer repeats. These observations provide a simple explanation of how natural selection for longer sl variants might occur. Of course, subrepeats apparently do not increase to many tens or hundreds of copies. Therefore, we must also hypothesize that too large a number of subrepeats can be deleterious. Perhaps multiple subrepeats would sequester a transcription factor not only from rRNA promoters in unlinked loci but also from promoters in adjacent repeat units (see Reeder, 1984, for detailed discussion of this model). This situation would likely lead to a reduction in efficiency of rRNA transcription and thereby be deleterious to the individual. Thus, it is possible that natural selection can *directly* mold the rDNA sl variant pattern and influence the frequency distribution seen in wild oats.

SUMMARY

Eleven classes of useful characters have been identified for plant nuclear ribosomal RNA genes. These classes and their approximate rates of evolution are as follows:

(1) The length of the plant ribosomal DNA repeat unit is highly variable within most species and this variability has great utility in studies of populations. A 100–200-bp sequence that is repeated many times in tandem in the IGS region of rDNA forms the molecular basis for this variation in that the number of tandem copies of this sequence differs among individuals as well as among rDNA repeats within an individual. Studies of these variants appear to be helpful in elucidating the molecular mechanisms of rDNA evolution.

(2) The nonrepeating portion of the IGS region is less variable than is the subrepeat region, but is variable in length within the genera *Pisum* and *Vicia*; this variability might have utility in assessing specific relationships within such genera.

(3 and 4) Ribosomal RNA coding sequences are invariant in length in restriction pattern analyses,

but length variation is observed in the internal transcribed spacer (ITS) region. The frequency at which length variations in the ITS are detected is lower than that for length variation in either segment of the IGS. It is not likely that length variation in this region will be useful phylogenetically.

(5 and 6) Modification of Bg<III cleavage sites in pea rDNA varies quantitatively among pure lines and between wild populations. Such variants might be useful in genetic studies, but only to a limited degree since they are not as frequently observed as IGS length variants. A second class of modification is extremely conservative, as is illustrated by one of the rDNAs BamHI cleavage sites, which is modified in all legume and cereal species so far examined.

(7-11) Nucleotide substitutions accumulate in plant rDNA at several distinct tempos in distinct segments of DNA, resulting in a minimum of five character classes. In the IGS region they are found in (a) the subrepeat segment, differing among rDNA repeats of single individuals, and (b) in the nonrepeating segment within and among species of the same genus. Comparison of ITS DNA sequences of pea and lupine reveals four blocks of sequence, each of which has accumulated base substitutions at one of two levels, both greater than within the 5.8S rRNA coding sequences as determined by comparing sequences of pea, broad bean, lupine, and wheat and restriction enzyme cleavage sites of pea, broad bean, runner bean, pumpkin, and wheat.

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DNA CONTENT VARIATION AMONG HIGHER PLANTS[1]

H. James Price[2]

ABSTRACT

DNA content varies well over 100-fold among diploid herbaceous angiosperms. Differences exceeding two- to three-fold commonly exist among congeneric species. There is no overall correlation between DNA content and evolutionary or genetic complexity, and apparently only a small percentage of a plant genome has coding functions. The question of adaptive versus nonadaptive roles of variation in nuclear DNA content is addressed. The geographic, ecological, and taxonomic distributions of DNA content are not random; they apparently represent the results of natural selection. Several examples of evolutionary changes of DNA content and of geographical and ecological correlates are presented. Variation in DNA content is discussed in terms of the nucleotypic theory. The nucleotype is determined by the total quantity of DNA, both genetic and nongenetic, that has been correlated with several factors, including nuclear volume, cell volume, mitotic cycle time, and the duration of meiosis. It is proposed that differences in DNA content have striking and multiple nucleotypic effects on plant development and adaptation. A precise technique for the scanning microspectrophotometric determination of DNA content from Feulgen-stained leaf epidermal cells is presented.

Extensive variation in genomic DNA content exists among plant and animal taxa (Bachmann et al., 1972; Sparrow et al., 1972; Bennett & Smith, 1976; Price, 1976). Nuclear DNA amount among diploid herbaceous angiosperm species varies well over 100-fold (Bennett & Smith, 1976; Price, 1976). For example, *Arabidopsis thaliana* (2C DNA content = ca. 0.5 pg) and *Trillium erectum* (2C DNA content = ca. 80 pg) both have a diploid chromosome number of ten, but *T. erectum* has very much larger chromosomes housing about 160 times more DNA. Even more variation is apparent when polyploid species are considered, e.g., *Fritillaria davisii* (2C DNA content = ca. 225 pg) (Bennett & Smith, 1976). Differences in genomic DNA content exceeding two- to three-fold commonly occur among congeneric species, including those in the genera *Gossypium* (Edwards & Endrizzi, 1975), *Vicia* (Chooi, 1971), *Crepis* (Jones & Brown, 1976), and *Microseris* and *Agoseris* (Price & Bachmann, 1975).

Among eukaryotes, there is no strong correlation between DNA content and organismic or genetic complexity (Sparrow et al., 1972). As stated above, even closely related species vary greatly in DNA content. Furthermore, it has been estimated that only a small percent of the base pairs of DNA are utilized for coding proteins in plants (Flavell, 1980). The general lack of a correlation between organismic complexity and DNA content, the variation in genome size (DNA amount per genome) among closely related species, and the apparent surplus of DNA above that coding for proteins have been called the DNA C-value paradox (Thomas, 1971; Raff & Kaufman, 1983).

Differences in DNA content apparently involve redundant nucleotide sequences that are without coding function (Flavell et al., 1974). It is not the purpose of this paper to discuss the nature of these sequences. The reader is referred to Murray et al. (1981), Walbot & Goldberg (1979), and Flavell (1980, 1986) for discussions concerning repetitive sequences within plant genomes.

The role of genome size variation will be discussed in terms of phenotypic effects independent of any biochemical or coding functions that the nucleotide sequences may have. Topics included are (1) selfish DNA, (2) the nucleotype, and (3) taxonomic, geographical, and ecological distribution of DNA content variation. Lastly, a critique

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of techniques for determining DNA content using scanning microspectrophotometry will be presented.

SELFISH DNA

Orgel & Crick (1980) and Doolittle & Sapienza (1980) proposed that processes involved with DNA replication might allow the accumulation of DNA sequences in a genome whose presence stimulates the further accumulation of similar sequences. These sequences were considered to have no effect on the phenotype and to contribute little or nothing to the fitness of the organism. They suggested that this "selfish" or "parasitic" DNA may explain much of the variation in DNA content observed among species. These papers have resulted in an array of responses (see Nature 285: 617–620, 645–648, 1980) both favoring and criticizing the concept. In spite of controversy, the concept of selfish DNA is important because it points out the futility of searching for a biochemical function for all DNA sequences and because it stimulates thought on the origins and turnover of sequences in the genome. However, selfish DNA by definition excludes any functions for the sequences and thus diverts attention away from questions concerning evolutionary significance of variation in DNA content. If the generation of selfish DNA sequences is regarded as a mutational event that generates variation in genome size (Cavalier-Smith, 1980), then the important question becomes how much variation in DNA amount, regardless of mode of origin, is tolerated before selection comes into force.

The puzzle of genome size variation probably will not be solved at the subcellular level. Rather, the cellular effects of DNA amount are more likely reflected as a whole-organism phenomenon that can be best studied at the developmental, populational, and ecological levels. It has been proposed that the mere bulk of all the DNA in the genome exerts an influence on the phenotype so that under some circumstances selection favors accumulation of nuclear DNA more or less independently of its nucleotide sequence, while under different conditions the loss of sequences not necessary to survival may bring about considerable adaptive advantage (Bennett, 1972; Price, 1976; Bachmann et al., 1985).

NUCLEOTYPIC EFFECTS

The nucleotype is defined as the effect of DNA quantity on the phenotype apart from the coding function (Bennett, 1972). The nucleotype is determined by the total quantity of DNA, both genetic and nongenetic, and influences several cellular and developmental parameters, including chromosome size, nuclear volume, cell volume, mitotic cycle time and the duration of meiosis.

General comparisons of karyotypes of plants with similar chromosome numbers showed that those with higher DNA contents have larger chromosomes (Sparrow & Evans, 1961; Sparrow et al., 1968; and others). Measurements of individual metaphase chromosomes indicated a strong positive correlation between DNA content, chromosome volume, and chromosome mass (see Rees & Jones, 1972; Levin & Funderburg, 1979). Furthermore, a strong correlation exists between the total length of the synaptonemal complex and genome size in plants (Anderson et al., 1985).

Baetcke et al. (1967) biochemically determined DNA content and measured nuclear volume from root meristems of 30 herbaceous angiosperms representing ten families. The DNA content varied over a 35-fold range among these species, and a linear relationship (slope = + 1) was demonstrated between DNA content and the mean nuclear volume of meristematic cells of root and shoot.

Price et al. (1973) measured cell and nuclear volume of apical meristem cells of species ranging over 100-fold in DNA content. The data indicated a direct correlation between nuclear volume, cell volume (slope = + 1), and DNA content. Additional data supporting a positive relationship between DNA content and cell volume include the research with unicellular algae by Holm-Hansen (1969), a study of a polyploid series of yeast, $1X$ to $8X$ (Gunge & Nakatomi, 1972), a correlation between the fresh weight and DNA content of root meristematic cells from thirteen angiosperm species (Martin, 1966), a relationship between DNA content and cell volume among *Gossypium* species (Edwards & Endrizzi, 1975), and an increase in cell size in rye with supernumerary chromosomes (Rees, 1972).

Nurse (1985) discussed the interaction of genes and DNA amount in the determination of cell volume. Although genes that influence cell volume have been studied, they cannot account for the correlation of cell size and DNA content. Factors other than DNA content that affect nuclear and cell volume of meristematic and differentiated cells include physiological differences, nutritional and environmental state of the plant, and the genotype (Price et al., 1973). However, in light of the strong correlation between DNA content, nuclear volume, and cell size, a reasonable hypothesis is to consider DNA content as determining a fundamental nuclear and cell size that is influenced by developmental, genetic, and environmental factors. Selection for

DNA amount may be partly through its effects on nuclear and/or cellular size.

The importance of cell size to plant adaptation needs much more research. Cutler et al. (1977) suggested that smaller cells help plants resist moisture stress because they maintain turgor with solute accumulation under lower water potential values than do larger cells. Nobel (1980) related water use efficiency (WUE = net rate of CO_2 uptake divided by net transpiration rate) in plant leaves to several factors, including diffusion across the cell wall and membranes, photochemistry, biochemistry, effects of the atmosphere, leaf temperature, stomatal opening, cellular properties, and leaf anatomy. The factor A^{mes}/A (mesophyll surface area per unit of leaf area) was mathematically modeled and experimentally demonstrated to affect WUE, i.e., an increase in A^{mes}/A results in an increase in WUE (Nobel, 1980). A^{mes}/A is strongly influenced by cell size, shape, and number, e.g., leaves of the same thickness but with smaller cells have a greater WUE (Nobel, 1980).

The effect of cell size on leaf physiology described by Nobel (1980) and others may be adaptive and related to the large changes in DNA content that have occurred during angiosperm evolution. Since cell size is positively correlated with DNA content, one major effect of varying DNA amount may be on traits related to WUE and osmotic adjustment. An evolutionary change for which decreased DNA amount might be adaptive is the ecological transition of a plant group from mesic to more xeric conditions. Individuals with less nuclear DNA may be better able to withstand water stress and higher temperatures due to the development of leaves with smaller cells, higher WUE, and turgor maintenance.

Many studies have established a relationship between nuclear DNA content and the minimum mitotic cycle time among diploid angiosperms (Van't Hof & Sparrow, 1963; Van't Hof, 1965; Price & Bachmann, 1976). Plants with higher DNA contents generally have a longer mitotic cycle. The average duration of the mitotic cycle increases at the rate of about 0.38 hr./pg of DNA (Evans & Rees, 1971). The increase is accounted for mainly in a longer period of DNA synthesis (Evans & Rees, 1971). An average difference of four hours in mitotic cycle time was shown between monocots and dicots of comparable DNA amounts; the difference is accounted for mainly in the increased length of the G_1 phase in dicots, which may be due to their more densely coiled chromatin (Evans & Rees, 1971; Evans et al., 1972).

The amount of DNA per nucleus also correlates with the duration of meiosis in diploid plants. The extremes reported are 18 hr. for *Petunia* ×*hybrida* (3C DNA content = 5.7 pg) and 274.0 hr. in *Trillium erectum* (3C DNA content = ca. 120 pg) (Bennett, 1971, 1977). The increase in the duration of meiosis with DNA content in these studies resulted from a similar increase in all meiotic stages.

The reasons for the DNA content differences among and within plant species remain matters of speculation. Certainly, the shorter mitotic cycle time and smaller cells may contribute to more rapid development of smaller annuals. However, additional factors should be considered. Mowforth et al. (1982) and Grime & Mowforth (1982) suggested that selection may operate on genome size through a differential effect of temperature upon cell division and cell expansion. They proposed that at low temperatures cell expansion is inhibited to a lesser degree than cell division. Therefore, growth under low temperatures was proposed to be promoted by cell enlargement, which would favor higher DNA content and larger cells. Under warmer temperatures, the advantage of growth dominated by cell enlargement should give way to that of growth involving higher rates of division of smaller cells with less DNA (Mowforth et al., 1982). Natural selection operating on such a phenomenon could have influenced both the inter- and intraspecific patterns of DNA content and ecological adaptation in higher plants.

Nucleotypic effects of variable DNA content are predictable and apparently of adaptive significance to higher plants (Price, 1976; Bennett, 1972; Bachmann et al., 1979). Evolutionary patterns of DNA content are discussed below.

TAXONOMIC, GEOGRAPHIC, AND ECOLOGICAL DISTRIBUTION OF DNA CONTENT VARIATION

Geographic, taxonomic, and ecological distributions of genome size among herbaceous angiosperms are not random, but rather apparently represent the results of selection (Price, 1976). Karyotypic studies of grasses by Avdulov (1931) showed plants of tribes and genera centered in the tropics, or those that grow only during warm seasons in temperate climates, had uniformly small to medium-size chromosomes and nuclei. Plants of species growing in cooler temperature regions tend to have larger chromosomes. Levin & Funderburg (1979) concluded that genome sizes are generally larger in temperate compared with tropical herbs. However, in large cosmopolitan families other than the Gramineae and Liliaceae, no significant differences in genome size were detected between temperate and tropical species. It was suggested that generally families indigenous to tropical and subtropical regions have substantially smaller genomes than those of temperate regions.

Bennett (1976a, b) studied DNA content in relation to the distribution of cereal grain crops, cultivated pasture grasses, and legume pulse crops. Cultivation of species with higher DNA content tends to be localized in temperate latitudes, or the seasons and regions at lower latitudes where conditions are similar to those normally found in temperate latitudes. Bennett (1976a) suggested that man had generally chosen species for cultivation that resulted in a distribution paralleling or exaggerating the natural tropical–temperate cline in DNA content.

DNA content variation within genera is common. In cases where the phylogeny or primitive versus advanced status of taxa can reasonably be deduced, it is apparent that both evolutionary increases and decreases in DNA content have occurred. For example, Rees & Hazarika (1967) observed a three-fold variation in genome size among diploid species of *Lathyrus*. The higher values were from outbreeding perennial species and the lower from inbreeding annuals. This represented an apparent evolutionary decrease of DNA amount. Large evolutionary decreases in DNA content apparently have occurred in the evolution of annual species of *Crepis* (Jones & Brown, 1976), and in *Microseris* and *Agoseris* (Price & Bachmann, 1975). In contrast, the evolution of the inbreeding annual species of *Lolium* was accompanied or followed by an increase of about 35% in the quantity of nuclear DNA (Rees & Jones, 1967). The monotypic diploid perennial *Phalacroseris bolanderi* has more than twice the DNA of its perennial relatives of the Microseridinae. The higher DNA values probably represent an evolutionary increase (Price & Bachmann, 1975).

There is a general correlation of growth form with genome size. Bennett (1972) surveyed 271 plant species representing monocot and dicot annuals and perennials. His study showed that annual monocots and dicots have a significantly lower mean nuclear DNA content than perennials; the range of nuclear DNA amount is smaller among diploid annual species for both monocots and dicots; ephemeral annuals have a lower mean DNA content than nonephemeral annuals; and among monocots mean DNA content of obligate perennials is significantly greater than that of facultative perennials, and the mean values for facultative perennials and annuals are not significantly different. Bennett (1972) presented the hypothesis that nuclear DNA content and minimum generation time are correlated in plants, and that DNA content is causally correlated with the rate of development. He considered attributes that allow an annual species to develop rapidly in a time-limited environment (i.e., rapid mitotic cycle and brief meiosis) to require a low DNA content. Because of these nucleotypic correlates, plants with very high DNA contents should be perennials (Bennett, 1972).

DNA content has been considered in terms of evolutionary advancement within and among genera (Price, 1976) and growth forms of the species (Bennett, 1972), but it has received little attention within an ecological context. A better understanding of the apparent developmental and evolutionary significance of DNA amount comes from populational studies of diploid species that have been demonstrated to possess both interspecific and intraspecific variability in DNA content, such as western North American species in the subtribe Microseridinae (Asteraceae, Lactuceae). This group has been studied extensively by taxonomic (Stebbins, 1953; Chambers, 1955, 1963; Feuer & Tomb, 1977; Harborne, 1977), ecological (Chambers, 1955, 1957; Stebbins, 1972a), genetic (Chambers, 1955, 1963; Bachmann & Chambers, 1978, 1981; Bachmann & Price, 1979; Bachmann et al., 1979, 1981, 1983), and cytogenetic methods (Stebbins et al., 1953; Chambers, 1955, 1963). The genera *Agoseris* and *Microseris* are closely related; similar evolutionary trends have occurred within each. The perennial species of *Agoseris* and *Microseris* are taxonomically and ecologically primitive, and putative transition species morphologically bridge the gap between the genera (Chambers, 1957; Stebbins, 1972a, b). Trends toward reduction in size of all parts of the plant, more rapid growth rate, shortening of the life cycle, change of breeding structure from allogamy to autogamy, and specialization in structure of fruits and involucres have occurred in the evolution of annual species of both *Agoseris* and *Microseris* (Chambers, 1955, 1963; Stebbins, 1972a, b). The annuals have undergone a major ecological adaptive shift to drier ephemeral habitats and generally grow in late winter and early spring when moisture is available.

Relative nuclear DNA contents have been determined by scanning microphotometry of Feulgen-stained nuclei isolated from eight species of *Microseris*, four species of *Agoseris*, and *Phalacroseris bolanderi* (Price & Bachmann, 1975). A 7.7-fold range in DNA content was detected among these diploid ($2n = 18$) species. A 2.8- and 3.1-

fold range was found among species of *Microseris* and *Agoseris*, respectively. Price & Bachmann (1976) demonstrated a positive correlation between mitotic cycle time and nuclear DNA amount in the Microseridinae. Within *Agoseris* and *Microseris*, the annuals have lower DNA contents and a more rapid mitotic cycle than do the perennials.

Intraspecific variation in DNA content has been demonstrated in two annual species of *Microseris*. DNA content varies over 20% within *M. bigelovii* (Price et al., 1981a) and within *M. douglasii* (Price et al., 1980, 1981b). Within *M. bigelovii*, the lower DNA values were from geographically disjunct populations growing at the latitudinal extremes of the species. It was suggested that the small genomes may have resulted from selection for low DNA content in stressful and time-limited environments (Price et al., 1981a).

The DNA contents of 222 plants of *M. douglasii* representing 24 geographically, ecologically, and morphologically diverse populations in California were determined (Price et al., 1981b). The quantity was relatively uniform in most populations, even when there was an abundance of morphological diversity. Variation up to 14% existed among the population means. Populations with higher-DNA-content plants were restricted to more mesic sites, i.e., habitats receiving a yearly average precipitation of 20 inches or more, generally with well-developed soil. Price et al. (1981b) concluded that the observed distribution of DNA content in *M. douglasii* was not that expected by random drift; it was suggested that natural selection may have been responsible for at least part of the observed distribution pattern of DNA content.

The DNA contents of an additional 210 plants of *M. douglasii* were determined (Price et al., 1986). These data supplemented those previously reported (Price et al., 1981b) and allowed temporal changes in DNA content over several years to be detected at three populations. At one collection site near Jolon, California, temporal shifts were observed from low DNA amount in the drought year of 1962 to higher DNA values in 1973 after several years of generally more abundant precipitation, and back to low DNA content in 1977, the second of two severe drought years. These results suggested that the DNA content of *M. douglasii* may be tracking the environment and be subject to selection over seasons of drought and nondrought, respectively. Further collections (1980–1982) during the near-average to above-average rainfall years of 1978–1982 detected no reversal to a higher mean DNA content of the population. Although some high-DNA-content biotypes were detected by sampling for extremely robust growth forms, these had not become predominant over five years with very favorable moisture conditions.

A second population located near the summit of the Parkfield–Coalinga road had a mixture of very high, high, and low DNA biotypes in 1977 (Price et al., 1981b). The plants collected from 1980 to 1982 showed a progressive increase in mean population DNA content and a narrowing of the variation about the mean (Price et al., 1986). These results were compatible with the hypothesis that increased moisture availability and/or the longer growing season associated with it is conducive to selection for higher DNA values.

At a third population site near Middletown, mean DNA content was high in 1977. Since rainfall was low in 1977 in California, we expected to find after the high precipitation years of 1978–1982 a high mean DNA level in this population. Instead, the average DNA content of the samples declined between 1980 and 1982. This appears to contradict the hypothesis that increased soil moisture causes selection for higher DNA amounts. However, this site, a flat grassy swale, accumulates standing water after heavy winter rains. Factors such as the depth and persistence of standing water might affect the date of germination and the length of the time for maturation. Our field observations of late April to mid May in 1981 indicated that the plants of this population had a late start in growth, were depauperate, and were being exposed to a rapidly drying habitat during fruiting. Biotypes with lower DNA content might be favored at this site during years when winter rains produce a persistent vernal pool, which shortens the period favorable for growth and development.

The studies with *Microseris* suggest that one factor influencing the selection for DNA content is soil moisture availability. Other factors, such as length of the growing season, edaphic parameters, temperature, grazing, and competition from other plant species, apparently are of importance. The interactions of these parameters in influencing selection for DNA amount, however, appear to be complex, and DNA amount does not necessarily respond to selection in the same way at different sites if only one or a few factors are considered.

Another example of apparent adaptive intraspecific variation in DNA content is *Zea mays*. It has long been known that knob number in maize is negatively correlated with latitude in North America (Brown, 1949) and with altitude in Mexico (Wellhausen et al., 1952; Bennett, 1976b). Rayburn et al. (1985) and Laurie & Bennett (1985) independently determined nuclear DNA content from 21 and 10 lines, respectively, of maize representing a geographical range from Mexico to

Nova Scotia. DNA content varied up to 37%. A significant negative correlation ($r = -0.45$ and $r = -0.75$) exists between DNA content and latitude in both studies. Significant positive correlations existed between knob number (detected as mitotic C-bands) and the amount of karyotype consisting of C-bands ($r = 0.87$), knob number and DNA content ($r = 0.59$), as well as percent C-band heterochromatin and DNA content ($r = 0.70$) (Rayburn et al., 1985).

Corn is considered to have arisen in Mexico or Central America and then to have been taken northward by man. The selective pressures imposed in the northward migration of maize included a shorter and cooler growing season and maximum plant size permitted by climatic constraints (Rayburn et al., 1985). This selection for maximum plant size and rapid maturation appears to have involved reduction in DNA content through its nucleotypic effect of a shorter mitotic cycle time. The DNA primarily eliminated is apparently the 185-bp simple sequence satellite DNA that has been shown to be associated with chromosome knobs of maize (Peacock et al., 1981). Other possible effects of knob heterochromatin, such as influencing the expression of closely linked genes, could be of adaptive importance. Such phenomena remain to be detected at the molecular level.

Succinctly, nuclear DNA amount apparently has predictable and multiple nucleotypic effects on plants. Studies of development and physiology of closely related species or biotypes with different DNA contents, in relationship to their ecological adaptations and restraints, should lead to a better understanding of the evolutionary role of genome size.

TECHNIQUES—DETERMINATION OF DNA CONTENT

DNA content of nuclei from plant tissues is most commonly determined by scanning microspectrophotometry following Feulgen staining. Other methods include the biochemical extraction and measurement of DNA from an estimated number of cells (Martin, 1966; Baetcke et al., 1967), flow cytophotometry of isolated nuclei (Galbraith et al., 1983), and various nonscanning microspectrophotometric methods. Specific precautions for Feulgen staining and scanning microspectrophotometry will be discussed along with a specific protocol for DNA-content determination (Price et al., 1980).

SOURCES OF ERROR

Estimates of DNA content can vary among experiments due to many factors, including source of tissue, different preparation of fixative and stain, length of hydrolysis, temperature fluctuation, and adjustment and sensitivity of the microspectrophotometer.

The source of tissue is very important for DNA-content determination. Nuclei from similar tissues at the same stage of development from healthy plants are necessary if small differences in DNA content are to be accurately detected. It is not proper to compare interphase nuclei from one plant with mitotic nuclei of another.

The fixation of tissue is critical. Generally ice-cold 3 : 1 absolute ethyl alcohol and glacial acetic acid for 24 hr. provide adequate fixation. Some species or tissues may require a shorter fixation period. Standard and experimental tissue should be fixed with freshly prepared fixative from the same bottle. The material is transferred to cold 70% ethyl alcohol and stored in a refrigerator for up to approximately two months before staining.

One potential source of error is in the hydrolysis of tissue prior to Feulgen staining. Error due to hydrolysis can be minimized by performing a careful hydrolysis scheme and choosing a hydrolysis time that results in maximum staining of nuclear DNA. Too little hydrolysis will give reduced staining, and prolonged hydrolysis results in extraction of DNA and hence reduced staining. Therefore, the use of a hydrolysis curve can greatly reduce experimental error. Once an optimal hydrolysis period is established, it is important to hydrolyze together the standard tissue and the tissue being compared so that each receives a similar hydrolysis. Most species analyzed in my laboratory have maximum Feulgen staining following hydrolysis in 5 N HCl for 40–50 min. at 25° C.

Another source of error may result from different densities of nuclei. Polyploid cells and nuclei with high amounts of heterochromatin tend to have DNA amounts underestimated by Feulgen densitometry (Verma & Rees, 1974; Narayan & Rees, 1974). This problem can be overcome by measuring interphase nuclei rather than mitotic figures.

A frequently cited source of error is glare (Goldstein, 1970; Bedi & Goldstein, 1974). Error involving well-spread metaphase or telophase mitotic figures is potentially greater than that involving prophase or interphase nuclei (Bennett & Smith, 1976). Glare can be partially corrected electronically in the microspectrophotometer and by careful measurement of nuclei, including severe restriction of the area illuminated. In actual practice, stray light effects have been found to be negligible with the procedures using most modern microspectrophotometers.

After all sources of potential error have been minimized, measurements are then subject to sensitivity of the microspectrophotometer. The assemblage initially used in my laboratory was a Zeiss Universal-II scanning microscope with a 03 photometer system, 0.5-μm scanning stage, modified 45-control unit, modified PMI-indicator, and a value average module. The latter three components have been recently replaced with a Zeiss Zonax, which contains a fully programmable set of controls and graphics system. Both systems allow for very accurate and precise measurement of DNA amount. The variance due to instrumentation in measurements accomplished with these systems is less than 1% of the mean.

In practice, the minimal differences in DNA content that can be detected by Feulgen microdensitometry are in the 2.0–5.0% range. To approach these, techniques must be used that minimize all sources of error, including slide-to-slide variation. This is achieved by the use of an internal standard on each slide (Dhillon et al., 1977; Price et al., 1980).

PROTOCOL FOR DNA CONTENT DETERMINATION

A technique for determination of DNA content from interphase leaf epidermal nuclei is outlined below. This technique leads to the highly controlled, internally standardized, and precise measurement of relative DNA content (Price et al., 1980) and has been successfully applied to several genera, including *Microseris*, *Agoseris*, *Coreopsis*, *Helianthus*, and *Zea*.

1. Peel epidermis from the middle third of nearly fully expanded healthy leaves of standard and experimental plants. It is best to use plants that have been grown in a growth chamber. The standard for *Microseris* is an inbred strain of *M. douglasii*.
2. Fix in ice-cold 3 : 1 absolute ethanol and glacial acetic acid for 24 hr., transfer to cold 70% ethanol, and store under refrigeration.
3. Place 5-mm squares of epidermis in a drop of H_2O on a cleaned (0.5 g gelatin, 1 g $CrK(SO_4)_2 \cdot 12\ H_2O$) microscope slide. Epidermis of the standard should be placed adjacent to that of the experimental.
4. Place coverslips over the epidermal squares with slight hand pressure and remove after freezing over dry ice. Floating slides over liquid nitrogen on a raft made of screen and styrofoam also works well and is more economical.
5. Air dry slides.
6. Hydrolyze for 40 min. in 5 N HCl at 25°C (hydrolysis time may vary in different species). Rinse in distilled H_2O.
7. Stain for 2 hr. in Schiff's reagent (see next section for preparation of Schiff's reagent).
8. Rinse for 10 min. in two separate SO_2 water (600 ml H_2O, 36 ml aqueous 1% $K_2S_2O_5$, 30 ml 1 N HCl) baths and 10 min. in H_2O. Blot away surplus H_2O with a paper towel.
9. Place a drop of enzyme solution (2% cellulysin (Calbiochem), 0.5% macerase (Calbiochem), 0.001 M EDTA, pH 5.6) over each epidermis for 30 min. (Feulgen staining is not affected by this treatment).
10. Dip slides gently into H_2O and absorb surplus water with a paper towel.
11. Place a cover glass on the tissue over a drop of 45% acetic acid. Apply moderate hand pressure. This releases nuclei from the cells and facilitates their movement to clear areas of the slide.
12. Remove cover glasses after freezing over dry ice or liquid nitrogen and air dry slides.
13. Mount No. 1 cover glasses over Permount. Let Permount harden for several days in the dark.
14. Spectrophotometrically measure (560 nm) DNA content of nuclei from the standard and experimental tissue on each slide. The values of individual nuclei of the experimental material on each slide are adjusted by multiplying the amount needed to increase or decrease the mean of the standard to a predetermined value. For the *M. douglasii* standard, it is 22.54 absorbancy units.
15. DNA values in picograms can be obtained by comparing the standard species with another species of known DNA amount.

PREPARATION OF SCHIFF'S REAGENT

Schiff's reagent quantitatively reacts with DNA during Feulgen staining and absorbs light at a peak wavelength of about 560 nm.

Prepare Schiff's reagent by dissolving 2 g basic fuchsin (Certified Biological Stain) in 400 ml boiling H_2O. After cooling, add 40 ml 1 N HCl and 4 g $K_2S_2O_5$. Store overnight in a dark stoppered bottle. Add 1 g decolorizing carbon, shake and vacuum-filter through No. 1 filter paper. The reagent should be used fresh; older reagent results in reduced staining of DNA.

ADVANTAGES OF EPIDERMAL PROCEDURE

The leaf epidermal technique with an internal standard on each slide has several advantages over root tips or other cell types for microspectrophotometric determination of DNA content. For most composites, nearly all leaf nuclei are arrested at the G_1 phase of the cell cycle and are 2C in DNA content (Brossard, 1977; Nagl, 1978; Price et al., 1980). With *Zea mays,* 2C and 4C nuclei are readily identifiable. The epidermis from an inbred line of the same species used as an internal standard on each slide reduces errors due to variation in hydrolysis and staining from slide to slide and experiment to experiment. All values adjusted to the internal standard are directly comparable between slides and staining batches (Price et al., 1980). Spherically shaped interphase nuclei released by enzyme treatment are preferable to mitotic nuclei for microspectrophotometry, since hydrolysis and potential optical problems with compacted chromatin (Duijndam & van Duijn, 1975) are minimized. Lastly, the variance of interphase nuclei is among the lowest reported, with a CV generally under 5 or 6%.

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RHIZOPHORACEAE–ANISOPHYLLEACEAE: A SYMPOSIUM

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The systematics and phylogeny of the Rhizophoraceae were discussed at a symposium held during the American Institute of Biological Sciences meetings in Amherst, Massachusetts, August 13, 1986. The following nine papers are a record and amplification of this event. The motivation for choosing such a topic was the uncertain ordinal status of the Rhizophoraceae, made evident at an earlier discussion of the Myrtales in Sydney, Australia (1981: see Ann. Missouri Bot. Gard. 71(3), 1984), together with increasing evidence for the exclusion of the tribe Anisophylleae from the family. In addition, the Rhizophoraceae are a very diverse group, both ecologically and morphologically, most obviously in the mangrove members of the family that form a discrete tribe, Rhizophoreae. Opportunity thus existed to examine a relatively small tropical family (about 140 species) from several points of view, and to assemble evidence for more reliable systematic and phyletic associations. Information was presented by a group of investigators having extensive acquaintance with the family in field and laboratory. The Rhizophoraceae are familiar to tropical biologists because of the widely distributed mangrove genera that often dominate intertidal forests. However, the symposium has made very clear the extent to which these genera are not entirely representative of the family, so that it is inappropriate to refer to the Rhizophoraceae as "the mangrove family." Nevertheless, the presence of mangrove species allows some assessment of the way in which systematic characters may or may not be useful in phylogenetic analysis depending on their obvious functional or adaptive significance. The symposium also generated a better understanding of the tribe Anisophylleae and indicated why it should be segregated as a separate family and, if excluded from the Myrtales, where its affinities might lie.

The objectives of the symposium were thus not only realized, but also serve as a model for the kind of systematic analysis that is needed for most groups of tropical plants, not necessarily because the information is all that complete for the Rhizophoraceae (the survey reveals just how limited is our knowledge of many of the plants under discussion), but rather it provides a model for the range of information from which phyletic conclusions might be drawn and demonstrates that this can only be assembled by extensive teamwork. It is noteworthy that the new evidence was generated by a range of techniques, from such simple approaches as phyllotactic analysis requiring minimal equipment, to the demonstration of distinctive ultrastructural features, as in sieve-tube plastid organization, requiring elaborate technology. The tropical investigator should take heart from this demonstration that simple approaches can produce worthwhile results that need not be overshadowed by the results obtained by otherwise unavailable technology. The overlying message is that syntheses of this kind are urgently needed for all tropical flowering plants if our appreciation of their phyletic relationships is to be developed to a greater degree of reliability.

The overview of the symposium was provided by Rolf Dahlgren as a critical re-evaluation of the ordinal position of Rhizophoraceae sensu stricto and Anisophylleaceae in a manuscript completed shortly before his untimely death. The tragedy of this accident is clearly perceived as we view the major intellectual achievement provided by his contribution. The paper is a monument to his own methodology; his line of reasoning is very clear and explicit. It demonstrates the unique ability he had to grasp intricate detail and from it to distill a balanced judgment. It is appropriate that the symposium be dedicated to his memory and that his summary paper be allowed to lead on to the panorama he was able to command so well.

We express our thanks to all the contributors whose collaborative efforts have made the venture entirely possible.

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RHIZOPHORACEAE AND ANISOPHYLLEACEAE: SUMMARY STATEMENT, RELATIONSHIPS[1]

Rolf M. T. Dahlgren[2]

Abstract

Each of Rhizophoraceae and Anisophylleaceae, as now defined by Tobe & Raven, are here considered to represent monophyletic units. Conspicuous autapomorphies of the variable Rhizophoraceae are, for example, the constellation of protein bodies of the sieve-tube plastids and the presence of colleters. Autapomorphies of the less variable and smaller Anisophylleaceae are sets of embryological, anatomical, and morphological characteristics as well as aluminium accumulation. The contributors of this symposium show convincingly from various fields how the two families differ in numerous details. These differences in combination support very strongly that the families are distinct from each other and are probably even rather distantly related. The Rhizophoraceae do not belong to Myrtales, from which they were excluded by all participants of a recent Myrtales symposium. Comparisons with various other groups show that Rhizophoraceae agree in many characters with especially Elaeocarpaceae, previously placed in Malvales, Celastraceae of Celastrales, and families of Geraniales, e.g., Erythroxylaceae, Humiriaceae, Linaceae, Lepidobotryaceae, and Oxalidaceae. This is supported in particular by a syndrome of embryological attributes, but also from morphological, anatomical, pollen morphological, and chemical evidence. Anisophylleaceae, which possess a combination of quite trivial character conditions, technically fit most closely with Rosales in the wide sense, i.e., Rosales–Cunoniales–Saxifragales, without approaching any particular family. Anisophylleaceae may have evolved from taxa related also to the ancestors of Myrtales.

At a previous symposium held in Sydney (1982) the circumscription of the order Myrtales was critically considered. It was concluded (Raven, 1984) that two anatomical character states can be considered diagnostic features ("autapomorphies" in evolutionary terms) of this order: vestured pitting of the vessels and presence of intraxylary phloem. This implies that these character states were established in the ancestor of Myrtales.

At the Myrtales symposium (Raven, 1984) Thymelaeaceae and Rhizophoraceae were excluded with some misgivings from that order. Whereas the Thymelaeaceae possess the two above-mentioned anatomical characteristics (but show important differences from the Myrtales), the Rhizophoraceae lack them. The relationships of Thymelaeaceae as well as Rhizophoraceae have remained uncertain. The purpose of this symposium is to analyze and settle the relationships of the Rhizophoraceae.

Each of the families Thymelaeaceae and Rhizophoraceae, in their wide circumscriptions, contains a group of somewhat erratic genera—the Gynystyloideae in Thymelaeaceae and the Anisophylleoideae in Rhizophoraceae. When included, these elements amplify the variation in the two families and make difficult a proper evaluation of their affinities and evolutionary backgrounds.

The history of the systematic treatment of four genera, which are here assigned to Anisophylleaceae, has been outlined by Tobe & Raven (1987b; see also Juncosa & Tomlinson, this volume). Ridley (1922) was the first to acknowledge Anisophylleaceae as a family. Although genera of Anisophylleaceae have occasionally been referred to other families such as Euphorbiaceae, Olacaceae, and Saxifragaceae, they are usually considered closely related to the Rhizophoraceae, which is nearly always so for the Anisophylleaceae as a family.

The Rhizophoraceae have generally been placed in Myrtales, which is partly explained by the great similarity between the most well-known rhizophoraceous genera, *Rhizophora* and *Bruguiera*, with,

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[1] *This contribution has been initiated on the request of Dr. Peter Raven, who has also continuously communicated information and encouraged the work. Dr. A. Juncosa has contributed new information on Rhizophoraceae embryology. Dr. A. Cronquist, Dr. A. Juncosa, Dr. P. H. Raven, and Dr. H. Tobe have given valuable remarks on the manuscript.*

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for example, *Sonneratia*, which is a clear member of Myrtales. Previously, this genus and *Duabanga* made up the family Sonneratiaceae, but recent evidence shows that both are best placed separately in Lythraceae.

Looking aside from parallel mangrove adaptations, there remain a number of vegetative, floral, chemical, and pollen morphological similarities between Rhizophoraceae and Myrtales, which together have justified a position in or next to this order until the structures were more fully analyzed and the relationships carefully reconsidered in connection with the recent Myrtales symposium (see above). These similarities extend to habit, phyllotaxis, occurrence of leaf sclereids, floral construction (e.g., diplostemony), and some embryological details. In fact, the occurrence of intercolpate grooves ("pseudocolpi") on the pollen grains in genera (at least *Anopyxis*) of Rhizophoraceae (see Vezey et al., this volume) are surprisingly reminiscent of those in several families of Myrtales, although they must be explained as convergence or parallelism. A misleading psychological reason for considering Rhizophoraceae and Myrtales closely related may be that the colleters in Rhizophoraceae resemble the axillary, rudimentary stipule homologues in many Myrtales; however, well-developed stipules occur beside the colleters in Rhizophoraceae.

The Rhizophoraceae have also occasionally been placed in Loranthales (Dumortier, 1829) but more often in Cornales (as by Cronquist, 1968; Thorne, 1968). A position of Rhizophoraceae—or Anisophylleaceae—in Cornales is unjustified in view of the embryological and chemical pattern in that order, largely defined by unitegmic, tenuinucellate ovules and cellular endosperm formation combined with common occurrence of iridoid compounds (Dahlgren, 1975). The placement of Anisophylleaceae in Cornales by Dahlgren (1980a) was explained by the record at that time of unitegmic ovules in *Anisophyllea* (Karsten, 1891), but embryological conditions were otherwise largely unknown.

Airy Shaw (1966) claimed relationships between Rhizophoraceae and Combretaceae, Elaeocarpaceae, and Tiliaceae, and (in 1973) with Combretaceae, Rubiaceae, and Elaeocarpaceae. Combretaceae are clear members of the Myrtales; the possible relationships between Rhizophoraceae and these have been commented on above. Rubiaceae agree with Rhizophoraceae in having opposite leaves, interpetiolar stipules, and colleters, but in floral, chemical, and especially embryological characters, they are extremely different, ruling out a close relationship. More interesting is the mention of Elaeocarpaceae. The similarity with this, for example in the laciniate petals, may first seem superficial, but other shared features (perhaps not considered by Airy Shaw), including some in embryology and chemistry, are worthy of careful consideration and will be evaluated below. Less obvious are the similarities between the Rhizophoraceae and the typically malvalean Tiliaceae.

In recent years, the Rhizophoraceae (without Anisophylleaceae) have sometimes been placed in an independent order, Rhizophorales, in either Rosidae (Cronquist, 1981) or in Myrtiflorae (Dahlgren, 1980a). The order Rhizophorales as established by van Tieghem & Constantin (1918) included Lecythidaceae in addition to Rhizophoraceae.

The position of the family Rhizophoraceae in any other order than its own has been regarded more or less unsatisfactory. Cronquist (1981) considered it, when placed in Myrtales, "as a giraffe in a herd of bison," and it is clearly out of place in both Cornales and Olacales.

Placing Rhizophoraceae in its own order solves no problem if our ambitions are to ally Rhizophoraceae with other groups of dicotyledons. It also remains to relate Anisophylleaceae with a family group and place it satisfactorily in an order.

When attempting to relate each of the Rhizophoraceae and Anisophylleaceae to other groups, the procedure has been to consider the variation pattern in each family in order to assess which character conditions can logically be regarded as relatively ancestral (plesiomorphic), that is, least advanced in the family, and which can be regarded as derived (apomorphic).

For the Anisophylleaceae, this poses no great problems, as the family is rather homogeneous. Tobe & Raven (1987b) have sketched the apomorphic conditions for the embryological features: unitegmic rather than bitegmic ovules; tapetal nuclei fused rather than not fused; a thin rather than thick seed coat; a base chromosome number $x = 8$ rather than $x = 7$; an *Allium*-type rather than *Polygonum*-type of embryo sac development; and unvascularized rather than vascularized integuments. These conclusions are based on common consensus and experience in evolutionary trends in dicotyledons and not on proper outgroup comparison, as is normally required in cladistic analyses. Actually, what we are still hunting is an acceptable outgroup of that family. In this case there is little controversy connected with the conclusions, but one can easily see risks in choosing which states are plesiomorphic first and concluding afterwards about an outgroup on the basis of biased opinions.

It is important that the choices of which features are considered plesiomorphic in a family are soundly based, since the plesiomorphic and not the apomorphic states decide the conclusions as regards relationships to other families, whereas the apomorphic states and not the plesiomorphic must govern the conclusions on evolution within the family.

Risks for biased opinions become more obvious when dealing with the much more variable Rhizophoraceae. Here, the logical step has been to regard the mangrove genera, the tribe Rhizophoraceae, as secondarily adapted in a number of characters ranging over vegetative and reproductive structures, a view for which Juncosa & Tomlinson (this volume) give ample evidence.

We are thus left mainly with the other tribes in Rhizophoraceae for conclusions on outward relationships, although presumably various chemical, anatomical, and embryological character states of tribe Rhizophoreae may have retained features of ancestral Rhizophoraceae, such as perhaps peculiar sieve-tube plastid inclusions, features of flavonoid and alkaloid chemistry, and presence of colleters, endosperm, and endothelium. Thus, emphasis is first laid on character states shared among all the tribes of the family, then on states common to tribes Macarisieae, Hypogyneae, and Gynotrocheae, or at least to some members in each of these tribes.

In my contribution I have disregarded completely the alignments between each of Rhizophoraceae and Anisophylleaceae and other groups in current systems of classification. I have compared character conditions of the kind just mentioned with those in various conceivably related families. It turned out that the current classifications help little in indicating groups with profound and all-around similarity to each of the two families.

Contrary to what was first expected, it has been much easier to suggest relationships for the larger and more variable Rhizophoraceae than for the small, more homogeneous Anisophylleaceae. This depends on the fact that Rhizophoraceae possess a number of rather unusual, presumably advanced attributes, such as a peculiar combination of embryological character states matched only in a few other families, peculiar alkaloid chemistry, and a characteristic seed coat. Luckily enough, the collective evidence all points in the same direction: toward a few families rarely or never considered previously as close relatives of Rhizophoraceae. Even though some of the similarities used in the forthcoming arguments are likely to be caused by convergent evolution, all are not likely to be so. According to the conclusions, the Rhizophoraceae are considered to be most closely related to families previously referred to three different orders, Malvales, Celastrales, and Geraniales, leading to a completely new view of their positions in the dicotyledons.

For Anisophylleaceae, the conditions are less favorable, since nearly all character states in which they differ from the Rhizophoraceae represent frequent states, some of them presumably less derived than the corresponding ones in Rhizophoraceae, giving fewer clues to the closest relationships.

Within some orders and superorders certain families possess many plesiomorphic character conditions, making them rather similar and difficult to place. Thus, a combination of various trivial character conditions, such as in Anisophylleaceae, with small to medium-sized, tetramerous, heterochlamydous, choripetalous, diplostemonous, and isomerous flowers, gives little guidance to any particular relationships.

CHARACTERIZATION OF RHIZOPHORACEAE

The Rhizophoraceae comprise a variable group of genera divisible into three tribes after the following model:

Tribus **MACARISIEAE**: *Anopyxis* (Pierre) Engl. (3 species); *Blepharistemma* Wall. ex Benth. (1 species); *Cassipourea* Aubl. (55 species); *Dactylopetalum* Benth. (15 species, if distinct from *Cassipourea*); *Comiphyton* J. J. Floret (1 species); *Macarisia* Thouars. (7 species); and *Sterigmapetalum* Kuhlm. (7 species).

Tribus **GYNOTROCHEAE**: *Carallia* Roxb. (9 species); *Crossostylis* J. R. & G. Forst. (10 species); *Gynotroches* Bl. (1–4 species); and *Pellacalyx* Korth. (8 species).

Tribus **RHIZOPHOREAE**: *Bruguiera* Lam. (6 species); *Ceriops* Arn. (2 species); *Kandelia* W. & A. (1 species); and *Rhizophora* L. (8 species).

The difficulty in defining the family by gross morphology is reflected in the fact that it comes out in 17 different places in the revised Thonner key (Geesink et al., 1981), although in this key Anisophylleaceae are included in Rhizophoraceae and account for four of these places.

Differences from the Anisophylleaceae are the opposite leaves and the interpetiolar stipules.

The most characteristic feature of Rhizophoraceae is perhaps the unusual type of sieve-tube plastids: with ca. 20 or more square to polygonal protein bodies of variable size (0.1–0.5 μm) (Behnke, this volume). These were found in *Bruguiera, Carallia, Crossostylis, Rhizophora* (Behnke, 1982), *Cassipourea, Ceriops, Kandelia,* and *Sterigmapetalum* (Behnke, 1984). Sieve-tube plastids of this type are known only in two more families: Erythroxylaceae and Cyrillaceae, both with somewhat fewer protein bodies, and the last family also with protein filaments in the plastids (Behnke, 1982). This character state represents a significant autapomorphy of the Rhizophoraceae. In Anisophylleaceae the sieve-tube plastids possess starch grains only (Behnke, 1982, 1984).

Another unusual feature, an autapomorphy found in both mangrove and nonmangrove genera of Rhizophoraceae, is the presence of colleters at the leaf bases (Hou, 1958, 1960). Lersten & Curtis (1974) described their construction in *Rhizophora mangle.*

These characters, especially when supplemented with some embryological features mentioned below—for instance, the combination of bitegmic crassinucellate ovules with integumentary tapetum (endothelium)—may suffice as arguments for considering Rhizophoraceae as a monophyletic unit, which could otherwise be doubted from the rich variation in vegetative, floral, wood anatomical, and other characters.

According to Keating & Randrianasolo (this volume), the leaves have brochidodromous or eucamptodromous venation. Lateral teeth are associated with mainly the latter kind of venation and are found in less coriaceous leaves of certain nonmangrove taxa, mainly in the tribe Macarisieae; they are called "macarisioid teeth." Whether occurrence of teeth represents a plesiomorphic or apomorphic state is uncertain, and perhaps no phylogenetic conclusions can be based on them. Stomata are confined to the lower surface of the leaves; the brachyparacytic type is most widespread in the family; and this was possibly the plesiomorphic state. Cyclocytic stomata are found in the Rhizophoreae and appear to represent a derived type in the family. It is interesting that prismatic crystals and crystal druses occur in Rhizophoraceae but are largely vicarious: prismatic crystals being found in the Macarisieae, where crystal druses are very rare (confined to *Blepharistemma*), while all other genera only have crystal druses. Thus crystals help with tribal division within the family. Laticifers, often articulated, are common in some species (Keating, 1984).

According to van Vliet (1976), the wood anatomy of the Rhizophoraceae is highly variable. The perforation plates of the vessels are usually scalariform, with 5–87 perforations. In this the Rhizophoraceae differ from the Anisophylleaceae, which have simple perforation plates. The vessel diameter in Rhizophoraceae is also typically smaller than in Anisophylleaceae. Furthermore, intervessel pits are alternate in Anisophylleaceae but opposite in most Rhizophoraceae. Within Rhizophoraceae, it is the tribe Gynotrocheae that approaches most the Anisophylleaceae, and within that tribe particularly the genus *Carallia,* in which vessel perforation may even be simple.

The inflorescences of Rhizophoraceae are generally few- to several-flowered cymes, or the flowers may also be simple. The inflorescences are situated in leaf axils.

Rhizophoraceous flowers vary from hypogynous to epigynous. They are, for example, hypogynous in Macarisieae, for some genera of which a particular tribe, Hypogyneae, has been proposed. Other genera have more or less perigynous, half-epigynous, or epigynous flowers. The hypogynous (or possibly somewhat perigynous) condition is likely to be plesiomorphic.

According to Juncosa & Tomlinson (this volume) Rhizophoraceae exhibit subepidermal floral laticifers of two tribally distinctive types. The numbers of sepals and petals each vary between 4 (as in *Rhizophora*) and 16 (in *Bruguiera*). The sepals are valvate. The sepal traces are of the split-lateral type (Juncosa, unpubl.). Apically laciniate petals are common in the nonmangrove genera. Among these, especially in *Cassipourea,* the petals recall the laciniate petals in certain genera of Elaeocarpaceae (Arena & Orsini, 1973). Fringed petals also occur in Anisophylleaceae and may represent the main reason why the genera of this group have so readily been included previously in Rhizophoraceae.

Interestingly, in the tribe Rhizophoreae the petals do not form a whorl, but each individual petal encloses one or more stamens opposite it. Juncosa & Tomlinson (1987) regarded this as an autapomorphy of this tribe. Stamens with a narrow filament and a well-defined truncate, tetralocular anther, as found in most nonmangrove genera, probably represent the plesiomorphic state, whereas the more specialized types of mangrove genera are derived. Tomlinson et al. (1979) showed that pollen is often released explosively, and pollen dispersal is highly variable: by wind, flies, other small insects, butterflies, night-flying moths, or even birds.

It is assumed that the plesiomorphic androecial condition for Rhizophoraceae is the diplostemonous, but many more stamens occur in some genera, e.g., about six times the petal number in *Kandelia* (Juncosa & Tomlinson, 1987). In *Ceriops tagal,* at least, all stamens belong to one whorl and arise on a ring primordium, whereas in *Bruguiera* two whorls of stamen initials are formed. This was used as evidence by Juncosa & Tomlinson (1987) that the remarkable explosive pollen discharge mechanism is derived independently in the two groups. The multistaminal condition is here regarded as derived by increase in number of initials. This is a common phenomenon in Myrtales, where increased stamen number has evolved in several families independently, and, for example, in Lythraceae obviously a few times.

Pollen grains of Rhizophoraceae according to Vezey et al. (this volume) are 3(–4)-colporate, and their exine has a rugulate-punctate (to psilate) surface. (The exine is proportionally thicker than that in Anisophylleaceae, where the surface sculpture is reticulate-punctate.) Vezey et al. (this volume) report "subsidiary colpi" or "pseudocolpi" on the pollen grains in some members of the tribe Macarisieae, this being a conspicuous similarity to the conditions in many Myrtales. The pollen grains in Rhizophoraceae are dispersed in the two-cellular stage.

The pistil is usually surrounded by a fleshy, often conspicuously lobate disc (said by Hou, 1958, to be lacking in *Pellacalyx*). The base of the stamens may be variably attached to this disc (Hou, 1968).

The pistil generally has a 2–12-locular ovary, each locule with from two to rather numerous (in *Pellacalyx* to ca. 25) ovules on an axile placenta. *Kandelia* is, however, an exception from this; its ovary is unilocular and contains about six apically inserted ovules.

The style is simple or slightly branched apically, as in *Gynotroches*; the latter state may be the most ancestral in the family. The stigma is terminal and capitate or more or less lobate; in *Gynotroches* the apical stylar branches are stigmatic. (The simple style contrasts to the separate stylodia in Anisophylleaceae.)

The embryological conditions in Rhizophoraceae (see, for example, Karsten, 1891; Cook, 1907; Mauritzon, 1938; and Juncosa, 1982, 1984a, b) are as follows. The ovules are anatropous or hemitropous, bitegmic, and crassinucellate, although sometimes rather weakly crassinucellate. The inner integument is three- to multilayered, and the outer two- to multilayered, depending on genus and stage of the ovule. The micropyle is at least usually zigzag. A parietal cell is always cut off from the primary archesporial cell and divides a number of times to form a modest parietal tissue. Embryo sac development, as far as known, is of the *Polygonum*-type. Endosperm formation is nuclear. During embryo sac development and the early stages of endosperm formation, the nucellar tissue lateral to the embryo sac disintegrates, so that this comes to border upon the inner integument. The inner layer of this develops an endothelium in at least several genera. The seeds are endospermous. The cells of the outermost layer of the inner integument (the exotegmen) become elongate and fibrous in most genera (comprising "Legnotidaceae" in Corner, 1976), although this is not the case with the genera of the tribe Rhizophoreae nor in *Carallia* of Gynotrocheae; see Juncosa, 1984a).

An aril is present in at least four genera of the tribe Macarisieae, e.g., *Cassipourea* (Schimper, 1892) and *Comiphyton* (Floret, 1974; Tobe, pers. comm.). This aril represents an expansion from the micropylar part of the outer integument, i.e., it is *exostomal.*

The fruits are normally capsular, dry or fleshy, although nonclassifiable in the viviparous genera. They are sometimes stated to be indehiscent. Frequently they do not have more than one seed per locule, sometimes only one seed altogether. The seeds (see above) have a chlorophyllous embryo (Schimper, 1892). The embryo has two well-developed cotyledons in the nonmangrove genera; in *Bruguiera* there are 2–4 cotyledons according to Schimper (1892); in *Rhizophora, Kandelia,* and *Ceriops* the cotyledons are fused into a handweight-shaped structure. In the mangrove genera the embryo grows continuously and the seed has no resting period, a condition called "vivipary." Vivipary and specializations connected with this are secondary adaptations.

The basic chromosome number according to Raven (1975) is $x = 18$ and $x = 32$.

Chemically, the Rhizophoraceae can be classified as tannin plants. Bark of some genera has up to 40% or more of condensed-type tannins (for references, see Hegnauer, 1973). Ellagic acid has rarely been detected, and then in low quantities (in *Cassipourea*). Both caffeic acid and proanthocyanin are present. Of flavonoid compounds, also kaempferol, quercetin, myricetin, leucodelphinidin, and leucocyanin are recorded within the family (Hegnauer, 1973).

Alkaloid chemistry in Rhizophoraceae is possibly important and will be further discussed below. Derivatives of tropane, pyrrolizidin, and hygrolin bases have been detected in different genera and, according to Hegnauer (1973), are probably all

TABLE 1. *Features judged to be primitive (plesiomorphic) in Rhizophoraceae sensu stricto.*

Sieve-tube plastids with several to numerous, square to polygonal protein bodies
Vessels with scalariform perforation plates
Intervessel pitting opposite
Laticifers probably present
Leaves opposite
Leaf venation at least partly brochidodromous
Stomata brachy-paracytic on lower surface of leaves
Prismatic oxalate crystals present (possibly also crystal druses)
Colleters at leaf bases
Inflorescences multiflorous cymes or cymules
Flowers hypogynous, probably pentamerous, diplostemonous
Disc present, prominent
Petals probably apically laciniate
Stamens with narrow filaments
Anthers well defined, ± ovate, tetralocular, with longitudinal dehiscence; insect pollination
Pollen grains tricolporate, with rugulate-punctate surface; without pseudocolpi(?)
Perhaps style simple, apically five-brachiate
Ovary with five locules
Ovules probably two per locule, axile
Ovules anatropous, bitegmic, crassinucellate, with three- to several-layered inner integument
Endothelium present
Seed coat exotegminal, with "fibrous" cells
Aril probably present, formed from the apex of the outer integument (exostomal)
Fruit capsular
Embryo chlorophyllous, with well-developed cotyledons
Alkaloids formed from the amino acid ornithine present

derived from ornithine. Some of the alkaloids are sulphated (Ettlinger & Kjaer, 1968). Rhizophoraceae (contrary to Anisophylleaceae) do not show aluminium accumulation. The endosperm of the seeds is nonstarchy and contains fatty oils.

The above evidence, in combination with the pantropical distribution pattern with Old World concentration, will form the basis for the following comparative remarks.

"RHIZOPHORACEOUS" CHARACTER CONDITIONS IN OTHER FAMILIES

METHODOLOGY

In the search for one or more families that are closely related to Rhizophoraceae it is essential to consider the character conditions judged to be plesiomorphic in Rhizophoraceae. These states have been indicated for a number of characters above.

The characters that should be most successful in the search for closely related families will simultaneously fulfill the following qualifications:

1. Character states that occur in most or all Rhizophoraceae or at least in a fair variety of the nonmangrove genera; these states are likely to be *plesiomorphic in Rhizophoraceae.*
2. Character states that are likely to be *apomorphic in a larger assemblage,* such as in a superorder; i.e., *character conditions that are not archaic in dicotyledons.*
3. Character states that are rather *unusual in dicotyledons at large, or have a defined distribution among them.*

Briefly expressed, we must first search for more or less advanced character states that are likely to have been established in an ancestor of a group of families that includes Rhizophoraceae.

Beyond individual peculiar character states present in Rhizophoraceae, *combinations* of character states should be considered, because unusual combinations are not likely to have evolved in different evolutionary lines. Exceptions are such combinations of character states that have evolved in response to a defined, extreme environmental pressure favoring special syndromes. Therefore, the mangrove genera, which are specialized in numerous respects and show multiple similarity to other mangrove genera, are unsuitable for comparison. It is true that also rainforest habitats favor certain morphs, but these are presumably less specialized than the mangrove ones.

Character conditions evaluated here include the following:

1. Presence of endothelium.
2. Presence of aril.
3. Exotegmic seed coat.
4. Chlorophyllous embryo.
5. Sieve-tube plastids with the protein bodies typical of Rhizophoraceae.
6. Presence of certain types of alkaloids.
7. Combined occurrences of the above (and other features).

Families found to share with Rhizophoraceae the unusual character conditions mentioned above will be compared further with Rhizophoraceae with regard to more general characters. If these turn out to be greatly divergent, the selected character conditions mentioned above are likely to reflect convergence rather than close relationship. If, however, a family shows similarity with Rhizophoraceae both in these selected characters and overall prop-

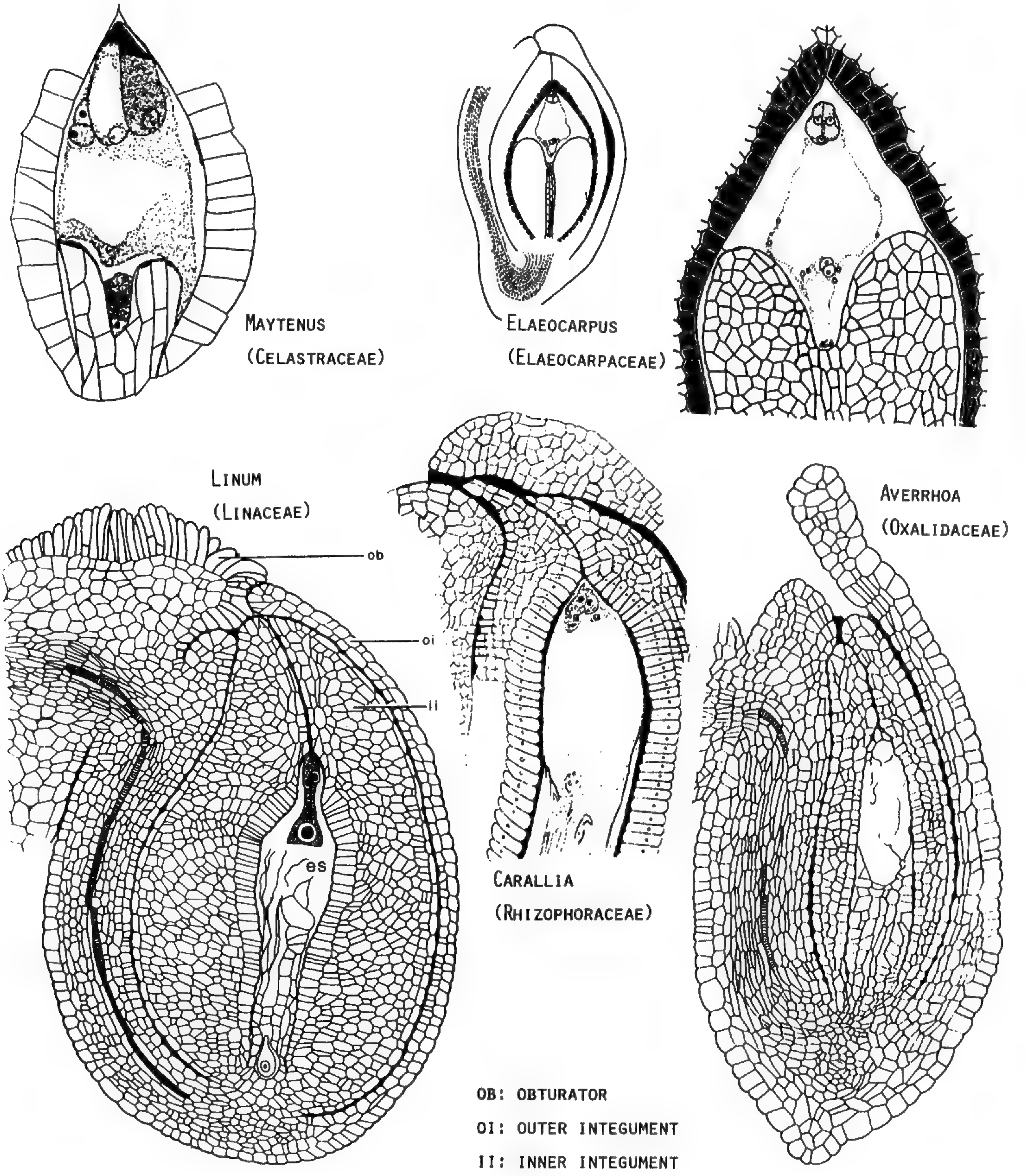

FIGURE 1. *Comparison of anatropous bitegmic ovules in several families having an endothelium lining the embryo sac. All have nuclear endosperm formation.* Maytenus *from Andersson (1931)*, Elaeocarpus *from Venkata Rao (1953)*, Linum *from Boesewinkel (1980)*, Carallia *from Karsten (1891), and* Averrhoa *from Boesewinkel (1985).*

erties, that family is likely to be closely related to Rhizophoraceae.

"RHIZOPHORACEOUS" CHARACTER CONDITIONS

For the following properties, most emphasis has been laid on families that are realistic as potentially related to the Rhizophoraceae. For example, monocotyledons, most sympetalous dicotyledons, taxa of Magnoliiflorae, Ranunculiflorae, Caryophylliflorae, and others have largely been ignored.

1. Presence of endothelium. Occurrence of endothelium (integumentary tapetum) was surveyed by Kapil & Tiwara (1978). In most groups having endothelium the ovules are unitegmic and tenuinucellate. These will not be considered here. Groups having a combination of endothelium and bitegmic ovules are shown as follows. They have nuclear (or rarely helobial) endosperm formation and include taxa with crassinucellate as well as tenuinucellate ovules.

Endothelium

I. In combination with crassinucellate ovules
  Rhizophorales: Rhizophoraceae (Narayana, 1970)
  Malvales: Elaeocarpaceae (Mauritzon, 1934; Venkata Rao, 1953)
  Geraniales: Erythroxylaceae (Boesewinkel & Geenen, 1980), Linaceae (Boesewinkel, 1985), Oxalidaceae (Boesewinkel, 1985), Zygophyllaceae, Balanitaceae (Narayana, 1957)
  Celastrales: Celastraceae (Andersson, 1931)
II. In combination with tenuinucellate ovules
  Theales: Lecythidaceae, Scytopetalaceae
  Ebenales: Ebenaceae
  Primulales: Myrsinaceae, Primulaceae

Most Rhizophoraceae probably have endothelium (although vestigial in the Rhizophoreae according to Juncosa, pers. comm.).

Rhizophoraceae were not mentioned by Kapil & Tiwara (1978), and the list thus is likely to be somewhat incomplete.

The endothelium will be further discussed below under the combination of character conditions.

2. *Presence of aril formed from the exostome.* Occurrence of arils is scattered and has restricted significance. Corner (1949, 1976) tended to regard the presence of arils as an archaic feature, while most other botanists seem to consider them polyphyletic and of rather recent origin. Arils comprise histologically diverse structures and are thus undoubtedly polyphyletic. However, it is likely that arils have developed early in some groups and then have been reduced or lost in some of their derivates, e.g., in combination with fruit evolution from capsules to berries or drupes. Occasional presence of arils, as in Rhizophoraceae, thus could be considered potentially useful and a possibly plesiomorphic character state.

What is of primary interest here is the occurrence of *exostomal arils*, as this is the kind present in Rhizophoraceae. Such arils occur at least in the following taxa:

Rhizophorales: Rhizophoraceae *pro parte* (at least 4 genera of tribe Macarisieae)
Malvales: Elaeocarpaceae: *Peripentadenia* (Hyland & Coode, 1982)
Celastrales: Celastraceae (common; see Andersson, 1931)
Theales: Clusiaceae *pro parte* (at least in *Clusia*)
Rutales: Meliaceae *pro parte* (at least in *Apanomixis*)
[Geraniales: Erythroxylaceae: *Aneulophus* (dubiously)]

Arils present in various other groups such as genera of Elaeocarpaceae (Malvales), Lepidobotryaceae (Geraniales), Gonystylidaceae (Thymelaeales), Connaraceae and Sapindaceae (Sapindales), Clusiaceae (Theales), and Rutaceae and Meliaceae (Rutales) according to Corner (1976) are mostly or wholly formed from the chalaza or raphe, or both. More studies are needed to clear up homology conditions for using aril structures.

3. *Seed coat with fibrous exotegmen.* According to Corner (1976), a fibrous exotegmen occurs in the following taxa:

Rhizophorales: Rhizophoraceae *pro parte*; probably all genera except the Rhizophoreae and *Carallia* of Gynotrocheae (Juncosa, pers. comm.).
Malvales: Elaeocarpaceae
Geraniales: Erythroxylaceae, Ixonanthaceae, Linaceae, Humiriaceae, and Oxalidaceae
Celastrales: Celastraceae
Euphorbiales: Euphorbiaceae: Phyllanthoideae
Sapindales: Connaraceae, Sapindaceae *pro parte*, and Staphyleaceae *pro parte*
Myrtales: Combretaceae, Lythraceae (including Punicaceae and Sonneratiaceae), and Onagraceae
Others: Aristolochiaceae, Capparidaceae, Caricaceae, Flacourtiaceae, Malpighiaceae, Violaceae, and additional families

Corner (1976) commented on *Gynotroches* and *Pellacalyx* (of his Legnotidaceae) that the exotegminal cells are long and sclerotic. This condition could represent the ancestral type in Rhizophoraceae and must be considered potentially useful in phylogenetic considerations (see Juncosa, 1984a).

Further notes on the seed coat will be given below.

4. *Chlorophyllous embryo.* The embryo in Rhizophoraceae is always or at least generally chlorophyllous (Schimper, 1892; Cronquist, 1981). A chlorophyllous embryo is often found in exendospermous seeds, a tendency that is marked in

monocotyledons but not as clear in dicotyledons; for instance, the seeds are endospermous in Rhizophoraceae.

Yakovlev & Zhukova (1980) and Dahlgren (1980b) have respectively listed and commented on the distribution of chlorophyllous embryos in seeds. In choripetalous dicotyledons their distribution is as follows (mainly according to Yakovlev & Zhukova, 1980):

Rhizophorales: Rhizophoraceae (all or most species; not included by Yakovlev & Zhukova)
Malvales: virtually all families: Bombacaceae, Cistaceae, Dipterocarpaceae, Elaeocarpaceae, Malvaceae (most taxa), Sterculiaceae, and Tiliaceae
Celastrales: Celastraceae
Geraniales: virtually all families, including Erythroxylaceae, Geraniaceae, Linaceae, Oxalidaceae, and Zygophyllaceae
Sapindales: various families, e.g., Aceraceae, Anacardiaceae, Hippocastanaceae, Sapindaceae, and Staphyleaceae
Rutales: most families, among them, Burseraceae, Meliaceae, Rutaceae, and Simaroubaceae
Polygalales: Polygalaceae
Rhamnales: Rhamnaceae
Fabales: all
Theales: Clusiaceae
Other groups: including scattered families of Myrtales; many Capparales, especially Brassicaceae; many Nymphaeales; many Caryophyllales; all Salicales; many Euphorbiales; many Santalales; Plumbaginales; and some taxa in Violales (Violaceae) and Cornales (Icacinaceae, Alangiaceae, Cornaceae)

This character previously has been quite overlooked in phylogenetic considerations.

5. Sieve-tube plastids with numerous, variably large, square or polygonal protein bodies. This type of protein has been found by Behnke (1982, 1984) in all genera of Rhizophoraceae studied (see above), *Erythroxylon* (Erythroxylaceae, Geraniales), and *Cyrilla* (Cyrillaceae, Ericales). In the last-mentioned family the sieve-tube plastids also contain thin protein filaments.

Cyrillaceae are so different from Rhizophoraceae in overall characters that they can probably be dismissed from consideration as closely related.

Of other families with different shapes and numbers of protein bodies in the sieve tubes may be mentioned Oxalidaceae (including *Averrhoa*), Connaraceae, Eucryphiaceae, and Vitaceae (Behnke, 1981).

The presence of the same type of protein configurations in Rhizophoraceae and Erythroxylaceae is of interest in light of a number of other similarities between the two families. If this type represents a synapomorphy of these two families, this would indicate a *very* close relationship (a sister group relationship). As will be commented on below under Erythroxylaceae, there is not sufficient evidence for that.

6. Presence of certain types of alkaloids. Rhizophoraceae contain three types of alkaloids (see Hegnauer, 1973): pyrrolidine, tropine, and pyrrolizidine alkaloids.

Hygroline, an alcohol of hygrine, is a *pyrrolidine alkaloid.* It is known in species of *Carallia* (Fitzgerald, 1965) and *Gynotroches* (Johns et al., 1967) of Rhizophoraceae, in at least two species of *Erythroxylon* of Erythroxylaceae, and in *Cochlearia* of Brassicaceae. Hygrine is also known in Convolvulaceae, Solanaceae, and Orchidaceae (Gibbs, 1974).

Of other pyrrolidine alkaloids, gerrardamine, gerrardine, and gerrardoline are known in *Cassipourea gerrardii* of Rhizophoraceae but not in other taxa (Gibbs, 1974). Pyrrolidine alkaloids are otherwise rather scattered in angiosperm families.

Tropane alkaloids, surveyed by Romeike (1978) are known in the following groups:

Rhizophorales: Rhizophoraceae (*Bruguiera*) (Loder & Russel, 1966)
Malvales: Elaeocarpaceae (*Peripentadenia*) (Johns et al., 1971)
Geraniales: Erythroxylaceae (*Erythroxylon*)
Euphorbiales: Euphorbiaceae (*Phyllanthus*)
Other groups: Solanaceae (numerous genera), Convolvulaceae, Brassicaceae, Proteaceae, Dioscoreaceae, and Orchidaceae

Bruguiera contains a few tropane alkaloids. Some, like brugine, are unique to *Bruguiera*; others are shared between *Bruguiera* and either of *Dyboisia* (Solanaceae) or *Erythroxylon* (Erythroxylaceae). *Peripentadenia* (Elaeocarpaceae) contains tropacocaine, as does *Erythroxylon*.

Pyrrolizidine alkaloids, surveyed by Culvenor (1978), are represented by cassipourine, a 1-aminopyrrolizidine derivative, in *Cassipourea* of Rhizophoraceae. Pyrrolizidine alkaloids are scattered in angiosperms and are known in the following groups (Culvenor, 1978; Seigler, 1977):

Rhizophorales: Rhizophoraceae (*Cassipourea*; Bull et al., 1968)
Malvales: Elaeocarpaceae (*Aristotelia*) (Bick et al., 1971)
Celastrales: Celastraceae (*Bhesa*)
Euphorbiales: Euphorbiaceae (*Phyllanthus*, *Securinega*)
Ebenales: Sapotaceae (*Mimusops*, *Planchonella*)
Santalales: Santalaceae (*Thesium*)
Other groups: Apocynaceae, Scrophulariaceae, Asteraceae (many genera), Ranunculaceae, Fabaceae, Boraginaceae (many genera), Poaceae, and Orchidaceae

It is difficult to judge the significance of these three alkaloids. According to Hegnauer (1973), they are all derived from the amino acid ornithine. A shared inherent ability to synthesize such alkaloids in taxa of Rhizophoraceae, Elaeocarpaceae, Celastraceae, and Erythroxylaceae (perhaps also some Euphorbiaceae: Phyllanthoideae) based on a common ancestry should be considered.

COMBINED OCCURRENCE OF EMBRYOLOGICAL AND SEED CHARACTERS

The following combination of character conditions is found in Rhizophoraceae. Its occurrence in other families will be considered particularly significant here in the evaluation of the closest relationships of the family.

1. Ovules anatropous (to hemianatropous).
2. Ovules bitegminal, with a micropyle tending to be zigzag.
3. Inner integument three- to several-layered.
4. Ovules modestly to weakly crassinucellate.
5. Parietal cell cut off from primary archesporial cell, dividing a few times.
6. Nucellus lateral to embryo sac disintegrating at an early stage.
7. Inner integument forming an integumentary tapetum of ± palisadelike cells (an endothelium).
8. Endosperm formation nuclear.
9. Endosperm retained and ± copious in the ripe seed.
10. Embryo of the ripe seed chlorophyllous.
11. Seed coat exotegminal, exotegmen fibrous.
12. Aril tending to be present, exostomal.

The first eleven states are found in the following groups:

Rhizophorales: Rhizophoraceae *pro parte*
Malvales: Elaeocarpaceae
Celastrales: Celastraceae
Geraniales: Erythroxylaceae, Humiriaceae, Linaceae, and Oxalidaceae

Exostomal arils, additionally, are found at least in Celastraceae. Apart from these families, certain other not yet sufficiently investigated minor families, e.g., Lepidobotryaceae of Geraniales, are likely to agree with these groups mentioned. Also, members of Theales (e.g., Clusiaceae), Euphorbiales (members of Phyllanthoideae, Dichapetalaceae), Thymelaeales (Gonystylaceae), and others agree in some of these characters and cannot be wholly excluded from consideration as potentially close relatives of Rhizophoraceae.

As regards alkaloids, it is also obvious that families like Elaeocarpaceae, Erythroxylaceae, and Celastraceae show similarity to Rhizophoraceae, supporting (rather than being neutral or contradictory to) the embryological evidence.

CONCLUSIONS

Having used a limited number of characters to select families that qualify as more or less closely related to Rhizophoraceae, each of the following families and orders will be briefly compared with this family with respect to all-around similarity.

1. Elaeocarpaceae, which are presumably incorrectly placed in Malvales.
2. Celastraceae (including Hippocrateaceae), which are generally placed in their own order Celastrales, often along with various minor and insufficiently known families.
3. Erythroxylaceae of Geraniales; their position in this order has never been questioned in recent years and they also agree well with other Geraniales (or Linales) such as Hugoniaceae, Linaceae, and Oxalidaceae.
4. Lepidobotryaceae and Ctenolophonaceae, two unigeneric families of Geraniales, which are unknown in practically all of the respects considered above but which in general morphology approach Rhizophoraceae tribe Macarisieae.
5. Other taxa of Geraniales.
6. Certain other groups of Theales, Ebenales, Sapindales, and Rutales.
7. The order Myrtales.

FAMILIES PUTATIVELY RELATED TO RHIZOPHORACEAE

1. Elaeocarpaceae. This family, with about 10 genera and 400 species, is usually placed at the "bottom" of the Malvales near Tiliaceae. In various systems, e.g., that of Hutchinson (1959), and some textbooks (Davis, 1966; Hegnauer, 1973), Elaeocarpaceae are even included in Tiliaceae. The absence of mucilage cells and cavities, stellate hairs, nectar hairs at the calyx base, and of fatty acids with a cyclopropenyl ring, in combination with the presence of imbricate sepals, a nectariferous disc at the base of the stamens, endothelium, and other features are all foreign to other Malvales and justify their exclusion from that order.

Elaeocarpaceae and Rhizophoraceae are woody, and in wood anatomy Elaeocarpaceae are more advanced than most Rhizophoraceae, having, as a rule, vessel members with simple perforations. Wood rays are heterogeneous, mixed uniseriate and pluriseriate, as in Rhizophoraceae. The parenchyma is usually paratracheal and very sparse (different from most primitive Rhizophoraceae); mucilage canals and cavities are present.

The nodes are trilacunar, as in Rhizophoraceae. The leaves are often alternate in Elaeocarpaceae. As in Rhizophoraceae, stipules are present; they may be persistent or caducous. The leaf venation is at least partly brochidodromous, as in some Rhizophoraceae, but sometimes eucamptodromous, although Hickey & Wolfe (1975) attributed Malvales in general with actinodromous venation. Furthermore, the leaf teeth in Elaeocarpaceae according to Hickey & Wolfe (1975) are mainly of the violoid type, this resembling the theoid type, which these authors reported for Celastraceae. The teeth in Elaeocarpaceae are obviously more or less different, however, from the peculiar macarisioid teeth in Rhizophoraceae (Keating & Randrianasolo, this volume). Stomata in Elaeocarpaceae are paracytic to cyclocytic and are restricted to the lower leaf surface, as in Rhizophoraceae. Crystals are present in the parenchyma and are generally solitary and prismatic, as are the crystals in Rhizophoraceae tribe Macarisieae. The hairs, when present, are simple and unicellular, as in Rhizophoraceae.

Likewise matching this family, the inflorescences are mostly axillary cymes or panicles, and the flowers are hypogynous and probably primitively pentamerous. The sepals are valvate to imbricate, and the petals are distinct (rarely basally connate) and frequently distally lobate or fimbriate, as in most nonmangrove Rhizophoraceae. A more or less conspicuous disc is present (Balgooy, 1982), as in nearly all Rhizophoraceae. The stamens are 1–3 times the petal number or usually more (van Heel, 1966), the diplostemonous condition being probably plesiomorphic. Haplostemony, as in Celastraceae, is found within *Sloanea*. Both in the basic state and in the increase of stamens, Elaeocarpaceae agree with Rhizophoraceae. The stamens have narrow filaments, as in Rhizophoraceae tribe Macarisieae, but the anthers are advanced, having at least in some genera a nonfibrous endothecium and, as a rule, apical dehiscence by short slits or pores.

The two families largely agree in pollen morphology, the pollen grains being mostly tricolporate, with rather thick exine and a rugulate-punctate surface. They are dispersed in the two-celled state in both families.

Carpel number is variable, as in Rhizophoraceae; the carpels are fused in the stylar region, the style being simple or apically lobate. The ovary is two- to several-loculed with axile placentation, in which the Elaeocarpaceae agree with Rhizophoraceae. As pointed out above under Rhizophoraceous Character Conditions, embryology in Elaeocarpaceae is essentially similar to that in Rhizophoraceae, although the arils when present in the former (according to Corner, 1976) are not exostomal but developed from the chalaza and raphe.

The fruit in Elaeocarpaceae is a capsule or drupe. The seeds have copious endosperm, with fat oils and protein and a chlorophyllous embryo, all the conditions in Rhizophoraceae. Arillate seeds occur in some species, and the aril in *Peripentadenia* is reportedly "a total covering of thick flesh outgrown from the distal cap" (Hyland & Coode, 1982).

Elaeocarpaceae agree with Rhizophoraceae in alkaloid chemistry (see above) and both are tannin plants. Ellagic acid is (rarely) present in both families. Both produce proanthocyanins as well as caffeic acid, and in both the flavonoids include myricetin, quercetin/kaempferol, and pelargonidin (Gornall et al., 1979). In fact, Elaeocarpaceae agree much better with regard to their secondary metabolites with Rhizophoraceae than with Tiliaceae, with which they are generally associated.

Briefly, the Elaeocarpaceae differ from the Rhizophoraceae mainly in some wood-anatomical details, in having usually alternate leaves and different anther morphology, and in basic chromosome number. Furthermore, the sieve-tube plastids accumulate starch, not protein. The floral receptacle is rarely as well developed as in Rhizophoraceae. Arils, when present, may be of different origin.

This supports the following conclusions: 1. Elaeocarpaceae make up a distinct family. 2. They are misplaced in Malvales. 3. They are closely related to Rhizophoraceae.

2. Celastraceae. Celastraceae comprise a fairly large family of roughly 50 genera and 800 species (Cronquist, 1981). The family is variable and somewhat difficult to define. All members are woody plants. Secretory canals ("laticifers") are often present in phloem of stem and leaves; this is also a feature met with in Rhizophoraceae (see, for example, Keating, 1984). Contrary to Rhizophoraceae, the Celastraceae are said to have unilacunar nodes. Vessel perforation is simple or rarely scalariform; variation is great in wood rays and wood parenchyma. Oxalate crystals of simple, prismatic type and as crystal druses (also crystal sand) occur in Celastraceae as well as in Rhizophoraceae. The leaves are opposite or alternate and simple and generally have small and/or caducous stipules or none at all (the stipules are generally larger in Rhizophoraceae). The venation is pinnate-brochidodromous with apically elongated arches; lateral teeth, where present, are of the theoid type (Hickey & Wolfe, 1975), agreeing probably more with Elaeocarpaceae than with Rhizophoraceae.

Hairs are infrequent and short and unicellular when present (Metcalfe & Chalk, 1950), as in Rhizophoraceae; in both families the stomata are generally confined to the lower surface of the leaves. In the Celastraceae they are anisocytic or anomocytic, only rarely paracytic, and thus mostly different from those in Rhizophoraceae.

The inflorescences in the Celastraceae and Rhizophoraceae are frequently axillary cymes or panicles (or solitary). The flowers are generally small and greenish, regular, 4–5-merous, and hypogynous, perigynous, or half-epigynous. In these respects the Celastraceae largely agree with Rhizophoraceae. However, the sepals are less developed and valvate to imbricate, the petals are often roundish, and the disc in most cases is more conspicuous and often square or 5-angular. The petals in Celastraceae to my knowledge are never fimbriate or laciniate apically, as is usual with Rhizophoraceae. Further, the androecium is restricted to a single alternipetalous whorl, although clearly derived from a diplostemonous condition (alternisepalous staminodes occur in *Lophopyxis*).

The pollen grains are mostly tricolporate, with sexine thicker than nexine, simplibaculate (Erdtman, 1952), and basically agree with the pollen in Rhizophoraceae. They are two- or three-celled when dispersed (Brewbaker, 1967).

The pistil consists of 2–5 carpels and has a single terminal style with capitate or lobate stigma. Each of the 2–5 locules contains as a rule two axile ovules. In these respects, as in nearly every detail of the embryology, the Celastraceae agree with the Rhizophoraceae tribe Macarisieae, including presence of endothelium, exostomal aril, and exotegminal, fibrous seed coat. The seeds have a chlorophyllous embryo.

The Celastraceae show a much wider chemical spectrum than Rhizophoraceae and Elaeocarpaceae but agree in being essentially tannin plants. They produce proanthocyanins and caffeic acid; ellagic acid has been reported in some individual species. Furthermore, the flavonoid spectrum agrees (Hegnauer, 1964) with the mentioned two families in presence of quercetin, kaempferol, myricetin, and other flavonoids. A pyrrolizidine alkaloid has been reported (see above), the significance of which is, however, uncertain. On the other hand, Celastraceae generally produce saponins (Bosser & Pernet, 1957) and often alkaloid amines, e.g., cathine (Cronquist, 1981), which are unknown in Rhizophoraceae and Elaeocarpaceae.

Besides other basic chromosome numbers, $x = 8$ is known in Celastraceae, as in some Rhizophoraceae.

Celastraceae obviously agree well with the Rhizophoraceae in essential characters but can be considered more derived in the haplostemonous flowers with little-developed calyx and generally massive disc. Further, they have the ability to produce saponins and certain amines and differ with regard to sieve-tube plastid inclusions. They form a more heterogeneous assemblage, with some genera having spread to temperate climates.

3. Erythroxylaceae. Erythroxylaceae consist of only the genera *Erythroxylon*, *Nectaropetalum*, *Pinacopodium*, and *Aneulophus*, the last often placed in Linaceae. *Erythroxylon* consists of ca. 200 species; the other genera are small. Erythroxylaceae are placed in Geraniales (or Linales) near Linaceae and Humiriaceae in all current classifications, and a number of shared features support this. Nevertheless, Erythroxylaceae (as well as some other families of Geraniales) agree with the Rhizophoraceae in several conspicuous features, warranting a close comparison between the two families.

Like the Rhizophoraceae, all Erythroxylaceae are woody but generally shrubby. The vessels have simple perforations in the end walls, a conspicuous difference from most Rhizophoraceae, but the wood rays are mostly heterocellular, mixed uni- and pluriseriate, as in that family. Essential oils are sometimes found in the wood.

A highly conspicuous similarity between Rhizophoraceae and Erythroxylaceae is the similar kind of protein bodies of the sieve-tube plastids (see above).

The leaves are alternate or rarely (*Aneulophus*) opposite and have brochidodromous venation of the secondary veins (Hickey & Wolfe, 1975), agreeing in this rather well with various Rhizophoraceae. Their teeth are mostly of the theoid type. Stipules are present, as in Rhizophoraceae; they are intrapetiolar and often tricuspidate. The stomata are paracytic and generally restricted to the lower surface of the leaves. Sclereids are sometimes present, while this in Rhizophoraceae is mainly the case with mangrove genera (tribe Rhizophoreae). Hairs are simple and unicellular when present. Solitary crystals of oxalate are found in some tissues.

The inflorescences are axillary panicles or cymes or consist of solitary flowers, as in Rhizophoraceae. A peculiarity of the Erythroxylaceae is that the axis of these inflorescences often bears a great number of bracteate leaves (raments, cataphylls). The flowers are small, actinomorphic, pentamerous in perianth and androecium, and hypogynous. The sepals are valvate or imbricate and basally connate. The petals are entire (not fimbriate or laciniate), free from each other, and usually adaxially appendaged. Unlike most Rhizophoraceae, Elaeocarpaceae, and Celastraceae, disc structures are lacking. The androecium is diplostemonous; the ten stamens are situated in a single whorl and the bases of their filaments are usually connate into a short tube. The anthers are tetrasporangiate, longitudinally dehiscent, and extrorse.

The pollen grains, as in most Rhizophoraceae, are tricolporate, with rather thick exine and often with a reticulate surface. They are, however, three-celled, whereas those in Rhizophoraceae are two-celled.

The pistil is 2–4-carpellary, with (2–)3(–4) locules and usually with 3 separate stylodia, each with a more or less expanded, often capitate stigma; sometimes, as in *Nectaropetalum*, there is a single, apically bilobate style (Verdcourt, 1981). Each locule contains one (or two) axillary and pendulous ovule(s); only one ovule usually develops in each fruit. The embryological characters are essentially as in Rhizophoraceae (see above). The fruit is generally a drupe, the single seed of which usually has copious endosperm (with starch) but may lack endosperm. Arils are lacking, except in *Aneulophus*, but the nature of the aril in this genus is uncertain, possibly exostomal (see Wilczek, 1958).

The chemical conditions are somewhat similar to those in Rhizophoraceae as regards alkaloids (tropane alkaloids—cocaine, for instance—are present and sometimes copious) and tannins; however, saponins, cyanogenic compounds, and ethereal oils are sometimes present, which is obviously not the case in Rhizophoraceae.

The basic chromosome number, $x = 12$, deviates from Rhizophoraceae.

Accordingly, Erythroxylaceae and Rhizophoraceae exhibit important differences and important similarities. The flowers in Erythroxylaceae lack a floral disc, in contrast with most Rhizophoraceae (but it is absent from *Pellacalyx* of this family). In Erythroxylaceae the floral receptacle is much less developed and never cupular, cataphyllous leaves are common (but probably evolved within Erythroxylaceae), and the pollen grains are three-celled.

Erythroxylaceae agree well with other Geraniales in most respects; in fact there are difficulties in delimiting them from, for example, Linaceae (*Aneulophus* and *Nectaropetalum* having been referred to both families). This is no argument against considering Rhizophoraceae (as well as Elaeocarpaceae and Celastraceae) as closely related to Erythroxylaceae and other families of Geraniales.

The following conclusions are drawn from the evidence presented here:

1. There are no arguments to exclude Erythroxylaceae from Geraniales (or from Linales, if this order is separated from Geraniales, as by Cronquist, 1981).
2. The Erythroxylaceae show numerous and essential similarities to Rhizophoraceae, which together support that they are relatively closely related.
3. This similarity is, however, not as far-reaching as that between Rhizophoraceae and Elaeocarpaceae, and there is not sufficient evidence that Rhizophoraceae and Erythroxylaceae can be "sister groups" in the phylogenetic sense.
4. Therefore, it is most likely that the very particular kind of sieve-tube plastids that the two families have in common has evolved by convergent evolution in the ancestors of each of the two families. (An alternative is that a certain disposition for them evolved in a common ancestor, although this is concealed or blocked in other related families.)

4. Lepidobotryaceae, Ctenolophonaceae. Lepidobotryaceae are often included in either Oxalidaceae or Linaceae. They may be circumscribed so as to include either only *Lepidobotrys* Engl. or also *Sarcotheca* Blume and *Dapania* Korth. *Lepidobotrys* occurs in Africa, *Sarcotheca* in Malaysia, and *Dapania* in Malaysia and Madagascar.

The present comments will be restricted to *Lepidobotrys* (see Leonard, 1950, 1958) without evaluating the circumscription of the family.

Lepidobotrys is a tree with alternate leaves, which have small stipules and one large leaf lamina; somewhat below this the petiole has a "joint" at which is situated a much smaller sheathing leaflet, often called a "stipel." The anatomical features remain insufficiently known, but according to Metcalfe & Chalk (1950), the vessels have scalariform perforation plates, and the intervascular pitting is minute and alternate.

Wood parenchyma is abundant and consists of scattered cells containing oxalate crystals. The rays are almost exclusively uniseriate and almost homogeneous (Metcalfe & Chalk, 1950). The inflorescences are small, axillary and racemelike; their axis bears densely set scales, in the axils of which the flowers are situated. Young inflorescences therefore are conelike. The flowers are fairly long-pedicelled, actinomorphic, mainly pentamerous, diplostemonous, functionally unisexual, and tricarpellary. The petals are imbricate, and the mutually free filaments of the 10 stamens are inserted on a lobate, well-developed disc. The pollen grains are tricolporate with reticulate exine (see Oltmann, 1971). The pistil is trilocular and has three free, apically bilobate stylodia. The functionally male and female flowers differ in having either well-developed stamens and rudimentary (but distinctive) pistil or smaller, nonfunctional stamens and a well-developed pistil. Each locule possesses two apical-axile ovules. The embryology is unknown. The fruit is a one-seeded capsule with a funicular aril.

This genus has a floral structure similar to that in certain species of Rhizophoraceae tribe Macarisieae, although in stylar conditions it more resembles Anisophylleaceae. It is an example of some rather isolated genera in Geraniales that have been variously treated as separate families or included in Oxalidaceae or Linaceae.

Another isolated genus, *Ctenolophon*, is sometimes treated as the separate family Ctenolophonaceae and is sometimes included in Linaceae. This genus has opposite, stipulate leaves, as in Rhizophoraceae, and a panicle of pentamerous, diplostemonous flowers with a prominent disc and a bilocular pistil with a single style, all known in Rhizophoraceae. The pollen grains are extraordinarily different, however (see, for example, Erdtman, 1952; Oltmann, 1971). The fruit is a nutlet with a single arillate seed. The nature of the aril is not quite clear. *Lepidobotrys* and *Ctenolophon* are mentioned here as a complement to Erythroxylaceae, as they are currently considered good members of Geraniales (or Linales) yet resemble the Rhizophoraceae in some respects in which the Erythroxylaceae differ from the Rhizophoraceae; *Lepidobotrys* in the more enlarged floral axis with a prominent, somewhat lobate disc and in the free filaments, a floral structure clearly similar to that in, for example, *Gynotroches*; *Ctenolophon* in the opposite leaves, distinct floral disc, separate filaments, and single (although apically bibrachiate) style.

5. *Other Geraniales.* Whereas it seems as if the Rhizophoraceae show closest similarity to Erythroxylaceae and certain variously placed genera such as *Lepidobotrys* and *Ctenolophon*, which deserve further embryological, anatomical, and chemical studies, there is also, as noted above, great embryological similarity with Linaceae, Oxalidaceae, and Balanitaceae. Woody members of the first of these families and of Balanitaceae, Humiriaceae, Hugoniaceae, and Zygophyllaceae need be considered as potentially closely related to Rhizophoraceae.

6. *Members of Theales, Ebenales, Sapindales, and Rutales.* It has been stated above that several character states of the above-mentioned combination of embryological attributes occur in other groups, mainly of these four orders.

The Theales are variously circumscribed, with Lecythidaceae included or not. Within this complex in the wide sense, endothelium is reported for Lecythidaceae and may well occur in other families; an exostomal aril is found in at least some species of *Clusia*, of Clusiaceae; within this family the embryo may also be chlorophyllous. Sapotaceae in the probably highly heterogeneous order Ebenales show quite a number of similarities to Rhizophoraceae (and various Theales). Presumably primitive Theales and, separately, primitive Malvales evolved from ancestors with rather simple tetra- or pentamerous, diplostemonous flowers; in each of the Theales and Malvales lines an increase in stamen number seems to have occurred. Such an increase of stamen number can also be observed *within* each of Rhizophoraceae and Elaeocarpaceae. It is probable that other evolutionary lines evolved from groups with such simple, diplostemonous flowers, e.g., Geraniales, Sapindales, and Rutales, each line retaining some of the plesiomorphies while developing its own specializations (autapomorphies).

7. *The Myrtales.* Myrtales also most likely evolved from an ancestor with penta- or tetramerous, actinomorphic, hypogynous, diplostemonous flowers with a disc (see Dahlgren & Thorne, 1984). The Myrtales are less specialized in embryological characters than the Rhizophoraceae, having a more persistently multicellular nucellus and no endothelium (Tobe & Raven, 1983) and having nonchlorophyllous embryo and exendospermous seeds. The

nodes in Rhizophoraceae are trilacunar, which is extremely rare in Myrtales (found only in *Alzatea*). Vessels in Rhizophoraceae are more primitive than those in Myrtales in having scalariform perforation plates. The alkaloid chemistry in Rhizophoraceae has no correspondence in Myrtales. Finally, Rhizophoraceae lack internal phloem and vestured pits. This evidence all supports the view held at the Myrtales symposium (see, for example, Dahlgren & Thorne, 1984) that Rhizophoraceae are not closely related with Myrtales.

For Anisophylleaceae, earlier included in Rhizophoraceae, most of these objections against a close relationship to Myrtales are lacking (although some others may be added, as lack of stipules).

MONOPHYLY AND CHARACTERIZATION OF ANISOPHYLLEACEAE

Anisophylleaceae consists of the genera *Anisophyllea* R. Br., *Combretocarpus* Hook. fil., *Poga* Pierre, and *Polygonanthus* Ducke.

Anisophylleaceae are trees and shrubs, sometimes of considerable size. Characteristic wood anatomical features according to van Vliet (1976) are the simple perforations in the vessels, fibers with distinctly bordered pits, very broad (up to 30 cells wide) multiseriate rays, and the half-bordered, alternate vessel–parenchyma pits. These character states do not distinguish the family absolutely and sharply from Rhizophoraceae; rather the variable Rhizophoraceae with the genera of the tribe Gynotrocheae, in particular *Carallia*, join up with the Anisophylleaceae. As regards vessel diameter, van Vliet (1976) showed that the Anisophylleaceae normally have higher values than Rhizophoraceae (Anisophylleaceae: tangential diameter mostly 160–340 μm, radial diameter to 370–420 μm; Rhizophoraceae: tangential diameter mostly 40–200 μm, tangential diameter mostly to 85–340 μm). As other character conditions argue against a close relationship between Rhizophoraceae and Anisophylleaceae, it is not adequate to discuss the wood anatomical "limits" between the families—*Carallia* and other Gynotrocheae are not really intermediate between other Rhizophoraceae and Anisophylleaceae; they are only extreme in the former family. Lysigenous secretory cavities are present in *Poga* (Metcalfe & Chalk, 1950).

The leaves in Anisophylleaceae are alternate, simple, entire, and exstipulate. According to Keating & Randrianasolo (this volume), the secondary venation in most Anisophylleaceae is transitional between brochidodromous and (basally on the lamina) eucamptodromous, but it is acrodromous in *Anisophyllea*. No teeth are present. There is marked anisophylly and often strong asymmetry in the leaves of *Anisophyllea*, which are generally two-ranked and strongly horizontally oriented on plagiotropic shoots.

The inflorescences are axillary and generally elongate and catkin- or spikelike.

The flowers are small, usually 4(–5)-merous, but 3-merous in *Combretocarpus* and rarely in *Anisophyllea*; they are actinomorphic, epigynous, diplostemonous, and often unisexual by partial reduction of stamens or pistil (Tobe & Raven, in press). The floral receptacle, which encloses and is fused with the ovary wall, continues as a variably long hypanthium, resembling the condition in many Myrtales.

The petals (see Tobe & Raven, in press) are usually deeply incised, generally with 3, 5, or 7 lobes, which may have an enlarged, glandular tip. These enlarged tips are present in taxa of *Anisophyllea* (*A. laurina*) and *Poga*, and they support these genera as closely related (although they belong to different main branches in the cladogram of Tobe & Raven, this volume). Only *Polygonanthus* has entire petals, although the margin is sometimes finely fimbriate.

Incised to fimbriate petals may represent an autapomorphy of Anisophylleaceae but also occur in most nonmangrove Rhizophoraceae, in most Elaeocarpaceae, in certain genera of each of Diapensiaceae, Primulaceae, Malpighiaceae, and others. The value of this character in connecting Rhizophoraceae and Anisophylleaceae is dubious in the light of the numerous differences. A striking condition, stressed especially by Tobe (pers. comm.), is that the above-mentioned swollen, glandular tips of the petal lobes in Anisophylleaceae are matched in at least *Ceriops* of Rhizophoraceae. However conspicuous this similarity may be, I consider this the result of convergent evolution; Juncosa & Tomlinson (1987) showed that in *Ceriops* these structures are hydathodes.

A lobate intra- and interstaminal, discontinuous disc surrounds the style base. Nectar is produced at the filamental bases. The (6–)8(–10) stamens are incurved in bud and have mutually free, narrow filaments and dorsifixed, ovoid, introrse-latrorse anthers (all from Tobe & Raven, in press.)

The pistil ends in (3–)4(–5) separate stylodia. The carpels each form a locule with 1–2 ovules in axile position.

The Anisophylleaceae (Tobe & Raven, in press) show a combination of frequent character conditions, from which there are various exceptions representing further evolutionary developments that contribute to elucidating the probable evolution within this small family (see cladogram in Tobe & Raven, in press). The endothelium is fibrous, the anther wall formation of the basic type, and the tapetum glandular with 2-nucleate or—by nuclear fusion—1-nucleate tapetal cells.

The pollen grains are tricolporate and, according to Vezey et al. (this volume), have a rather thin tectum with reticulate-punctate surface. Tobe & Raven (1987b) showed that the pollen grains are two-celled when dispersed.

The ovules are bitegmic or (*Anisophyllea* and *Combretocarpus*) unitegmic, with the inner integument in bitegmic ovules only two cells thick, a difference from the Rhizophoraceae; in bitegmic ovules the micropyle is formed by both integuments. The ovules are clearly crassinucellate; the primary archesporial cell cuts off a parietal cell that gives rise to a parietal tissue. The nucellar tissue persists longer than in Rhizophoraceae. No endothelium is formed. Embryo sac formation is of the *Polygonum* type or, in *Combretocarpus*, of the *Allium* type, the latter obviously an autapomorphy for that genus. Endosperm formation is nuclear. The endosperm is used up in the course of seed maturation. The embryo has a long hypocotyl and small to rudimentary cotyledons or no cotyledons at all. The latter conditions are possibly potentially valuable in the search for the relationships of Anisophylleaceae. (Information all according to Tobe & Raven, 1987b.)

Contrary to the Rhizophoraceae and Elaeocarpaceae, the seed coat of the mature seed is not exotegminal-fibrous but consists of the testal epidermis only (exotesta), as in *Poga*, of a multilayered testa (*Polygonanthus*), or of the multilayered or ultimately thin single integument (*Anisophyllea* and *Combretocarpus*, respectively) (Tobe & Raven, this volume). This variation makes difficult comparisons and conclusions on relationships based on seed coat structure.

Chemical information is somewhat incomplete. Aluminium accumulation is highly characteristic (Chenery, 1948), a major difference from Rhizophoraceae but a similarity to various Myrtales. The Anisophylleaceae are clearly tanniniferous plants. Ellagic acid is known in *Anisophyllea* (Lowry, 1968). Alkaloids are unknown.

The above evidence will form the basis for an attempt to evaluate approximate relationships of the Anisophylleaceae, which show no autapomorphy with strong significance comparable to that of the kind of sieve-element plastids in Rhizophoraceae. The homogeneity of Anisophylleaceae therefore rests on the combination of numerous, rather frequently occurring, and trivial character conditions. These include the similar states of wood characters (see above), accumulation of aluminium, the floral structures (epigyny, tri- or tetramery, presence of hypanthium, generally incised petals, presence of a disc, diplostemony, and separate stylodia), and the combination of general embryological characters (see above). Thus, multiple similarities rather than singularity binds together the four genera and support them as a monophyletic unit.

RELATIONSHIPS OF ANISOPHYLLEACEAE

Technically the Anisophylleaceae can be defined as follows: woody; vessel perforation simple; leaves alternate, exstipulate, simple, entire; flowers mostly tetramerous, actinomorphic, isomerous in all whorls but diplostemonous, with sepals and petals; filaments free from each other and from the corolla; anthers dehiscing with longitudinal slits; disc present; stylodia free; ovules 1–2 per locule, axile, anatropous, crassinucellate, with nuclear endosperm formation; fruit fleshy, indehiscent; seeds exendospermous, with straight embryo.

Such a combination of features is restricted to Anisophylleaceae but may coincide with that in Rosaceae as broadly defined to include Malaceae; however, it is not present in one and the same member of any Rosaceae.

Neglecting tetramery (in all whorls) does not increase the choice, but neglecting also absence of endosperm in the seed, a presumably advanced and recently derived character condition, also adds Flacourtiaceae and Anacardiaceae. Neglecting also the fruit type, the lack of stipules, and the free stylodia would bring some Myrtales in agreement with Anisophylleaceae as well, but then the anatomical peculiarities of Myrtales (intraxylary phloem and vestured pitting) are not considered either.

Thus, in gross morphology Anisophylleaceae are largely Saxifragalean–Rosalean in nature, and I agree with Cronquist (1981), who placed Anisophylleaceae in Rosales in the broad sense. Also chemical characters agree, largely with those in, for example, Rosaceae in the narrow sense. However, within the Rosales no obvious group agrees particularly well with the Anisophylleaceae, and the alternative families Flacourtiaceae and Anacardiaceae must be considered.

FLACOURTIACEAE

Flacourtiaceae comprise a very variable group of often cyanogenic plants with mostly stipulate leaves. Their flowers are nearly always hypogy-

TABLE 2. *Differences between Rhizophoraceae and Anisophylleaceae.*

Character	Rhizophoraceae	Anisophylleaceae
Leaves	opposite	alternate
Stipules	present, interpetiolate	lacking
Vessel perforation	usually scalariform	simple
Vessel diameter	narrow	wider
Sieve element plastids	with particular protein bodies	with starch only
Aluminium accumulation	none	present
Colleters	reported in several genera	none
Inflorescence	pauciflorous, cymules, solitary flower	multiflorous; panicle or panicle-derived
Merism	4-, 5- or > 5-merous	3- or 4-merous
Ovary, style	superior to inferior, a single style	inferior, separate stylodia
Tectum of pollen wall	relatively thick	relatively thin
Subepidermal floral laticifers	present, different types	none
Nucellar tissue	consumed early	persisting longer
Endothelium	present	none
Seeds	endospermous	exendospermous

nous, and the stamens are generally numerous. Furthermore, the ovary generally has parietal placentae. No single genus of Flacourtiaceae to my knowledge has the combination of character condition of the Anisophylleaceae, and it is solely due to the variability (or heterogeneity) of the Flacourtiaceae that it agrees, in most respects, with the Anisophylleaceae.

ANACARDIACEAE

Anacardiaceae are members of Sapindales. They are rich in tannins and have well-developed schizogenous or lysigenous ducts or channels with resins, which is not the case with the Anisophylleaceae. The leaves are variable in Anacardiaceae but are more frequently compound than simple, as in Anisophylleaceae. The small flowers are reminiscent of those in Anisophylleaceae but are more often pentamerous; they vary from hypo- or perigynous to epigynous and are often diplostemonous, with free stamens and a well-developed disc. The carpels are often solitary (sometimes several and free from each other) but when fused are generally three. The fruit is usually drupaceous. Anacardiaceae, apart from the resin canals, compound leaves, and numerical conditions of the flower (especially gynoecium), agree fairly well with Anisophylleaceae.

CONCLUSION

Anisophylleaceae are difficult to place, as most of their characteristics are of very common occurrence. Rosales(–Saxifragales–Cunoniales) seem to be the group in which they would be fairly well placed, but without obvious links. These orders have a clearly temperate(–boreal) concentration, which somewhat contrasts with the tropical concentration of Anisophylleaceae. The floral morphological (Tobe & Raven, 1987c) and embryological conditions in Anisophylleaceae agree completely with those common in Rosaceae sensu stricto, for example: exendospermous seeds and a bitegmic, crassinucellate ovule with nuclear endosperm formation. That in both families the ovules are bitegmic in some and unitegmic in other genera is a coincidence. The basic chromosome numbers, $x = 7$ or $x = 8$, are also present in Rosaceae sensu stricto, especially the former number (Raven, 1975).

It is probable that Anisophylleaceae comprise a rather isolated family evolved from ancestors shared between those in Rosales, Cunoniales, and Saxifragales. It is also probable that these were not very remote from the ancestors of Myrtales, although the last order is distinctive in several respects, including the anatomical features mentioned above.

PROPOSED CLASSIFICATION

Ordinal composition around Rhizophoraceae:

GERANIALES: Zygophyllaceae, Nitrariaceae, Peganaceae (position uncertain), Balanitaceae, Vivianiaceae, Geraniaceae, Ledocarpaceae, Biebersteiniaceae, Dirachmaceae, Ixonanthaceae, Humiriaceae, Hugoniaceae, Ctenolophonaceae, Erythroxylaceae, Linaceae, Lepidobotryaceae, Oxalidaceae

CELASTRALES: Celastraceae, Elaeocarpaceae, **Rhizophoraceae**

Ordinal composition around Anisophylleaceae:

CUNONIALES: Cunoniaceae, Baueraceae, Brunelliaceae, Davidsoniaceae, Eucryphiaceae

ROSALES: Crossosomataceae, Rosaceae, Neuradaceae, **Anisophylleaceae**, Malaceae, Amygdalaceae (plus perhaps some smaller families such as Rhabdodendraceae)

SAXIFRAGALES: Saxifragaceae, Penthoraceae, Vahliaceae, Francoaceae, Greyiaceae, Brexiaceae, Grossulariaceae, Iteaceae, Cephalotaceae, Crassulaceae, Podostemaceae.

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A HISTORICAL AND TAXONOMIC SYNOPSIS OF RHIZOPHORACEAE AND ANISOPHYLLEACEAE[1]

Adrian M. Juncosa and P. Barry Tomlinson[2]

ABSTRACT

Even from its time of formal recognition by Robert Brown in 1814, the Rhizophoraceae has been known as a family with both terrestrial and mangal representatives so that the tendency to regard it as the "mangrove family" is inappropriate, even though one of its major subdivisions, the tribe Rhizophoreae, is made up exclusively of mangroves. This association of terrestrial and mangrove species adds a piquancy to the study of the systematics of the group because it allows the diagnostic usefulness of "adaptive" characters to be assessed. The progressive enlargement of our knowledge of the family is reviewed, including the status of Anisophyllea *and related genera, now regarded as constituting a separate family Anisophylleaceae. Brief tribal and generic diagnoses are provided, with generalized illustration of geographical distribution. Some portraiture of the more common genera is attempted.*

This symposium had as an objective the segregation of the small family Anisophylleaceae from the Rhizophoraceae (sensu lato), with a discussion of the evidence upon which this distinction was based (cf. Dahlgren, this volume). A further objective has been a discussion of where the two families might be placed in a natural system. Although the mangrove Rhizophoraceae are familiar to botanists and laymen alike, the systematic characteristics and even the existence of the inland genera are not well known. The Rhizophoraceae and Anisophylleaceae together include about 18 genera and some 140 species of tropical shrubs and trees (Table 1). The families exhibit a wide variety of character states and have had a checkered taxonomic history. It seems now generally agreed that the Anisophylleaceae are a distinct, probably unrelated family; for a detailed systematic comparison see our other contribution in this volume. Unless otherwise noted, "Rhizophoraceae" is therefore used sensu stricto, i.e., without the four genera now removed as Anisophylleaceae. In addition to describing this history, we present a synopsis of genera. No such complete synopsis appears elsewhere, so it should prove a useful reference for this symposium volume. A detailed comparison of the systematic and biological characteristics of the two families appears separately (Juncosa & Tomlinson, this volume).

TAXONOMIC HISTORY OF RHIZOPHORACEAE (SENSU LATO)

The family Rhizophoraceae, in a broad sense, originates with the genus *Rhizophora* of Linnaeus (1753), preceded by *Mangium* of Rumphius (1741–1755). Both of these authors used their generic names to designate a group of species growing in tropical tidal swamps, which modern ecologists would call "mangal" (Macnae, 1968). Of the seven species named by Linnaeus in *Rhizophora*, only one, *R. mangle* L., is still valid and forms the type species of the genus and hence of the family. *Mangium* has disappeared entirely, except in *Acacia mangium*, a terrestrial plant. A list of the Rumphian and Linnean names with their

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TABLE 1. *Summary of genera of the Rhizophoraceae (s. str.) and Anisophylleaceae (after Ridley, 1922; Alston, 1925; Ding Hou, 1958; Melchior, 1964; Floret, 1974; van Vliet, 1976; Willis, 1973; Steyermark & Liesner, 1983). Tribal classification of Rhizophoraceae follows that accepted in the literature; recent studies indicate that changes are necessary (Tobe & Raven, this volume).*

Family or Tribe	Genus	Number of Species	Distribution
ANISOPHYLLEACEAE			
(= Anisophylleae)	*Anisophyllea*	25	Africa to South America and Malesia
	Combretocarpus	1	Borneo
	Poga	1	Africa
	Polygonanthus	2	Brazil
RHIZOPHORACEAE			
Gynotrocheae[1]	*Carallia*	9	Madagascar to Australia
	Crossostylis	12	South Pacific
	Gynotroches	1[2]	Indochina, Malesia, Pacific Islands
	Pellacalyx	8	Malesia to S China
Macarisieae[1]	*Anopyxis*	2	Africa
	Blepharistemma	1	India
	Cassipourea (including *Lasiosepalum* and *Weihea*)	55	Sri Lanka to Central America
	Comiphyton	1	Equatorial Africa
	Dactylopetalum[3]	15	Africa, Madagascar
	Macarisia	7	Madagascar
	Sterigmapetalum	7	South America
Rhizophoreae	*Bruguiera*	6	Africa to Australia
	Ceriops	2	Africa to Australia
	Kandelia	1	Malaysia to Japan
	Rhizophora	8[4]	pantropical

[1] Tobe & Raven (this volume) segregate *Crossostylis* as its own tribe and create two subtribes each in Macariseae and their modified Gynotrocheae.

[2] Ding Hou (1958) described much variation in *Gynotroches* and only reluctantly accommodated it in a single species. Juncosa & Tobe (this volume) describe some characteristics of two of the several distinct taxa.

[3] Floret (1976) presented evidence for the elevation of *Dactylopetalum* to generic rank.

[4] Includes putative hybrids or varieties (Tomlinson, 1986).

modern equivalents forms Table 2. This demonstrates an intrinsically ecological concept for their initial circumscription.

The family was formally designated (as the "order" Rhizophoreae) by Robert Brown in his account of the botany of Terra Australis (Brown, 1814) and included the genera *Rhizophora* Linnaeus, *Bruguiera* Lamarck, and *Carallia* Roxburgh "all of which are found in the equinoctial part of New Holland." Consequently, even at its erection the family already included plants of terrestrial as well as mangal habitats. Robert Brown drew attention to the "affinity of Rhizophoreae to Cunoniaceae" and rejected Jussieu's attempt to combine some of its elements with loranthaceous genera (cf. Dumortier, 1829). The subsequent development of our knowledge of the family is summarized in Table 3.

Endlicher (1840) subdivided the family into Legnotidae (*Cassipourea* and *Dryptopetalum* = *Gynotroches*) and Rhizophoreae sensu stricto, which still included *Carallia*. Blume (1849) raised these two divisions to family status but transferred *Carallia* to Legnotidae so that the first recognition of the Rhizophoreae (not in Brown's sense) as "mangrove Rhizophoraceae," i.e., a named taxon capable of ecological designation, is from this date, even though Blume's "families" have scarcely been recognized by subsequent authors. Corner (1976) did recognize Legnotidaceae in his description of seeds of dicotyledons. Bentham & Hooker (1865), treating the Rhizophoraceae as a family, maintained Rhizophoreae and Legnotidae as tribes but added Anisophylleae as a third tribe to include the terrestrial genera *Anisophyllea* and *Combretocarpus*.

This system was essentially followed by Baillon (1876), who split the Legnotidae into two separate

TABLE 2. *Present probable status of some Linnean and Rumphian names in* Rhizophora *and* Mangium *(see Salvoza, 1936).*

	Present
A. *Rhizophora* Linnaeus (1753)	
R. mangle	*R. mangle* L.
R. gymnorhiza	*Bruguiera gymnorrhiza* (or *gymnorhiza*) (L.) Lamk.
R. cylindrica	*Bruguiera cylindrica* (L.) Bl.
R. candel	*Kandelia candel* (L.) Druce
R. caseolaris	*Sonneratia caseolaris* (L.) Engl.
R. majus	*Aegiceras corniculatum* (L.) Blanco
R. corniculata	*Aegiceras corniculatum* (L.) Blanco
B. *Mangium* Rumphius (1741–1755)	
M. candelarium	*Rhizophora apiculata* Bl.
M. celsum	*Bruguiera gymnorrhiza* (L.) Lamk.
M. minus (p.p.)	*Bruguiera gymnorrhiza* (L.) Lamk.
M. digitatum	*Bruguiera cylindrica* (L.) Bl.
M. minus (p.p.)	*Bruguiera cylindrica* (L.) Bl.
M. caryophylloides	*Bruguiera cylindrica* (L.) Bl.
M. caryophylloides *parvifolium* *latifolium*	*Ceriops tagal* (Perr.) C. B. Rob.
M. caseolare rubrum	*Sonneratia caseolare* (L.) Engl.
M. floridum	*Aegiceras floridum* R.&S.

tribes, Macariseae and Barraldeieae (= Gynotrocheae) from *Barraldeia* (= *Carallia*). Ridley (1922) raised the three tribes to families (his "orders," viz. Rhizophoraceae, Legnotidae, and Anisophylleae) but considered only the Malayan genera.

Schimper (1898) retained the traditional one-family concept but departed dramatically from the general consensus by splitting the family on morphological characters that he considered to be more fundamental than the structure of the fruit and seedling, since he considered their specializations to be features adapting the plants to their habitat (Anpassungsmerkmal) and therefore comparable to those found in other isolated mangrove taxa like *Aegiceras, Avicennia, Lumnitzera,* and *Sonneratia*. This may be seen as a complete reversal of the Linnean view. Schimper developed an elaborate subdivision, cutting across ecological characteristics as follows:

subfamily I. Rhizophoroideae
  tribe 1. Gynotrocheae
    subtribe 1a. Gynotrochinae [*Crossostylis* (as *Crossostyles*), *Gynotroches, Rhizophora, Ceriops, Kandelia*]
    subtribe 1b. Carallinae [*Pellacalyx, Bruguiera, Carallia*]
  tribe 2. Macarisieae [*Blepharistemma, Dactylopetalum, Macarisia, Weihea, Cassipourea*]
subfamily II. Anisophylloideae [*Anisophyllea, Combretocarpus*]

This arrangement has been summarily rejected by all subsequent authors, in particular it leads to Ding Hou's statement (1958), which might well be placarded in all institutes of systematic botany: "Schimper's clearly wrong classification provides again a good example of what danger is involved if a taxonomist introduces pre-occupied theoretical ideas into classification." In fairness to Schimper, it should be pointed out that he had a better idea of fruit and seed construction than most of his predecessors, since he recognized that the family Rhizophoraceae, which Brown had characterized as exalbuminous, did indeed possess well-developed endosperm (Juncosa, 1982), and that *Bruguiera* was appreciably different from the other mangrove taxa in some basic features. However, the sum of all vegetative features and especially of wood anatomy (Marco, 1935; van Vliet, 1976) shows that the habitat distinctiveness of the Rhizophoreae, even though it can be said to be primarily based upon "adaptive" or "ecological" characteristics, is well founded at the systematic level. The family therefore provides an interesting example for phyletic study since the Rhizophoreae are clearly derivative and must have had an ancestry in taxa that are now represented by the terrestrial genera. The most recent accepted intrafamilial classification (Table 1) was initially presented by Melchior

(1964). It recognizes three tribes: Macarisieae, with a center of distribution in Africa; Gynotrocheae, centered in Malesia; and Rhizophoreae, also centered in Malesia.

Monographs and partial revisions of varying utility exist for some genera of Rhizophoraceae. Alston (1925) discussed the largest genus, *Cassipourea*, including within it *Dactylopetalum*, *Weihea*, and *Lasiosepalum*. The related genus *Comiphyton* was described by Floret (1974), who subsequently discussed relationships of African Macarisieae further (Floret, 1976). *Sterigmapetalum* was recently revised by Steyermark & Liesner (1983). Several systematic treatments of *Rhizophora* or portions thereof exist (Salvoza, 1936; Ding Hou, 1960; Breteler, 1969, 1977). Yet only in the western Pacific, where the plants have been studied largely in the field rather than as dried material, is our understanding of the taxa adequate (Tomlinson, 1978; Duke & Bunt, 1979), although many basic questions about distribution, hybrids, and specific limits still remain unanswered. Excellent revisions of other Malesian genera, both mangrove and inland, are found in Ding Hou (1958). Our present understanding of the mangrove Rhizophoraceae is summarized in Tomlinson (1986).

In looking at the history of this family, one is impressed by the relative recentness of our present taxonomic and nomenclatural understanding. For example, the clarification of the full range of morphology in *Bruguiera* only comes with Ding Hou (1958); *Ceriops decandra* was correctly designated for the first time in this monograph. The difference between the two species of *Ceriops* is quite striking when floral function is considered. Some African taxa have been discussed by J. J. Floret (1976), while the New World taxa have been treated incompletely by a few authors (e.g., Prance et al., 1975).

One might conclude that any discussion of the phylogeny of this family is premature in the absence of detailed information about many species, but the situation reflects our ignorance of tropical plant families generally. If we can devote at least as much time to observation as we are doing to speculation about phylogenies, then our understanding is likely to improve.

AFFINITIES WITH OTHER FAMILIES

Rhizophoraceae (sensu lato) have traditionally been placed in the Myrtales (Bentham & Hooker, 1865; Melchior, 1964; Takhtajan, 1980), although more recently they have sometimes been aligned with Cornales (Cronquist, 1968; Thorne, 1976). These assignments and the long-obsolete suggestions of affinities with Loranthaceae or Santalaceae were based on the incorrect assumption that Rhizophoraceae (s. str.) characteristically have an inferior ovary; on the contrary, this is a rare and derived condition in the family. Furthermore, there are many fundamental vegetative differences between Rhizophoraceae (s. str.) and all of the aforementioned groups. Suggestions of relationship with Rubiaceae, Cunoniaceae, or Dialypetalanthaceae are based solely on the common possession of interpetiolar stipules and are as indefensible as are most systematic judgments based upon a single character. Cronquist's (1981) separation of Anisophylleaceae and Rhizophoraceae and assignment of the latter to its own order, Rhizophorales, is a wiser phylogenetic policy but still begs the question of affinities. We strongly favor Dahlgren's approach that leads to the surprising but very well-supported suggestion, proposed and discussed in detail elsewhere in this volume, of affinities between Rhizophoraceae, Celastraceae, Elaeocarpaceae, and possibly several other families.

FIELD RECOGNITION OF RHIZOPHORACEAE

Because of the great infrafamilial variation in most morphological characters, the family diagnosis, given below for completeness, is unwieldy and nearly useless to both field and herbarium botanists. Much of the year the mangrove genera are easily recognized by the hypocotyls protruding from the fruits. Vegetatively, the family is recognized by having opposite (or verticillate) leaves with interpetiolar stipules; the leaves are generally bitter-tanniniferous and usually minimally toothed in inland genera. In mangal, only one nonrhizophoraceous genus has interpetiolar stipules (to only 3 mm long—the weak-stemmed Old World shrub *Scyphiphora* (Rubiaceae)). Inflorescences are axillary and basically cymose, condensed in many common genera. The sole diagnostic floral feature, present in all species of which we are aware and otherwise known only in Rhamnaceae, is that each petal (fringed in all but two genera) individually encloses either a single antipetalous stamen or a group of 2–6 stamens, depending mainly upon whether the androecium is diplostemonous or polyandrous. Rhamnaceae are easily distinguished by their isomerous stamens and entire petals and of course many other characters.

FAMILY RHIZOPHORACEAE R. BROWN

Shrubs or trees (to 50 m) of dry to wet forests or mangrove swamps; leaves opposite or verticillate, toothed, crenate, or entire. Stipules interpetiolar, valvate and pubescent or imbricate and gla-

TABLE 3. *History of tribal classifications of Rhizophoraceae (s.l.).*

This Article, 1987—Family and Tribe	Brown, 1814—Family	Endlicher, 1840—Tribe
RHIZOPHORACEAE		
(i) Rhizophoreae	Rhizophoreae	(i) Rhizophoreae
Rhizophora (1753)	*Rhizophora*	*Rhizophora*
Bruguiera (1797)	*Bruguiera*	*Bruguiera*
Kandelia (1834)	*Carallia*	*Kandelia*
Ceriops (1838)		*Ceriops*
		Carallia
(ii) Gynotrocheae		(ii) Legnotidae[2]
Crossostylis (1776)		*Cassipourea*
Carallia (1811)		*Gynotroches*
Pellacalyx (1836)		
Gynotroches (1844)		
(iii) Macarisieae		
Cassipourea[1] (1775)		*Crossostylis* not classified
Macarisia (1836)		
Blepharistemma (1858)		
Dactylopetalum (1859)		
Sterigmapetalum (1925)		
Anopyxis (1960)		
Comiphyton (1974)		
ANISOPHYLLEACEAE		
Anisophyllea (1824)		
Combretocarpus (1865)		
Poga (1896)		
Polygonanthus (1932)		

Blume,[3] 1849—Family	Bentham & Hooker, 1865—Tribe	Baillon, 1876—Tribe
(i) Rhizophoreae	(i) Rhizophoreae	(i) Rhizophoreae
Rhizophora	*Rhizophora*	*Rhizophora*
Bruguiera	*Bruguiera*	*Bruguiera*
Kandelia	*Kandelia*	*Kandelia*
Ceriops	*Ceriops*	*Ceriops*
(ii) Legnotideae	(ii) Legnotideae	(ii) Gynotrocheae (as Barraldeieae)
Carallia	*Carallia*	*Carallia*
Cassipourea	*Cassipourea*	*Gynotroches*
Gynotroches	*Gynotroches*	*Crossostylis*
	Crossostylis	*Pellacalyx*
	Pellacalyx	
	Macarisia	
	Blepharistemma	
		(iii) Macariseae
		Cassipourea
		Macarisia
	(iii) Anisophylleae	(iv) Anisophylleae
	Anisophyllea	*Anisophyllea*
	Combretocarpus	

TABLE 3. *Continued.*

Schimper, 1898—See Text	Ridley,[4] 1922—Family	Melchior, 1964—Family and Tribe
I. Rhizophoroideae	(i) Rhizophoreae	RHIZOPHORACEAE
1. Gynotrocheae	*Rhizophora*	(i) Rhizophoreae
(a) Gynotrochineae	*Bruguiera*	*Rhizophora*
Rhizophora	*Kandelia*	*Bruguiera*
Kandelia	*Ceriops*	*Kandelia*
Ceriops		*Ceriops*
Gynotroches		
Crossostylis		
(b) Carallinae	(ii) Legnotidae	(ii) Gynotrocheae
Bruguiera	*Carallia*	*Carallia*
Carallia	*Gynotroches*	*Gynotroches*
Pellacalyx	*Pellacalyx*	*Crossostylis*
		Pellacalyx
2. Macarisieae		(iii) Macarisieae
Cassipourea		*Cassipourea*
Dactylopetalum		*Macarisia*
Weihea		
Macarisia		
Blepharistemma		
II. Anisophylloideae	(iii) Anisophylleae	ANISOPHYLLEACEAE
Anisophyllea	*Anisophyllea*	*Anisophyllea*
Combretocarpus		*Combretocarpus*
		Poga

[1] *Cassipourea* includes *Weihea, Lasiosepalum, Dactylopetalum* (p.p.), and *Petalodactylis.*
[2] From *Legnotis* a synonym of *Cassipourea.*
[3] Miquel (1855) added *Crossostylis* and *Anisophyllea* (as *Anisophyllum*) to Legnotidae.
[4] Non-Malaysian taxa not considered.

brous, always bearing colleters. Inflorescences axillary, cymose, dichotomous, or fasciculate. Flowers actinomorphic, bisexual or rarely unisexual, clearly articulated at juncture with pedicel. Calyx valvate, 4–many-lobed; petals equaling the number of sepals, usually with both a terminal arista and filiform appendages on the two lobes (rarely entire), each petal individually enclosing 1–5 stamens. Androecium diplostemonous to polyandrous, the filaments sometimes connate at base; nectariferous ring ("disc") intrastaminal, entire or lobed. Ovary superior to inferior, 2–many-carpellate (locules often incompletely or not at all separated by septae at anthesis); stigma capitate or with pronounced lobes, generally papillate. Ovules 2 or many per carpel, anatropous, usually apically inserted. Fruit capsular or baccate; seeds 1–many, naked, arillate, or winged, albuminous. Embryo green, usually straight, with laminar cotyledons and epigeal germination, or with thick cotyledons (or cylindrical cotyledonary body) and viviparous germination.

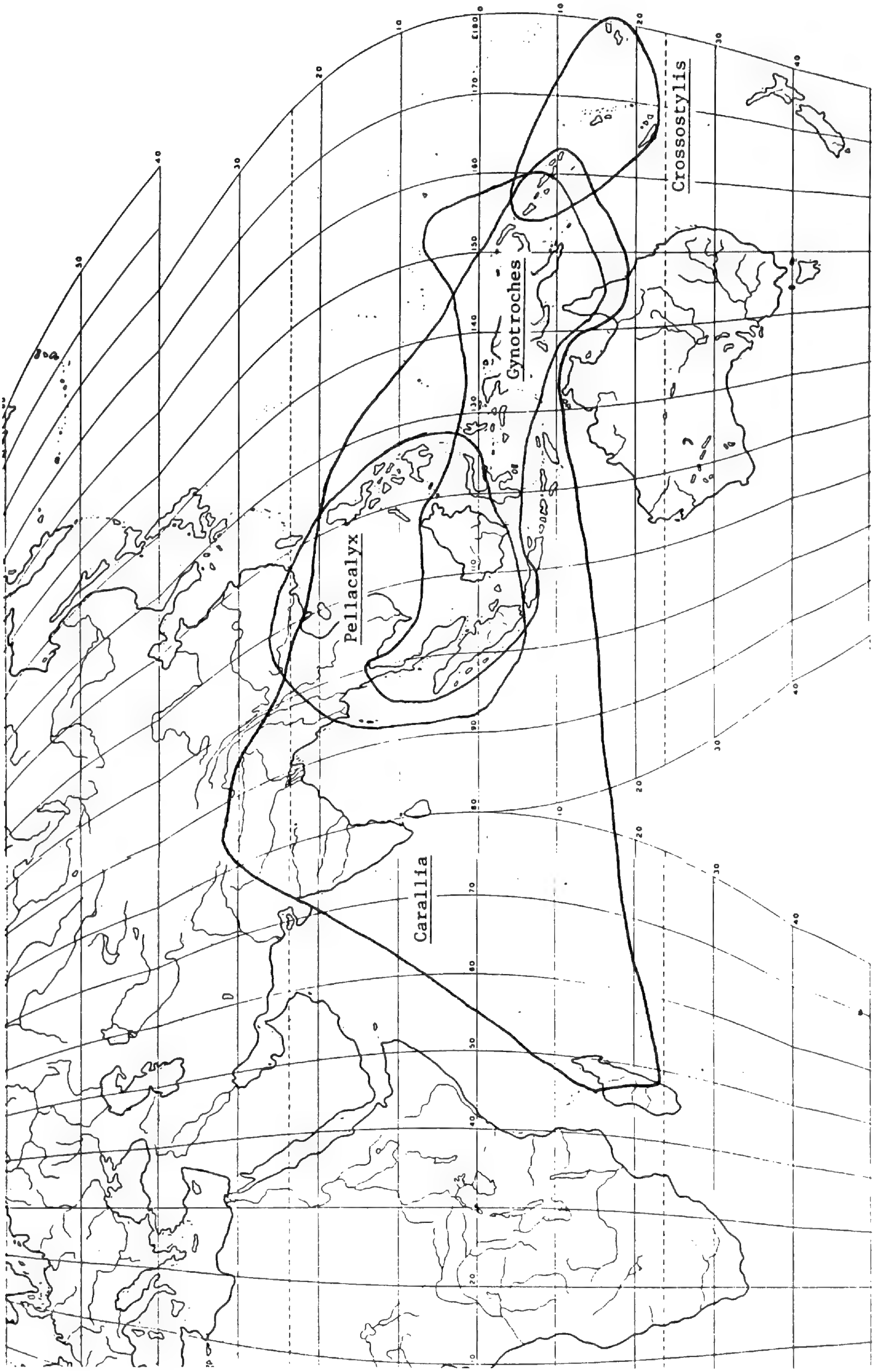
Genera. 15 (names listed by tribes); about 145 species.

Distribution. Pantropical.

In the synopsis that follows, genera are organized into the traditionally recognized tribes (e.g., Melchior, 1964), despite evidence already in hand that suggests some rearrangements (Tobe & Raven, this volume). Complete diagnoses are not given; instead, only some of the more distinctive characteristics of each tribe or genus are mentioned. References are likewise selectively cited. Listing of tribes and genera is alphabetical.

TRIBE GYNOTROCHEAE

Shrubs to large trees, some species weedy and characteristic of highly disturbed vegetation. Prominent aerial roots known in all genera but *Pellacalyx*. Leaves bijugate (not decussate), generally crenate. Stipules glabrous and imbricate (except in *Pellacalyx*). Flowers bisexual (except in *Gynotroches*); stamens twice the number of petals; ovary


Crossostylis
Gynotroches
Pellacalyx
Carallia

inferior (except superior in *Gynotroches*), 5- or many-carpellate; ovules 2 or many per carpel (locules incompletely separated). Fruit ± baccate, 1–many-seeded; seeds naked (except arillate in *Crossostylis*). This highly variable tribe has been the source of much confusion and is undoubtedly paraphyletic. Its proposed subdivision by Tobe & Raven (this volume) aids in clarification.

Genera. *Carallia, Crossostylis, Gynotroches, Pellacalyx.*

Distribution. Centered in Malesia, except *Crossostylis* (South Pacific) (Fig. 1).

Carallia Roxb., 9 species (Brandis, 1911; Ridley, 1922; Ding Hou, 1958). Figure 2.

Distribution. Indochina, Malesia, Philippines to New Guinea; *C. brachiata* also ranges to Madagascar, India, Nepal(!), S China, Solomon Islands, and N Australia.

Stilt roots reported only in *C. brachiata*. Large stalked glands (up to 5 mm) present outside stipules in several (all?) species. Inflorescences usually lax-cymose. Flowers 5–8-merous, diplostemonous, the ovary fully inferior. Seeds 1–several. Embryologically similar to Rhizophoreae.

Crossostylis J. R. & G. Forst., about 12 species (Smith, 1981). Figures 3, 4.

Distribution. S Pacific Islands.

Inflorescences dichotomous. Largest flowers in the family (to 6 cm wide) in *C. grandiflora* (Fig. 4). Petals with very reduced appendages, even appearing entire at maturity. Stamens variable in number, sometimes basally connate and bearing odd appendages that retain the copious nectar in pendulous flowers. Ovary multicarpellate (up to about 20), nearly superior to inferior; stigma with long lobes. Fruit dehiscent or a partially dehiscent "salt-shaker" capsule.

This genus shares some characteristics (e.g., appendaged seeds) with Macarisieae, but many others with Gynotrocheae. It is placed in its own tribe, Crossostylieae, by Tobe & Raven (this volume).

Gynotroches Blume, 2–4 species (Ding Hou, 1958; Backer & Bakhuizen, 1963). Figures 5, 6.

Distribution. Burma through Malesia to Micronesia and Melanesia.

Weedy tree; branches often drooping. Plants dioecious. Inflorescences fasciculate. Flowers 4–5-merous, diplostemonous (Fig. 6). Ovary superior, 4–5-carpellate, with 3–8 ovules per locule; stigmatic lobes sometimes elongate. Fruit a berry; seeds several to many.

The most recent revision (Ding Hou, 1958) recognizes only one species (*G. axillaris* Blume) but points out that the variation in floral characters is such that with further study several distinct species will be recognized. Juncosa & Tobe (this volume) provide some details separating two of these taxa.

Pellacalyx Korth., 8 species (Ding Hou, 1958). Figure 7.

Distribution. Burma and South China to Malesia.

Some species weedy; branches often drooping. Stipules valvate, the edges folded sharply inward. Indumentum of stellate hairs, unique among Rhizophoraceae. Pairs of bracteoles fused into a toothed cup. Number of stamens and of carpels twice the number of petals, this usually 4 or 5. Each carpel or locule with 8–25 ovules.

Despite its distinctive indumentum and superficially very different flowers, this genus shares many vegetative and embryological synapomorphies with *Gynotroches*; the two are clearly sister genera.

TRIBE MACARISIEAE

Shrubs to large (50 m) trees, generally of moist primary forest; but some species found in dry or deciduous forest. Stilt roots absent or weakly developed. Leaves toothed, at least in juvenile growth phases, verticillate or opposite, decussate in bud but often reoriented on branches. Stipules valvate, pubescent, also bearing colleters. Inflorescences fasciculate or lax-cymose. Flowers bisexual, except in *Sterigmapetalum* and *Blepharistemma* (?). Androecium diplostemonous (polyandrous only in *Cassipourea*). Ovary superior in four or five of the six genera, not in only two as sometimes stated; locules 2–6. Fruit a capsule, sometimes indehiscent; seeds arillate or winged.

Detailed information is lacking for most genera, and characterizations reported here are based largely upon the literature, much of which is very

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FIGURE 1. *Geographical distribution of genera of tribe Gynotrocheae.*


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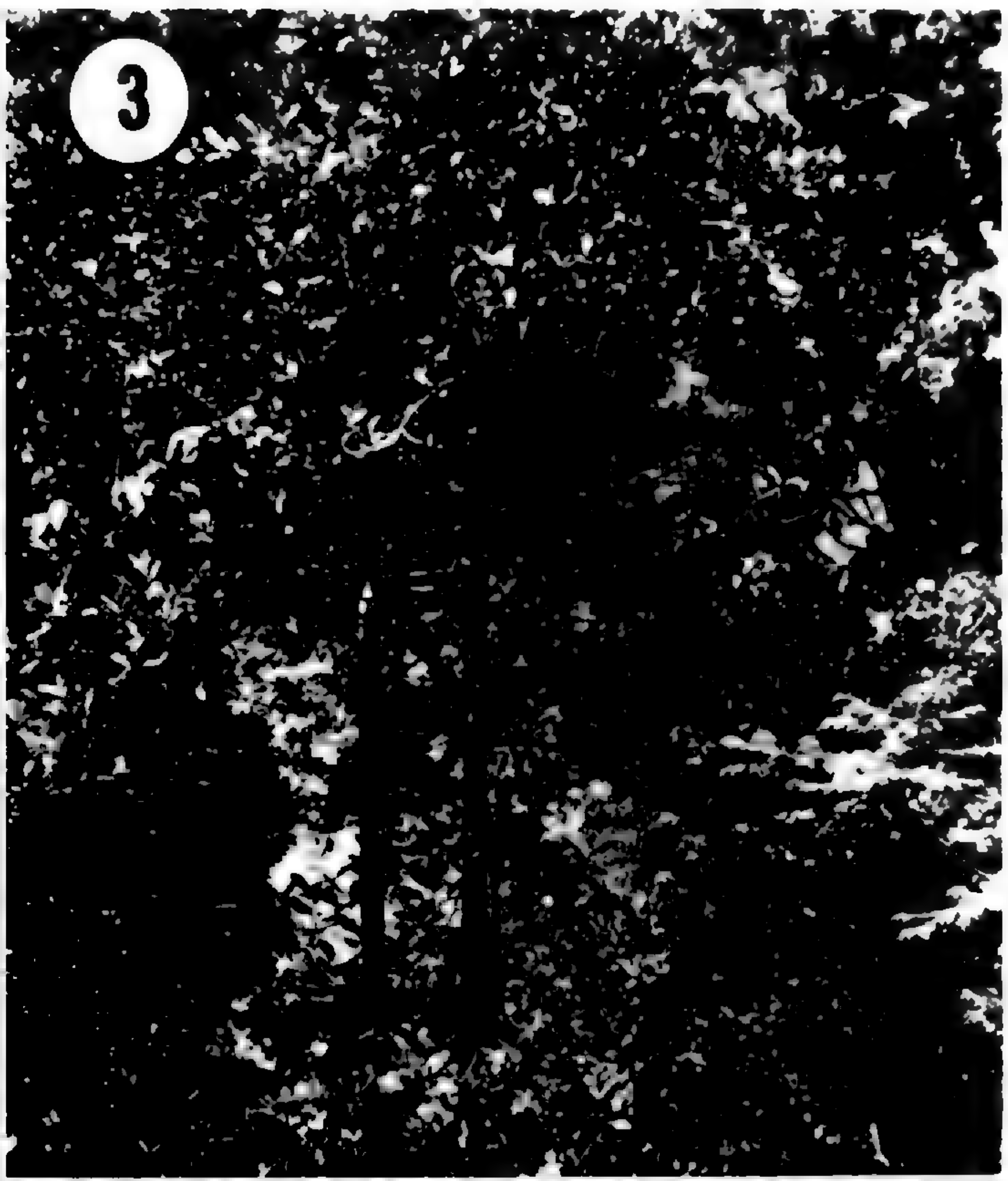
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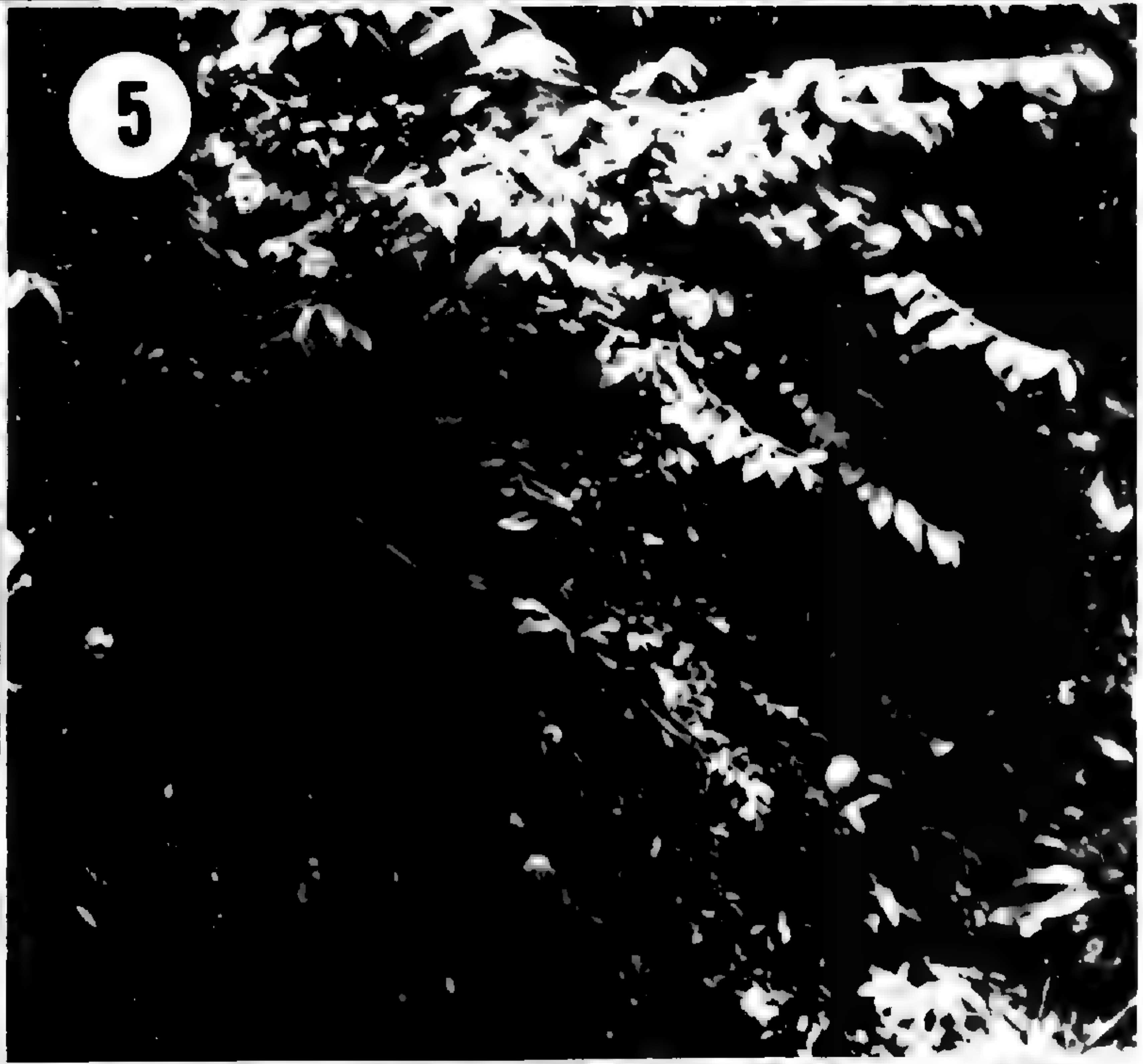
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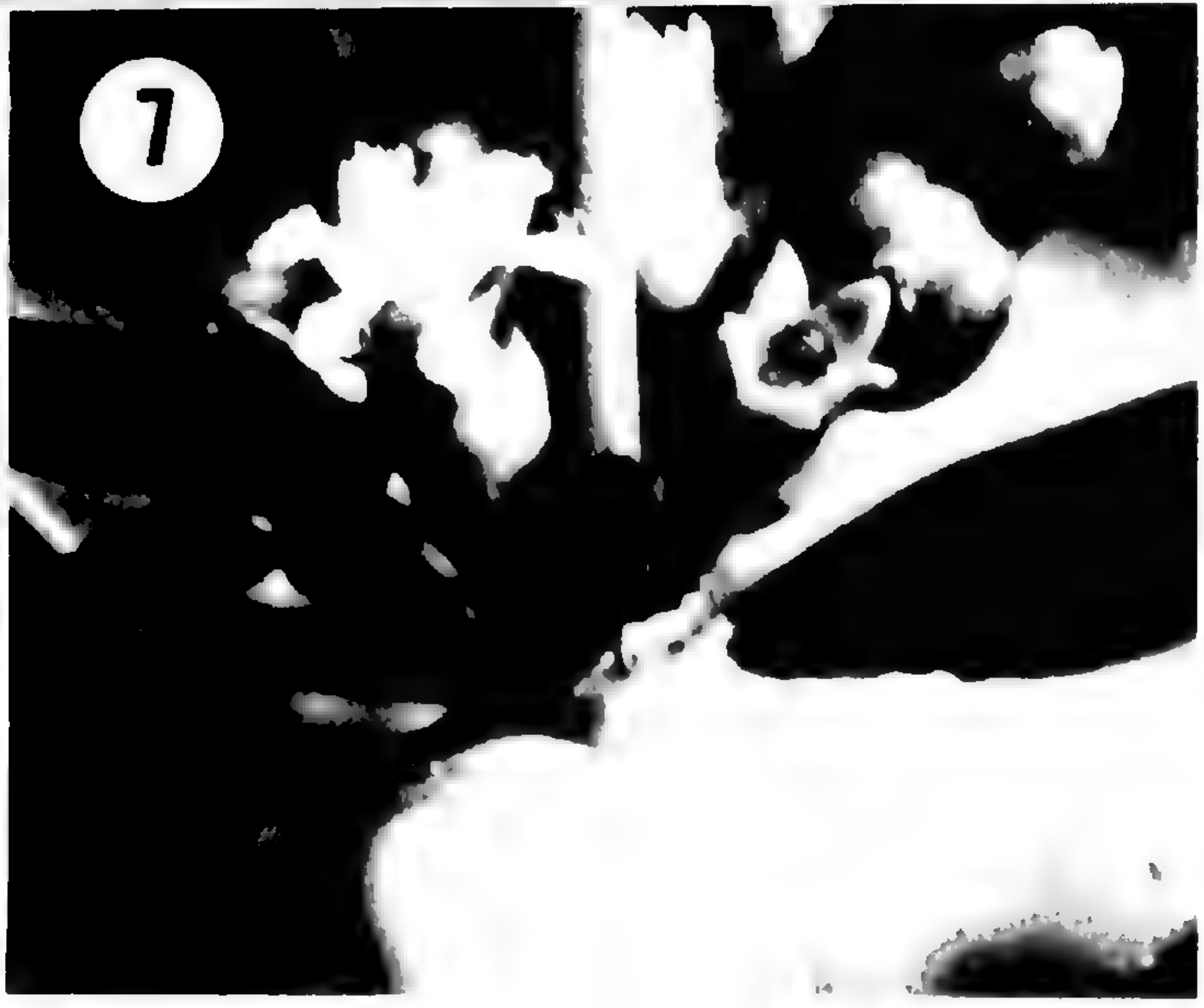
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incomplete and not illustrated. This basal tribe is the most poorly known group of Rhizophoraceae, largely due to the unavailability of fixed material and the rarity of certain key taxa. The three subgenera of *Cassipourea* are distinguished by several characters of calyx, androecium, and petal appendages, although three species exhibit combinations of character states of more than one subgenus (Floret, pers. comm.). *Dactylopetalum*, here re-elevated from a subgenus of *Cassipourea* to generic rank, and *Blepharistemma* are dubiously distinct at the generic level. Anatomical and monographic work in progress promises to clarify the relationships of all these arillate-seeded Macarisieae. Distinctions between the winged-seeded genera (*Anopyxis, Macarisia,* and *Sterigmapetalum*) are clear.

Genera. Anopyxis, Blepharistemma, Cassipourea, Comiphyton, Dactylopetalum, Macarisia, Sterigmapetalum.

Distribution. Centered in Africa, extending to Madagascar and India (Sri Lanka) and to South and Central America (Fig. 8).

Anopyxis (Pierre) Engl., 1–3 species (Sprague & Boodle, 1909; Hutchinson & Dalziel, 1954; Irvine, 1961).

Distribution. Tropical Africa.

Tallest inland genus (to 50 m), often dominant. Leaves opposite or in whorls of 3. Calyx, petals, and ovary 5-merous. Stamens 10, filaments connate over their entire length. Petals sometimes entire. Fruit woody, indehiscent (?); seeds winged.

Blepharistemma Wall. ex Benth., 1 species (Schimper, 1898; Gamble, 1919).

Distribution. SW India.

Bracteoles absent (?); flowers polygamodioecious, 4-merous. Ovary 3-locular; fruit fleshy, indehiscent (?); seeds arillate.

Cassipourea Aublet (including subgenera *Weihea* and *Lasiosepalum*), about 55 species (Alston, 1925). Figures 9, 10.

Distribution:

subgenus *Cassipourea*: tropical Americas, West Indies, West Africa.
subgenus *Lasiosepalum*: West Africa.
subgenus *Weihea*: Africa, Madagascar, India, Sri Lanka.

Many species occurring in dry habitats; commonly shrubby, also some tall (30 m) trees (Fig. 9). Inflorescences usually condensed. Flowers (4–)5(–6)-merous. Stamens indefinite in number (15–40), in one (or more?) whorls. Ovary superior, 3(–4)-locular. Seeds 1–4; aril white, yellow, or orange.

Comiphyton Floret, 1 species (Floret, 1974, 1976).

Distribution. Gabon to E border of Zaire; not yet known from the belt defined by 2°N or S, thus one of the most narrowly equatorial ranges of any plant.

Distinguished from *Cassipourea* by its inflorescence, diplostemonous androecium, anthers, and placentation (Floret, 1974, 1976); not sharply differentiated from *Dactylopetalum*.

Dactylopetalum Benth., about 15 species (Alston, 1925; Floret, 1976).

Distribution. Equatorial Africa, Madagascar.

After consideration of remarks by Floret (1976) and other literature (Bentham & Hooker, 1865; Oliver, 1871; Dale & Greenway, 1961), we prefer to recognize this genus as distinct from *Cassipourea*; distinguishing characteristics include the diplostemonous androecium, 2-carpellate ovary, and indehiscent (?) fruit.

Macarisia Thouars, 7 species (Schimper, 1898; Arènes, 1954).

Distribution. Madagascar.

Diplostemonous, 4–5-carpellate, seeds winged.

Sterigmapetalum Kuhlmann, 7 species (Steyermark & Liesner, 1983).

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FIGURES 2–7. *Habit and flowers of Gynotrocheae.—2. Fully open flowers of* Carallia borneensis *growing in Brunei. Those at left opened the previous day and are now in their pistillate phase (stigmas receptive); those at right are at (staminate) anthesis.—3.* Crossostylis grandiflora *growing in New Caledonia in lowland rain forest, typical habitat for inland Rhizophoraceae.—4. Flowers of* Crossostylis grandiflora, *some at anthesis, others past. Buds are white to red, petals white.—5.* Gynotroches *sp. growing by a stream in Sarawak, E Malaysia, showing opposite bijugate leaves reoriented into one plane on horizontal or drooping branches.—6. Flowers of* Gynotroches *sp.; they were being visited (pollinated?) by numerous small ants.—7. Flowers and young fruits of* Pellacalyx cristatus *growing in Sarawak; overall habit in this genus is similar to that of* Gynotroches.

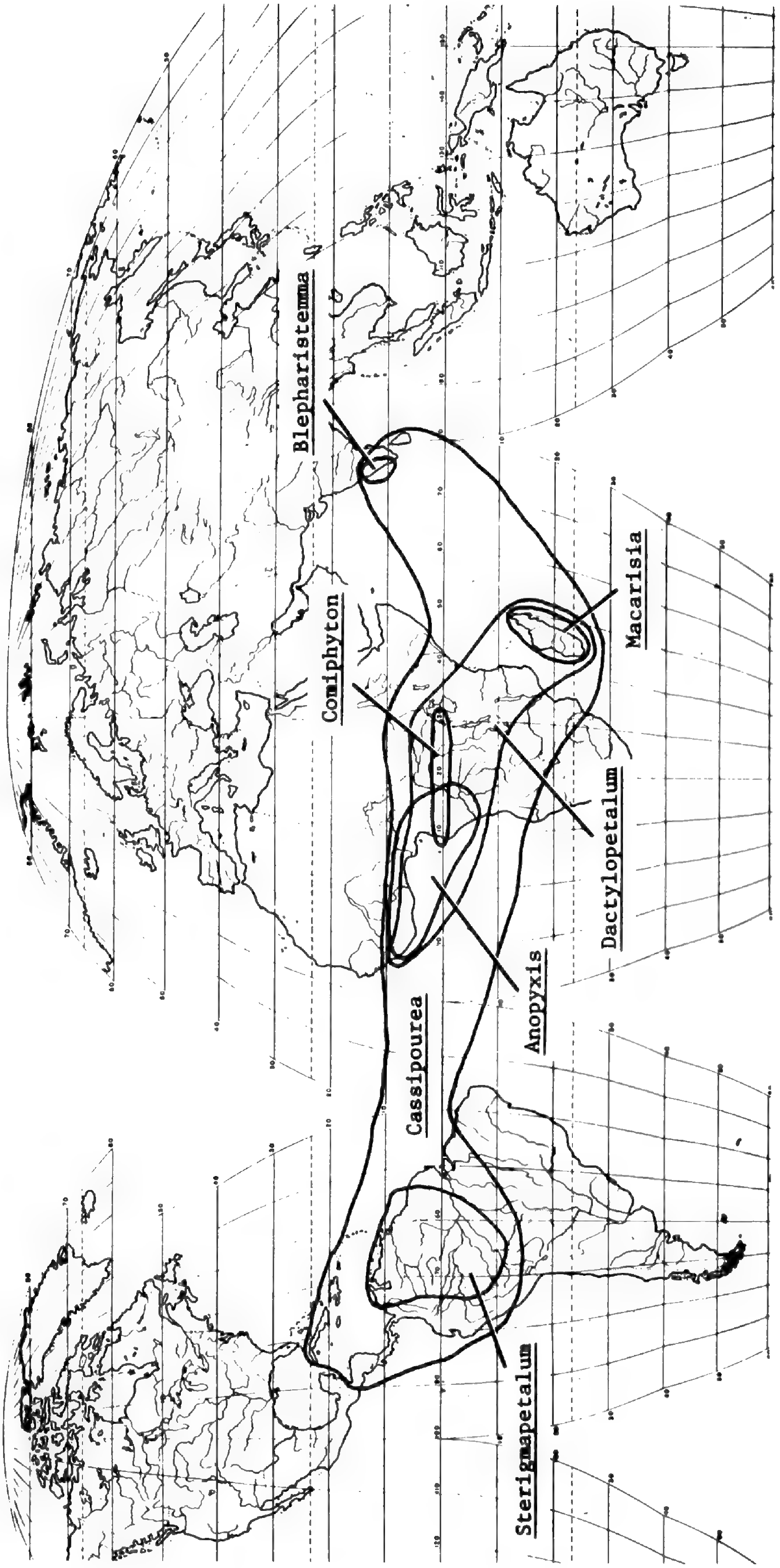
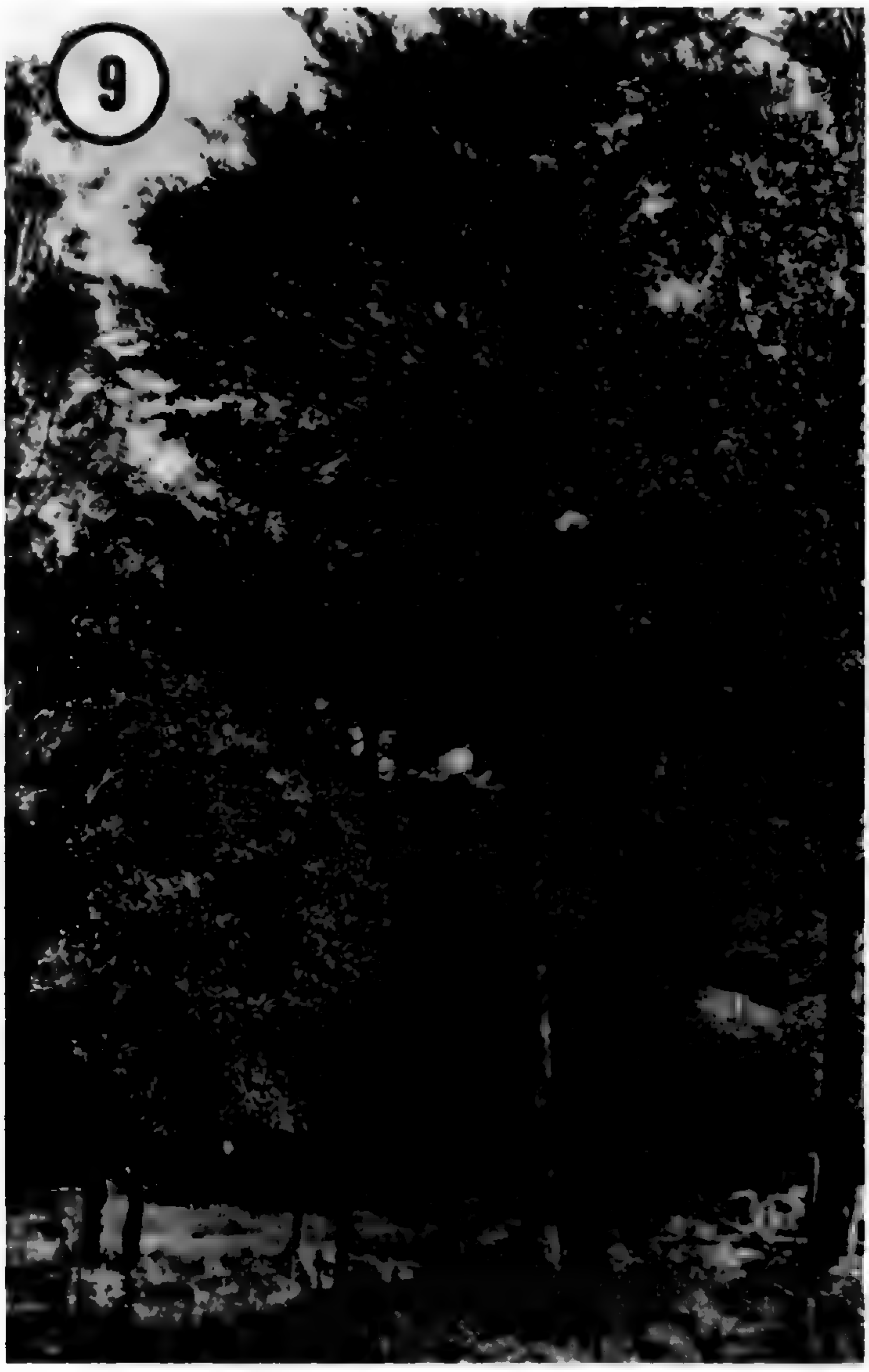
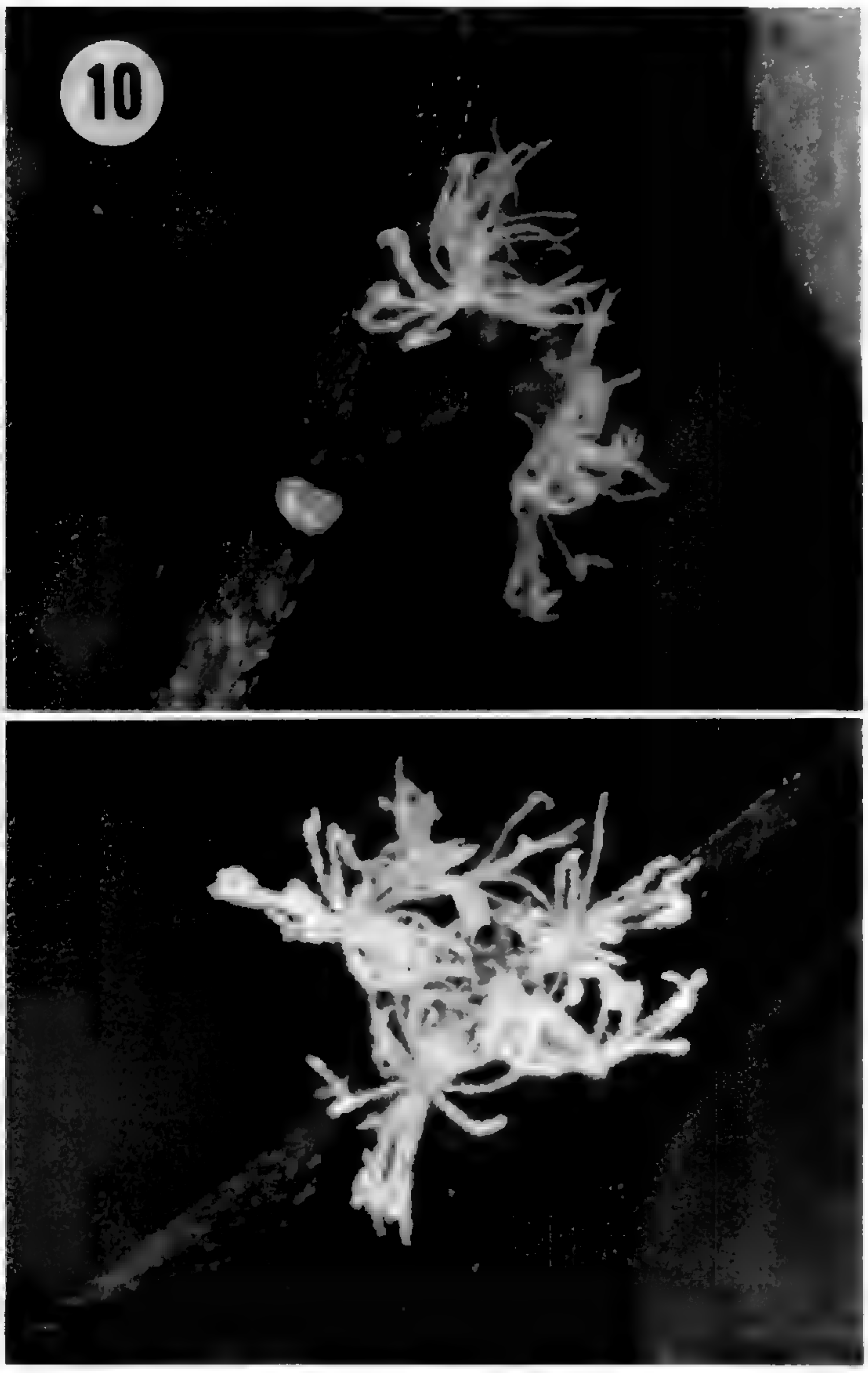


FIGURE 8. *Geographical distribution of genera of Macarisieae.*





FIGURES 9, 10. *Habit and flower of* Cassipourea *(Macarisieae)*.—*9.* Cassipourea *sp. growing by pasture on Monteverde, Costa Rica. Smooth unbuttressed bole and dense crown are typical of the genus.*—*10. Flower of* Cassipourea *sp. cf.* killipii *(Chocó, Colombia) at anthesis, showing both side and top views; plumose petal appendages greatly increase apparent size of flower.*

Distribution. NW South America.

Plants dioecious. Leaves usually verticillate. Flowers 4–6-merous, diplostemonous. Seeds winged.

TRIBE RHIZOPHOREAE

Shrubs or trees of mangrove swamps; flowering plants 1.5–50 m tall. Aerial stilt roots always produced, prominent only in *Rhizophora*. Leaves entire, bijugate. Inflorescences variable, generically diagnostic. Flowers 4–multimerous, mostly diplostemonous, the petals variously specialized for diverse pollination mechanisms. Ovary half to fully inferior, 2–3-carpellate; ovules 2 per carpel. Fruit baccate, fibrous, 1-seeded. Germination viviparous, the huge seedling axis (to 1 m) emerging from both seed coat and fruit up to 9 months before abscission.

This familiar tribe is unfortunately morphologically atypical of the family; this has led to considerable confusion in phylogenetic decisions.

Genera. *Bruguiera, Ceriops, Kandelia, Rhizophora.*
Distribution. Pantropical (Fig. 11).

Bruguiera Lam., 6 species (Ding Hou, 1957, 1958). Figure 12.

Distribution. SE Africa through Malesia to Pacific Islands and Northern Australia.

Inflorescences cymose or reduced to 1–3 flowers, sometimes ebracteolate. Flowers polymerous, diplostemonous; ovary deeply inferior, 3-carpellate. Each petal encloses two stamens, releasing them explosively when stimulated. Petal appendages often reduced, the petals variably pubescent abaxially.

Ceriops Arn., 2 species, 1 variety (Ding Hou, 1958). Figures 13, 14.

Distribution. SE Africa through Malesia to Australia.

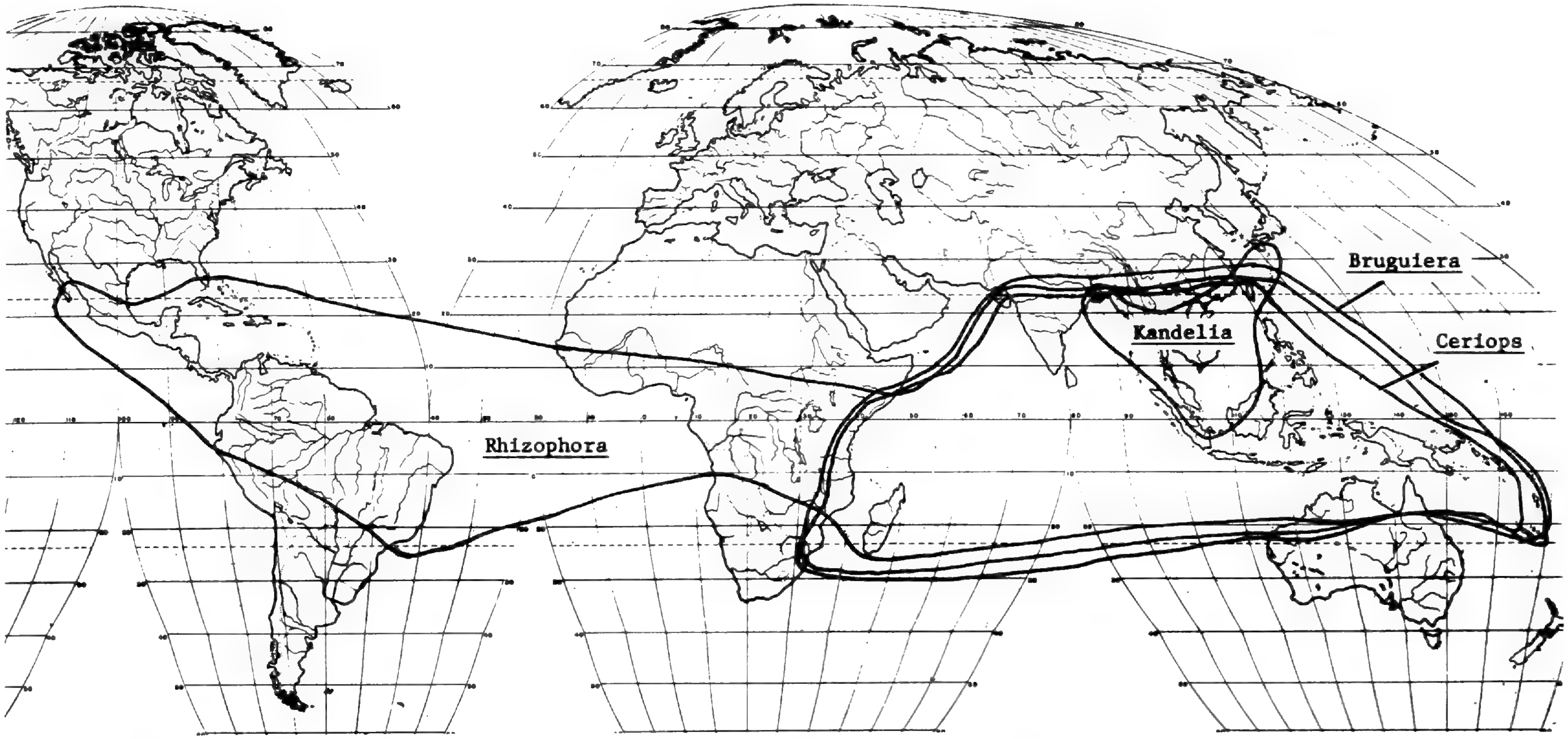
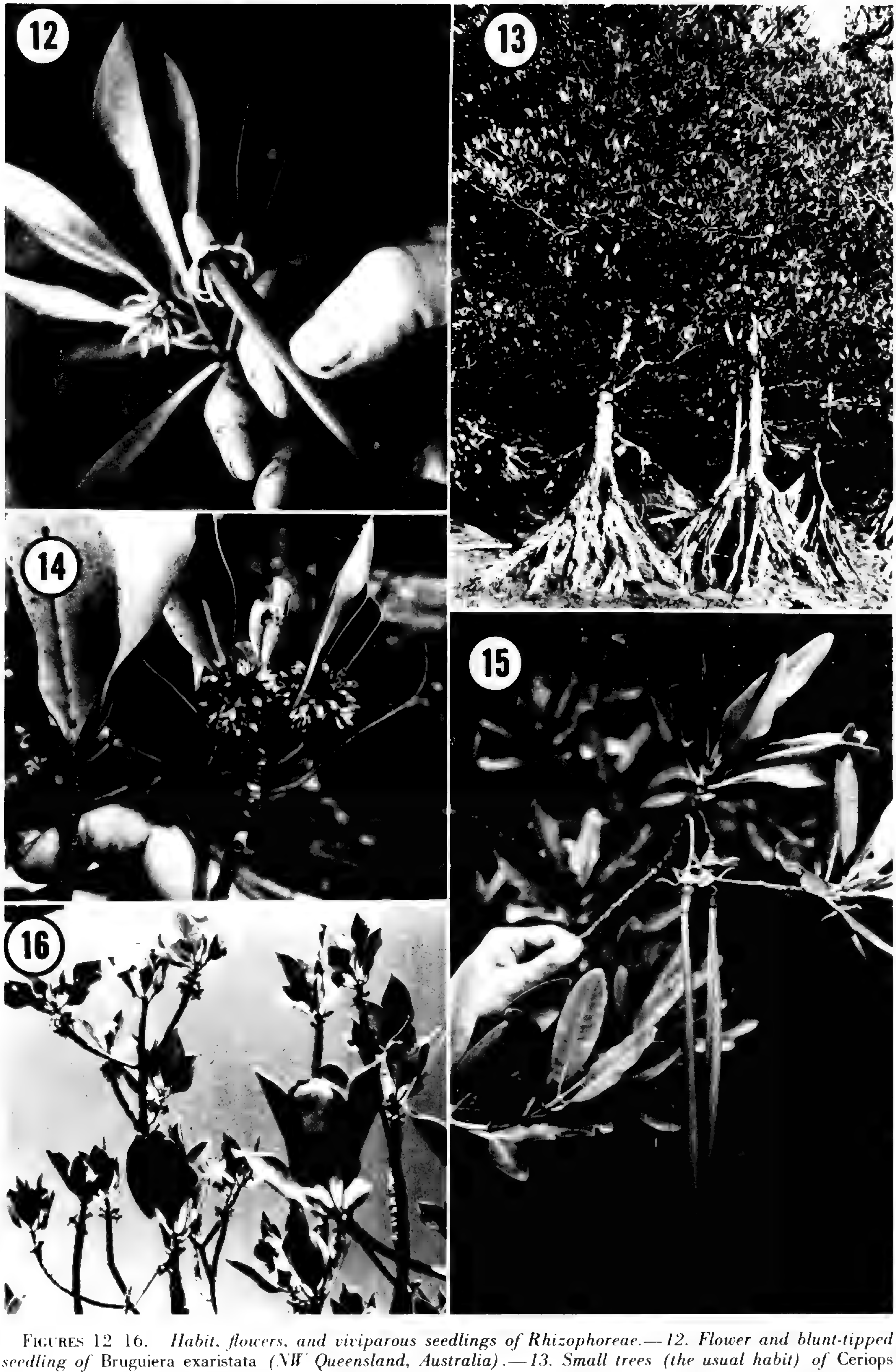


FIGURE 11. *Geographical distribution of genera of tribe Rhizophoreae.* Rhizophora *and* Bruguiera *have been introduced and are becoming naturalized in Hawaii (not shown).*



FIGURES 12–16. *Habit, flowers, and viviparous seedlings of Rhizophoreae.—12. Flower and blunt-tipped seedling of* Bruguiera exaristata *(NW Queensland, Australia).—13. Small trees (the usual habit) of* Ceriops tagal *(Sarawak), showing low cone of stilt roots that coalesce to form buttresses; leaves of this very drought- and salt-tolerant species are curled and upright.—14. Branch tip with fasciculate inflorescences of* Ceriops tagal *(Sarawak).—15. Branch tip of* Kandelia candel *(Sarawak) with mature viviparous seedlings. The long-acuminate seedlings of this genus have a mode of establishment unlike that of other Rhizophoreae.—16. Habit of* Rhizophora apiculata *(New Caledonia). In this species, highly adapted to anemophily, flowers are borne well below leaves, and petals and dehisced stamens may abscise before the flower opens.*

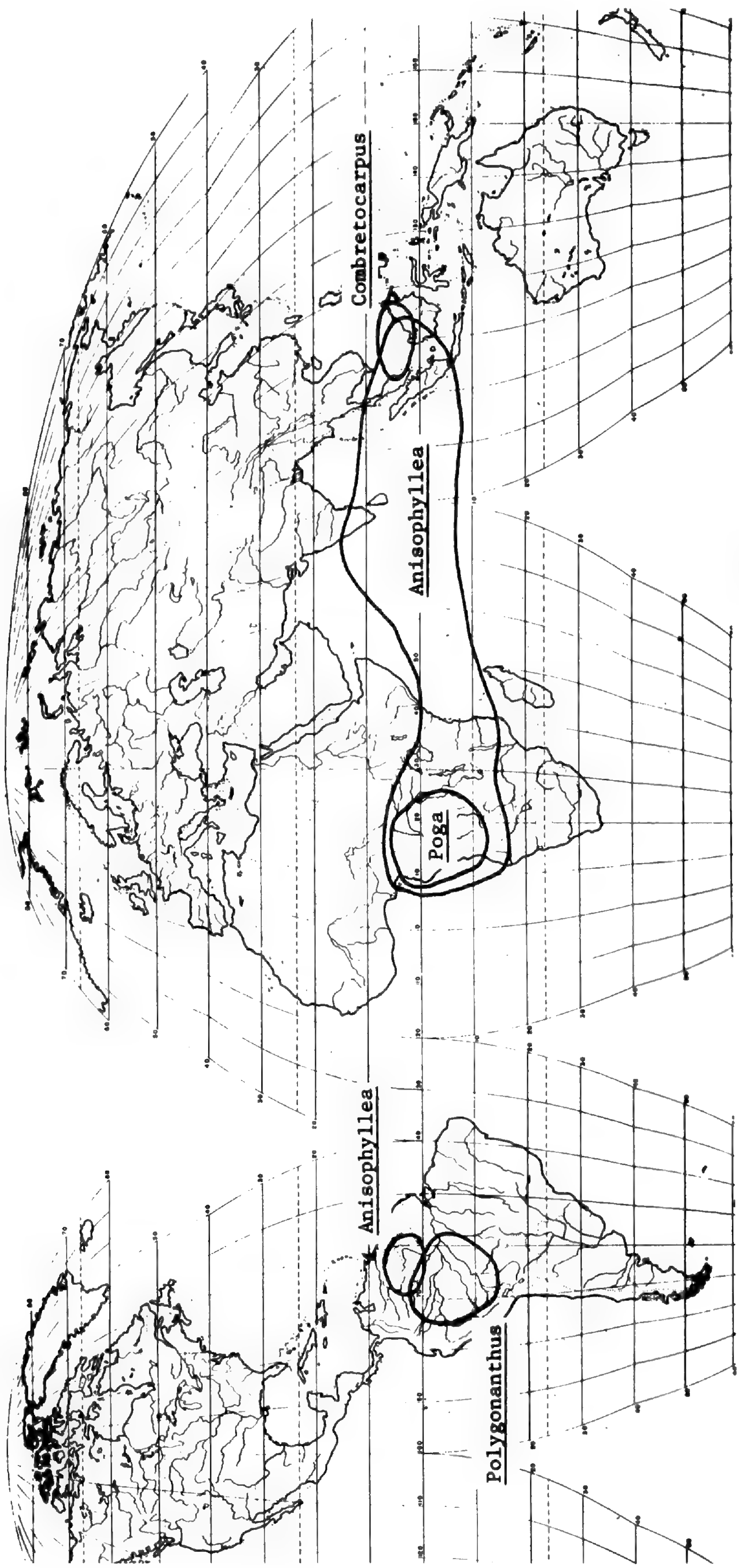
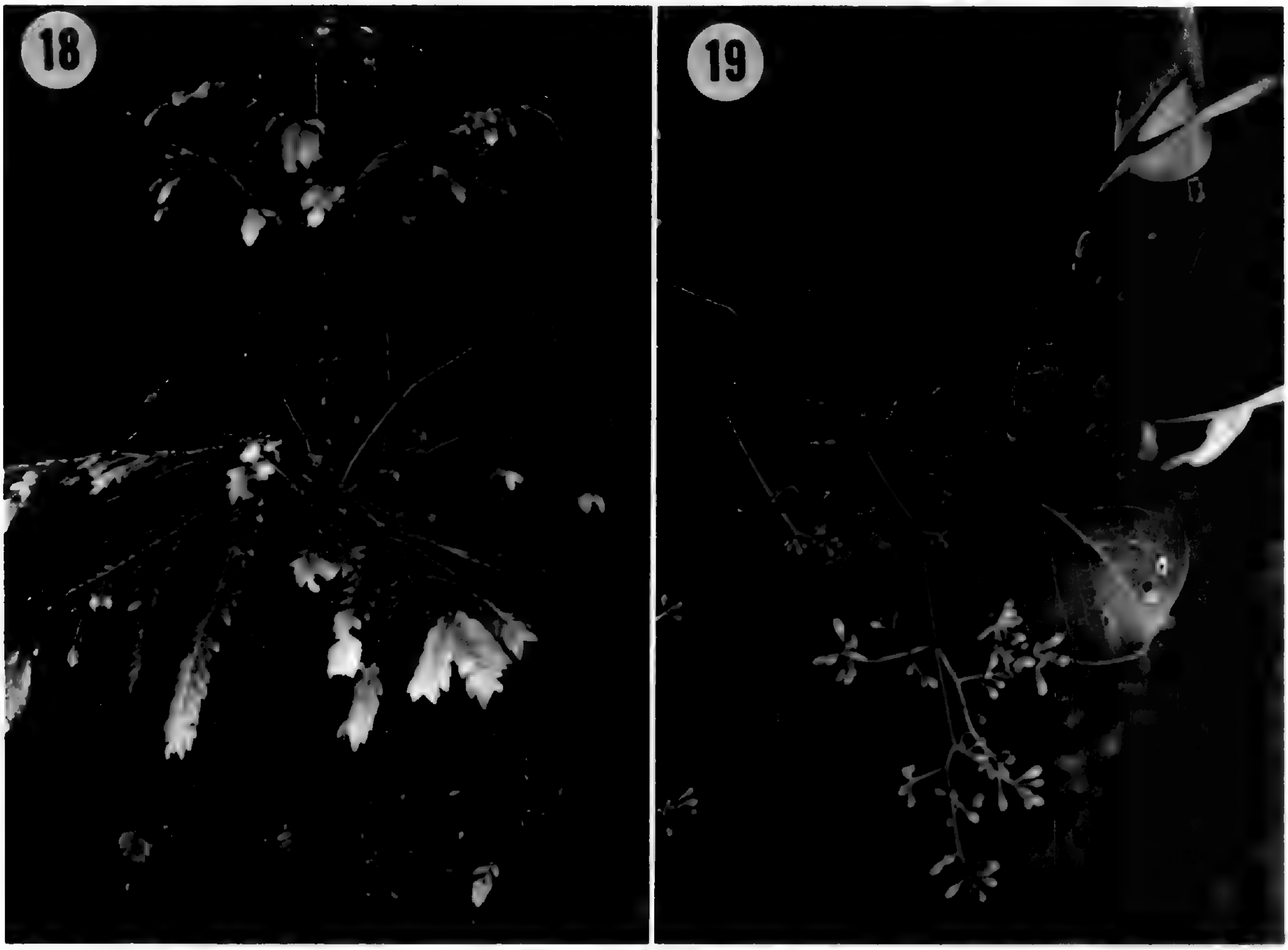


FIGURE 17. *Geographical distribution of genera of family Anisophylleaceae. In Peninsular Malaysia,* Combretocarpus *may now be extinct.*



FIGURES 18, 19. *Habit and inflorescence of Anisophylleaceae.—18.* Anisophyllea disticha *(Brunei), a common understory shrub in Malaysia; large trees in this genus have similar architecture and phyllotaxis, albeit less obvious.—19. Foliage and paniculate inflorescence of* Combretocarpus rotundatus *(Also from Brunei).*

Most salt-tolerant genus of the tribe; frequently shrubby; bark pale (unlike all other genera of the tribe). Inflorescences fasciculate (Fig. 14), trichasial changing to monochasial. Flowers pentamerous, diplostemonous; ovary half-inferior, 3-carpellate. Hypocotyl generally ridged.

Kandelia (DC.) Wight & Arn., 1 species (Ding Hou, 1958). Figure 15.

Distribution. Bangladesh to S Japan, through Indochina to Malaysia, Sumatra, Borneo. Characteristically found on riverbanks.

Inflorescences dichotomous; bracteoles connate and corky. Flowers 4–5-merous; petals to 2 cm, 3–7-lobed nearly to base; stamens about 30; ovary half-inferior, 3-carpellate. Hypocotyls long-acuminate.

Rhizophora L. Either 8 species or 4 species, 2 distinct varieties, 3 hybrids (Salvoza, 1936; Ding Hou, 1958; Tomlinson, 1978). Figure 16.

Distribution. Pantropical, barely extending to subtropics.

Large stilt roots. Inflorescences dichotomous, bracteoles of most species tiny. Flowers 4-merous; ovary half-inferior, 2-carpellate. Petals entire (this unique in the family) but usually densely pubescent, the edges barely enclosing each antipetalous stamen. Stamens 8, in two whorls, except 3 times the number of petals in *R. apiculata*; multilocellate in all species. Wind pollinated.

FAMILY ANISOPHYLLEACEAE RIDLEY

Trees and shrubs of wet primary forest; leaves alternate, dimorphic (except in *Combretocarpus*), exstipulate or with highly reduced stipular homologues. Inflorescences axillary, racemose to paniculate. Flowers mostly unisexual (plants monoecious), except bisexual in *Combretocarpus*. Calyx and petals valvate, 3–5-merous. Petals lobed or laciniate (except entire in *Polygonanthus*). Androecium diplostemonous. Nectary crenate. Ovary inferior, 3–

4-locular, the styles separate. Ovules 1–2 per carpel. Fruit a drupe or dry, winged (*Combretocarpus*), usually 1-seeded. Endosperm lacking; embryo with reduced or no cotyledons. Germination hypogeal.

Genera. Anisophyllea, Combretocarpus, Poga, Polygonanthus.

Distribution. South America, Africa, India to Malesia (Fig. 17).

Anisophyllea R. Brown ex Sabine, 25 species (Hutchinson & Dalziel, 1954; Ding Hou, 1958). Figure 18.

Distribution. South America, Africa, India to Malesia.

Shrubs 1.5 m tall through large trees. Axes strongly differentiated; plagiotropic branches of most species anisophyllous, with unique tetrastichous phyllotaxy (Fig. 18). Serial axillary buds numerous. Staminate and pistillate flowers either in separate inflorescences or mixed, often not strongly heteromorphic, usually 4-merous. Drupes 2–15 cm, usually 1-seeded.

Combretocarpus Hook. f., 1 species (Ding Hou, 1958). Figure 19.

Distribution. Borneo.

Large tree of peat swamps. Leaves isomorphic, distichous. Inflorescence paniculate (Fig. 19). Flowers bisexual, usually trimerous. Petals linear or irregularly 3–4-lobed. Fruit winged.

Poga Pierre, 1 species (Hutchinson & Dalziel, 1954).

Distribution. Equatorial Africa.

Large tree. Leaves anisophyllous. Inflorescences on specialized leafless branches. Flowers unisexual, strongly heteromorphic. Fruits with 3–4 edible oily seeds.

Polygonanthus Ducke, 2 species (Prance et al., 1975).

Distribution. Brazil (Amazonia).

Small trees. Leaves anisophyllous. Flowers unisexual, strongly heteromorphic; petals unlobed, nearly linear.

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SYSTEMATIC COMPARISON AND SOME BIOLOGICAL CHARACTERISTICS OF RHIZOPHORACEAE AND ANISOPHYLLEACEAE[1]

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P. Barry Tomlinson[3]

ABSTRACT

Systematic and biological characteristics of Rhizophoraceae and Anisophylleaceae are detailed. Comparison of a wide variety of vegetative and reproductive characters reveals virtually no points of agreement between the two families. Characters such as the basically diplostemonous androecium are of such wide occurrence in choripetalous dicotyledons as to be phylogenetically insignificant. One apomorphy found in both families, divided or appendiculate petal margins, occurs in several unrelated families also and is judged to be a homoplasy. Cladistic analysis of Rhizophoraceae shows that, not surprisingly, information now in hand about most Macarisieae is inadequate to resolve the relationships of the genera and clades of this tribe. The remainder of the proposed phylogenetic tree is very robust and shows that, as traditionally circumscribed, tribe Gynotrocheae is paraphyletic. Carallia *is evidently the inland genus most closely related to the mangroves.* Bruguiera, *although characterized by several remarkable autapomorphies, is the most primitive of the mangrove genera, and* Rhizophora *is the most derived.*

The Rhizophoraceae (used sensu stricto throughout this article) and Anisophylleaceae have often been treated as a single family, although some recent phylogenetic treatments of the angiosperms have placed them separately (Cronquist, 1981; Dahlgren, 1980), as originally suggested by Ridley (1922). We believe that this lack of consensus stems largely from the absence of detailed information on a wide variety of systematic characters of the two families, rather than from differences in interpretation. Detailed discussions of several specific suites of characters, such as pollen and leaf architecture, appear elsewhere in this volume, so we have emphasized other, mostly morphological, characters that are either not widely understood for these two families or not generally considered in systematic comparisons. A summary of the systematic differences between Rhizophoraceae and Anisophylleaceae in these characters forms Table 1.

Despite the fact that most botanists are somewhat familiar with the mangrove Rhizophoraceae, particularly the genus *Rhizophora*, the biology of these plants is widely misunderstood. Accordingly, in a second section of this article, we discuss some of the biological adaptations to the mangrove habitat that are found in Rhizophoraceae, with as much comparative reference to the inland genera as the current state of our knowledge permits.

SYSTEMATIC COMPARISON

DISTRIBUTION AND HABITAT

Rhizophoraceae and Anisophylleaceae are tropical families of shrubs and trees; only a few species of mangrove Rhizophoraceae stray beyond 22° lat-

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FIGURES 1, 2. *Aerial roots of mangrove Rhizophoraceae. Localities given in parentheses.—1. Stilt roots of* Rhizophora harrisonii *(Costa Rica).—2. Stilt and knee roots of* Bruguiera gymnorrhiza *(Queensland). Development of knee roots is illustrated in Figure 29.*

itude, and then only on coastlines with warm currents. Taxa of both families occur in most of the major moist-tropical floristic regions. The preponderance of genera with only one or two species and the narrow geographic ranges of those genera (Juncosa & Tomlinson, this volume) suggest that both may be relictual families.

For its size, the Rhizophoraceae have an exceptionally wide ecological and geographic range. The mangrove taxa are found on virtually all tropical coasts, and inland species grow in many moist forest types, both primary and successional. A few species, mostly in the genus *Cassipourea*, grow in drier habitats. Several genera of Rhizophoraceae (both inland and mangrove) may form very large trees (to 50 m), but most species are small trees and may begin flowering at heights of only 1–2 m.

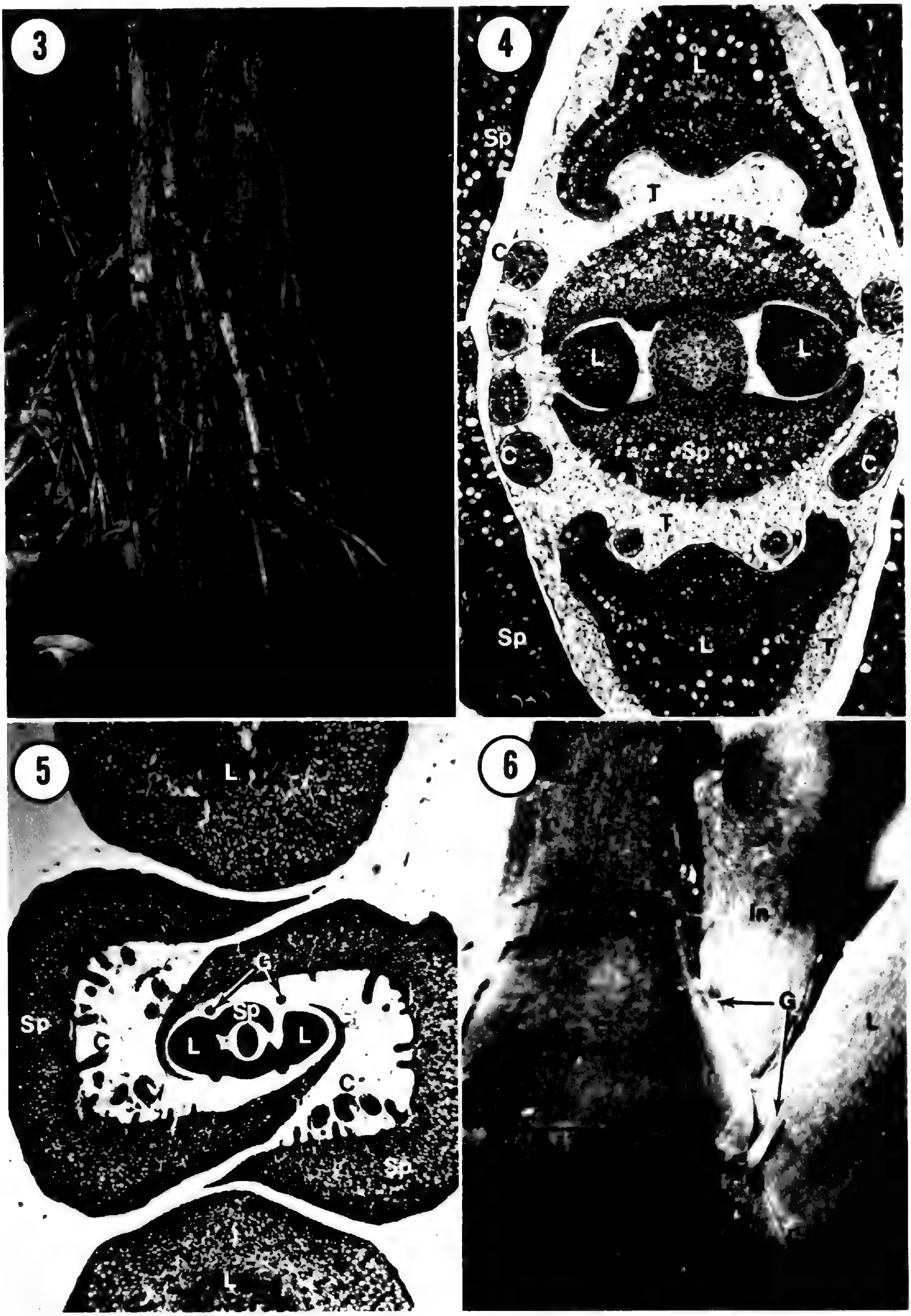
Anisophylleaceae are characteristically large trees of wet lowland primary forest, although the genus *Anisophyllea* also includes some elegant small shrubs (e.g., *A. disticha*). *Combretocarpus* is a dominant tree of Bornean (fresh water) peat swamp forest, apparently now extinct in peninsular Malaysia (F. S. P. Ng, pers. comm., 1981).

AERIAL ROOTS

Members of at least seven genera of Rhizophoraceae characteristically form aerial stilt roots, which have been described in greatest detail for the mangrove taxa (Troll, 1943). The genus *Rhizophora* ("root-bearer") is justly famous for its remarkable stilt roots (Fig. 1), the development, anatomy, and function of which were not understood until recently (Gill & Tomlinson, 1971, 1977; Scholander et al., 1955). *Ceriops tagal* and species of *Bruguiera* also form stilt roots on the hypocotyl and base of the trunk, which coalesce to form the fluted, conical trunk base that is seen in older plants (Fig. 2).

Among the inland genera, *Gynotroches* and *Crossostylis* (Gynotrocheae) normally form thick stilt roots on the lower trunk; *Crossostylis grandiflora* is known as "palétuvier de montagne" in New Caledonia for this reason (Fig. 3). At least one species of *Carallia*, *C. brachiata*, forms abundant stilt roots in peat swamps (Ding Hou, 1958). Thus, prominent aerial roots occur in three of the four genera of Gynotrocheae, the inland tribe that is probably most closely related to the mangroves. Although aerial roots in Rhizophoraceae may be formed more abundantly in swamps (e.g., in *Gynotroches*), they are not limited to plants found in that habitat; *Crossostylis grandiflora* is characteristically found in hilly sites. It may well be the humidity of the air rather than the inundation of the soil that is a factor in the development of aerial roots in inland taxa.

Another root character that is not often considered in systematic analyses is the presence of root hairs. These are formed on roots of *Cassipourea* seedlings but are not found in any of the members of the Gynotrocheae or Rhizophoreae that we have studied. Absence of root hairs from Rhizophoreae



FIGURES 3–6. *Stilt roots and vegetative bud morphology of inland Rhizophoraceae.—3. Stilt roots of* Crossostylis grandiflora, *one of at least three inland genera in which they occur (New Caledonia).—4. Transverse section of branch tip of* Cassipourea elliptica, *showing decussate phyllotaxy and valvate stipules.—5. Transverse*

may have a simple functional explanation if, as suggested by Tomlinson (1986), the endodermis is the site of the salt excluding mechanism, rendering an elaborated root surface unnecessary. Consequently, the root surface instead is elaborated by production of capillary rootlets (Attims & Cremer, 1967). This does not account for the absence of root hairs from Gynotrocheae, however.

Only one genus of Anisophylleaceae is known to possess any kind of aerial roots. *Combretocarpus* sometimes produces unique, diminutive (1–4 cm), negatively geotropic aerial roots on the trunk, usually 1–2 m above the soil (or water) level. However singular these may be, they bear no resemblance to the stilt roots of Rhizophoraceae, neither in development nor in mature anatomy and morphology, and cannot be considered a synapomorphy between the two families.

WOOD ANATOMY

A more detailed consideration of the wood anatomy of Rhizophoraceae and Anisophylleaceae appears elsewhere (Keating & Randrianasolo, this volume), but several specific points merit brief mention here. Indisputably, wood anatomical character states are very variable within Rhizophoraceae (Marco, 1935; van Vliet, 1976); however, we deem it poor systematic practice to use this variability as license to draw a relationship between the woods of these two families without any consideration of adaptive significance of wood structure. A number of significant differences could be discussed, but we wish to cite only a few. All Anisophylleaceae have alternate intervessel pitting with coalescent apertures, which are not found in any Rhizophoraceae. A limited amount of alternate pitting occurs in some species of *Carallia*, clearly as a specialization that has arisen within that genus and is thus not relevant to interfamilial relationships. The narrow vessels and scalariform perforation plates of Rhizophoreae are distinctive and related to the low negative pressures induced by the saline environment, as discussed in Tomlinson (1986).

At the request of P. Baas, E. Wheeler (pers. comm.) compared wood anatomical characteristics of Anisophylleaceae with those of the Gynotrocheae and her computerized data base of 5,000 species. Although the character set was not specified and clearly did not include coalescent apertures, absent from Rhizophoraceae (van Vliet, 1976), the coded characters of woods of Anisophylleaceae match those of at least some species of *Carallia* and, to a lesser extent, *Gynotroches* and *Crossostylis*. Significantly, woods of Anisophylleaceae are similar neither to those of the mangrove genera nor, more importantly, to those of any Macarisieae. Therefore, if the wood anatomical similarities between Anisophylleaceae and *Carallia* were taken as synapomorphies, it would then be necessary to include the Anisophylleaceae as a subtribe of Gynotrocheae (see Fig. 27), which in turn requires us to hypothesize parallel reversals in at least 20 (probably closer to 50) vegetative, chemical, embryological, floral, fruit, seed, embryo, and seedling characters (see Table 1 and Dahlgren, this volume). As this is both extremely unparsimonious and biologically completely implausible, we conclude that the similarities in wood anatomy represent homoplasies and are not systematically significant in this case.

PHYLLOTAXY AND NODAL ANATOMY

Phyllotaxis is the one systematic difference between Rhizophoraceae and Anisophylleaceae that seems to be widely known: Rhizophoraceae have opposite leaves with interpetiolar stipules, whereas most Anisophylleaceae have alternate, exstipulate leaves. Certain additional details may ultimately prove helpful in understanding infrafamilial systematics.

In all Rhizophoraceae, the interpetiolar stipules bear colleters that secrete gummy substances onto the buds. In *Rhizophora stylosa*, this secretion contains galactose (Primack & Tomlinson, 1978), but whether its primary function is to deter herbivory (either through direct toxicity to insects or by attracting insectivorous birds) or merely to lubricate the expanding leaves while protecting them from desiccation is uncertain.

There are tribal distinctions in bud morphology within Rhizophoraceae. In *Cassipourea*, the stipules are valvate and pubescent (in addition to bearing colleters), and the leaves are truly decussate, that is, successive pairs of leaf primordia are initiated at exact right angles to one another (Fig. 4). Some reorientation of the leaves may occur during and after expansion. However, the usual descrip-

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section of branch tip of Carallia borneensis, *showing imbricate stipules and bijugate phyllotaxy (successive pairs of primordia not perpendicular).—6. Extrastipular glands of* Carallia borneensis. *C, colleter; G, gland; L, leaf primordium; Sp, stipule; T, unicellular trichomes.*


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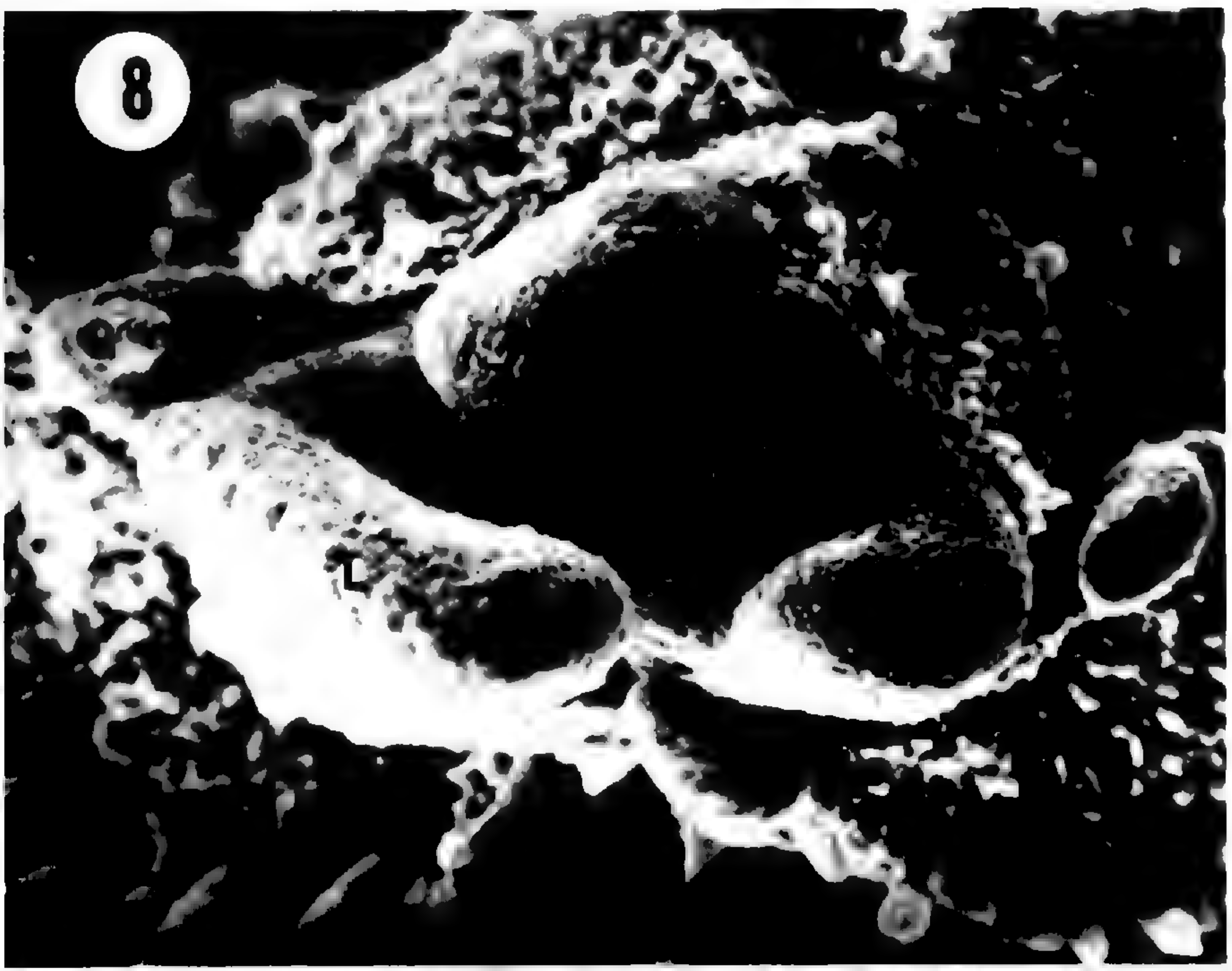
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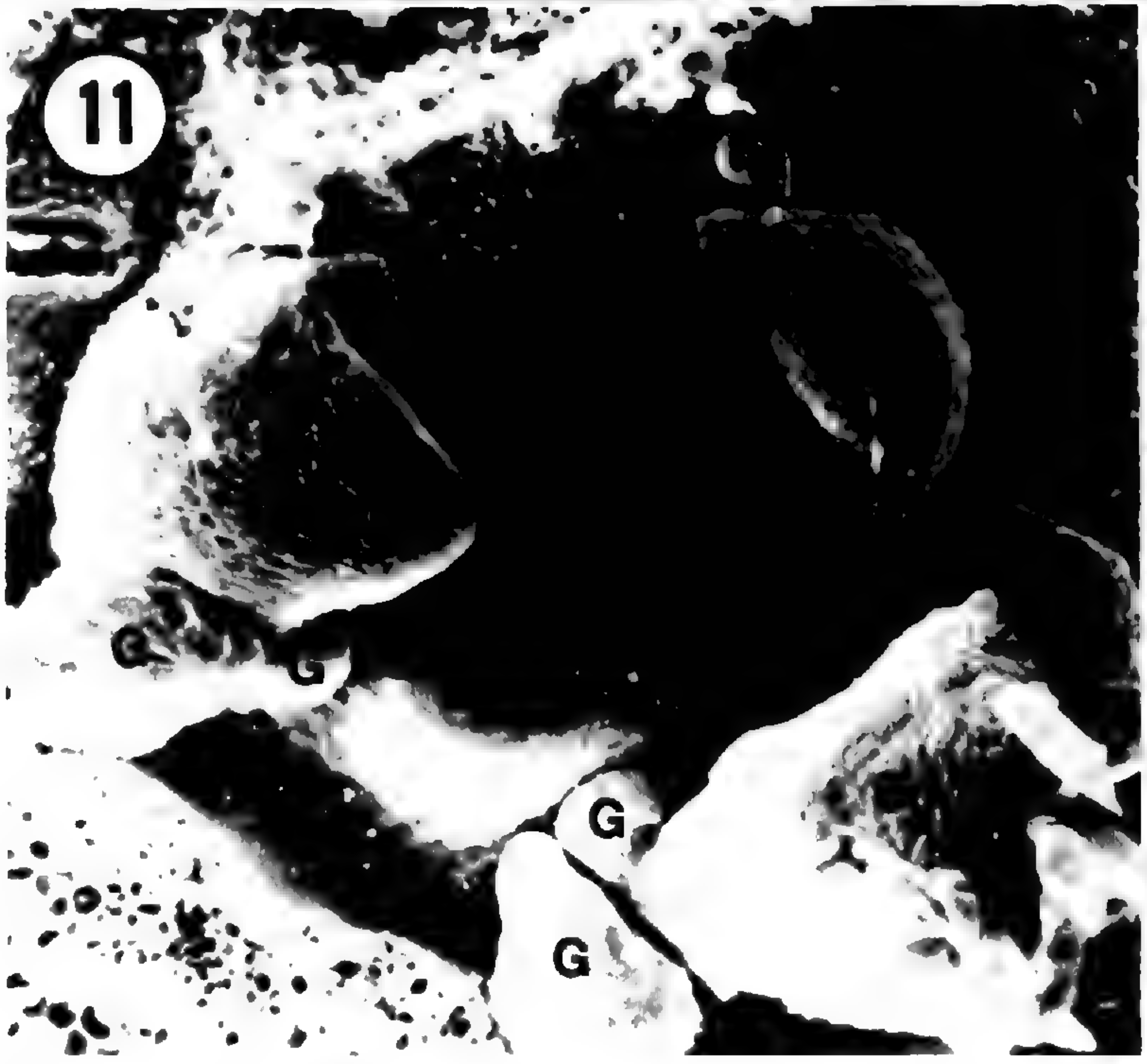
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tion of phyllotaxis in all Rhizophoraceae as decussate holds only for the tribe Macarisieae and for *Pellacalyx* (Gynotrocheae). Tomlinson & Wheat (1979) showed that phyllotaxis in all genera of Rhizophoreae is actually bijugate, with successive leaf pairs offset by angles of 70°–80°. Except for *Pellacalyx*, which has many autapomorphic features, all genera of Gynotrocheae also have bijugate phyllotaxy (Fig. 5). At least several species of *Carallia* bear extrastipular glands in addition to the colleters (Fig. 6). Interestingly, all genera with bijugate phyllotaxy have imbricate stipules, whereas those with decussate leaves have valvate stipules.

As discussed in greater detail later, overall tree architecture in Rhizophoraceae is variable, to some extent in relation to habitat differences. However, the basic architectural character of systematic interest is that the trunk and branches are only minimally or not at all differentiated; plagiotropic axes may be lacking altogether.

Anisophylleaceae are universally characterized as having alternate, exstipulate leaves, but at least one species of *Anisophyllea*, *A. disticha*, has structures interpretable either as minute stipules or large glands (Figs. 8, 11). The phyllotaxy of plagiotropic branches of this genus is unique among angiosperms: there are four orthostichies of leaves, two of reduced leaves on the upper side, and two of full-sized leaves along the lower side (Figs. 7–9). Orthotropic axes, in contrast, bear helically arranged reduced leaves in a conventional 2/5 helix (Figs. 10–12; Vincent & Tomlinson, 1983); thus, differentiation of axes is pronounced, at least in this genus.

Based primarily on study of herbarium material, Ding Hou (1958) stated that anisophylly of this kind is characteristic of only two species of *Anisophyllea*. However, our fieldwork shows that anisophylly is also the rule in plagiotropic axes of at least *A. cinnamomoides*, *A. ferruginea*, *A. griffithii*, and *A.*, sp. nov. Ding Hou (1958), but that the reduced leaves in these species are sometimes very small and caducous and hence are rarely seen in herbarium specimens. (Their scars, ordinarily lacking axillary buds, can often be detected.) It thus seems likely that both anisophylly and the unique tetrastichous phyllotaxy are uniform for Asian species of the genus. *Anisophyllea cinnamomoides*, which forms a moderate-sized tree, has the same architecture as a sapling that has been described in detail for adult *A. disticha* (Vincent & Tomlinson, 1983). Consequently, one may interpret the latter species as a permanently juvenile form. Herbarium study of virtually all other described species of the genus revealed that anisophylly occurs in all but a group of two or three closely related species (Juncosa, pers. obs.), a conclusion corroborated by the field studies of Floret (pers. comm.). He additionally communicated that in at least one rhizomatous shrubby species of a habitat subject to both severe seasonal drought and periodic fires, axis differentiation is seasonal rather than architectural.

Our knowledge of phyllotaxy and architecture in other genera of Anisophylleaceae is even poorer than in *Anisophyllea*; no reference mentions anisophylly in the other three genera. It does occur in *Poga* and *Polygonanthus*, although the strict alternation of leaf types seen in *Anisophyllea* is not preserved in all parts of the axes of *Polygonanthus*: several small leaves occur in succession at the bases of some branches, but these reduced leaves may be lacking distally (Juncosa, pers. obs.).

A more detailed discussion of leaf anatomy appears elsewhere in this volume, but a few characters bear mention here. It is not generally understood that in most inland Rhizophoraceae, juvenile and usually also the adult leaves are variously toothed or crenate, not entire as is usually stated. Only in Rhizophoreae are the leaves consistently entire, one of many characters in which derived states (within the family) are exhibited by the specialized mangrove genera. Other leaf characteristics of this tribe, such as the succulent hypodermal layer, terminal tracheids, and frequently abundant sclereids, are probably all adaptations to the mangrove hab-

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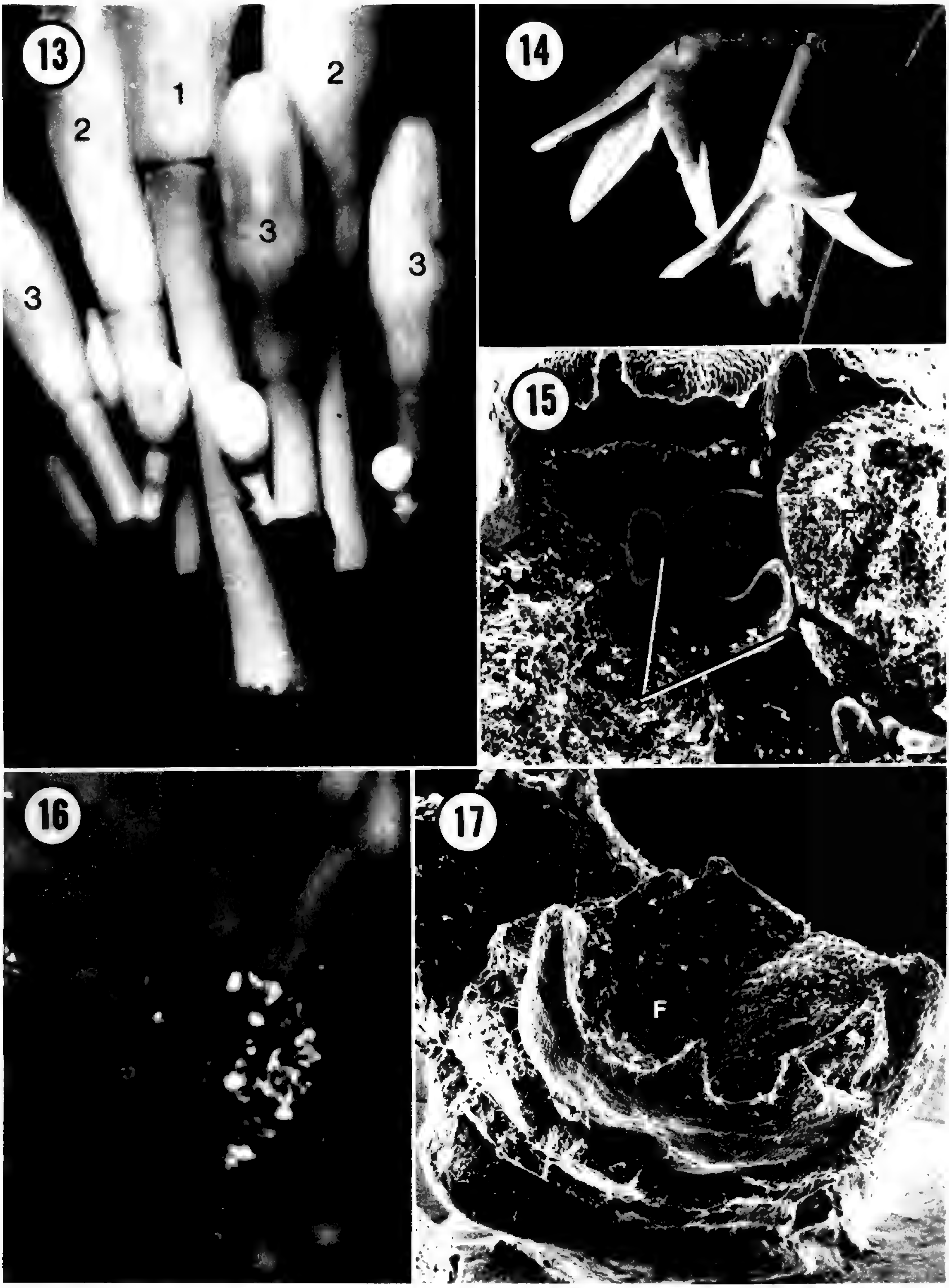
FIGURES 7–12. *Habit and development of axes of* Anisophyllea disticha.—*7. Plagiotropic branch of large-leaved Sarawak variety of* A. disticha. *Both ranks of scale leaves (arrows) are on upper side of branch.*—*8. SEM of apex of plagiotropic branch. Nonvascularized "glands" are of uncertain homology, although they do occur in stipular sites. (Micrograph courtesy of Nancy Dengler.)*—*9. Transverse section of plagiotropic branch tip at level of shoot apex. Scales leaves (Sc) have rather empty (vacuolate) cells; foliage leaves (L) have densely staining (meristematic) mesophyll.*—*10. Top of plant of* A. disticha *(photographed in Brunei), showing pseudowhorls of plagiotropic branches and orthotropic axis bearing only scale leaves (arrows).*—*11. SEM of apex of orthotropic axis. All leaf primordia are of scale leaves. "Glands" are very evident at stipular sites. (Micrograph courtesy of Nancy Dengler.)*—*12. Transverse section of orthotropic axis at level of shoot apex; leaves are arranged in a normal phyllotactic spiral.*



FIGURES 13–17. *Inflorescence morphology of Rhizophoraceae.—13. Open-branched cymose inflorescence of* Bruguiera parviflora *(Malaysia). Order of maturation of flowers is indicated by numbers. First branching event is dichasial, others generally monochasial.—14. Bifurcate inflorescence of* Rhizophora mangle *(Florida). In other species, up to 32 flowers occur in evenly bifurcating inflorescences.—15. SEM of developing inflorescence of* R. mangle, *showing aborted bracteole and terminal floral apex (bracket) between the sites where maturing flowers were removed (F).—16. Fasciculate inflorescence of* Gynotroches sp. *(Sarawak).—17. SEM of ultimate inflorescence branch of* Pellacalyx cristatus. *Opposite bractlets are fused into a toothed cup; terminal flower has been removed (site marked F). Axillary branch (A) is enclosed by fused prophyllar bractlets.*

itat. An achlorophyllous hypodermal layer is also found in at least three genera of Gynotrocheae, but not in *Cassipourea* (Macarisieae), so that character may be of phylogenetic significance as well.

Nodal anatomy also seems to distinguish the two families, as the Rhizophoraceae are characterized by multilacunar nodes with split-lateral traces (Howard, 1970, 1979), whereas Anisophylleaceae have unilacunar nodes (*Anisophyllea*: Geh & Keng, 1974; Vincent & Tomlinson, 1983; *Combretocarpus*: Juncosa, unpubl. obs.).

INFLORESCENCE

The inflorescence in Rhizophoraceae is fundamentally cymose, both in open-branched and fasciculate forms. Flowers of large-flowered species of *Bruguiera* are solitary, presumably by reduction. The first branching event is dichasial (sometimes trichasial in *Ceriops* and in *Carallia brachiata*); subsequently, branching is usually monochasial (Fig. 13). In *Rhizophora*, *Kandelia*, and *Crossostylis*, inflorescences bifurcate throughout (Fig. 14), but the division appears to be pseudodichotomous. Although the apices terminating the sympodial units do not develop into flowers in these genera, their vestiges can often be found (Fig. 15). Interestingly, both open-branching and fasciculate forms (in which the branch internodes do not elongate; Fig. 16) are found in all three tribes. It therefore appears that condensation of the inflorescence evolved in parallel three times. A single bract subtends each branch, thus there is a pair of bracts at each node, even when further development of one of the two branches is suppressed in the monochasial portions of the inflorescence. Pairs of bracteoles also subtend each flower. The bracteoles bear colleters similar in distribution, development, and mature anatomy to those of the stipules and secrete a sticky, rubbery coating over the floral primordia. In *Pellacalyx*, the pairs of bracts are fused into a toothed cup-shaped structure superficially resembling an epicalyx, but subtending minute axillary buds in addition to the terminal flower (Fig. 17).

Inflorescences in the Anisophylleaceae are paniculate or racemose and usually somewhat open-branched. A single bract subtends each branch and flower. In *Anisophyllea disticha*, male and female flowers occur in separate inflorescences, but in most other species and genera in the family, the two floral types are mixed in all inflorescences. Thus, although the differences are to some extent an extension of the phyllotactic differences of the vegetative shoots, there is no inflorescence character state common to both Rhizophoraceae and Anisophylleaceae.

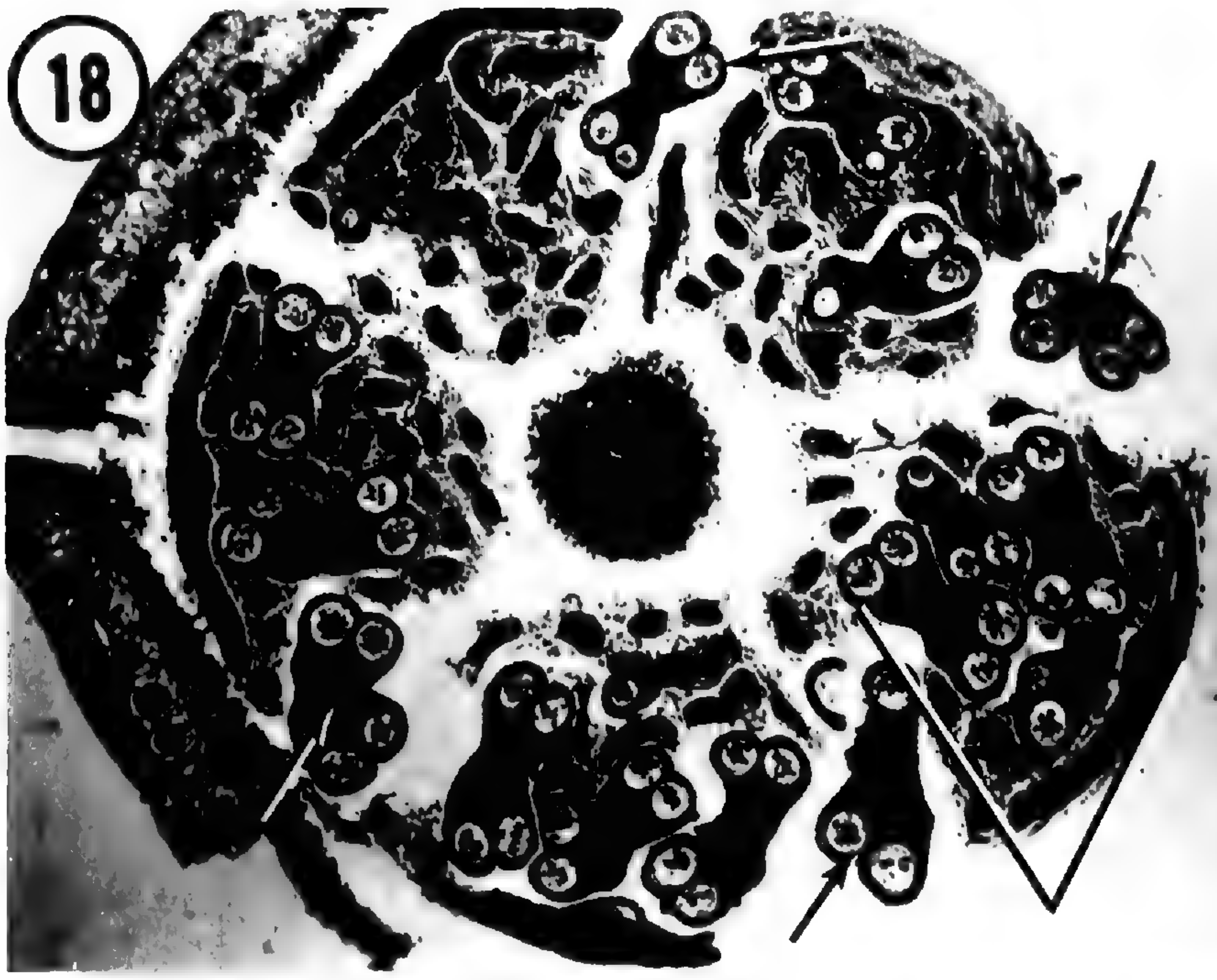
FLORAL MORPHOLOGY AND DEVELOPMENT

In most Rhizophoraceae the flowers are bisexual, but exceptions are found in both inland tribes. *Gynotroches* (Gynotrocheae) is dioecious; in male flowers, the ovary and ovules develop and at least the early stages of megagametogenesis occur, but the style atrophies distally instead of elongating. In female flowers, anthers and sporogenous tissue develop, but normal microsporogenesis seems to be interrupted shortly after meiosis. At least some species of *Crossostylis* (Gynotrocheae) are polygamodioecious, with many individuals bearing only functionally female flowers (Smith, 1981). Among the Macarisieae, *Blepharistemma* and *Sterigmapetalum* are reported to be polygamodioecious and dioecious, respectively, but developmental details are lacking.

Although mature floral structures in Rhizophoraceae are remarkably diverse, especially in relation to contrasted pollination mechanisms (Juncosa & Tomlinson, 1987), early developmental stages are generally very similar. Floral characters that unify the family include petal development and mature morphology, the generally diplostemonous androecium, and the presence of laticifers.

These generalizations are based upon study of nine of the fourteen genera of the family, including all genera of tribes Gynotrocheae and Rhizophoreae and one of Macarisieae (*Cassipourea*). Inasmuch as the mature morphology of flowers of Macarisieae varies very little, especially in comparison with that of genera of the other two tribes, this survey may be taken as encompassing nearly all aspects of floral evolution in the family.

Petals in rhizophoraceous taxa are fundamentally bifid, with a prominent terminal arista, and they enclose groups of one or more stamens individually, rather than forming a whorl that collectively surrounds the androecium as a whole (Fig. 18). This distinctive petal vernation is to our knowledge found in only one other family of dicotyledons, Rhamnaceae. Usually, several to many filamentous appendages develop on the distal margins of the two main lobes of the petal (Fig. 19). Mature petals of *Crossostylis* appear to lack appendages, but this results from the suppression of development of appendages that are initiated in exactly the same mode and position as in other genera. This may also be the case in *Anopyxis*, which is described as having entire petals. Only in *Rhizophora*, the most specialized genus in the family, are the marginal petal appendages truly absent, even though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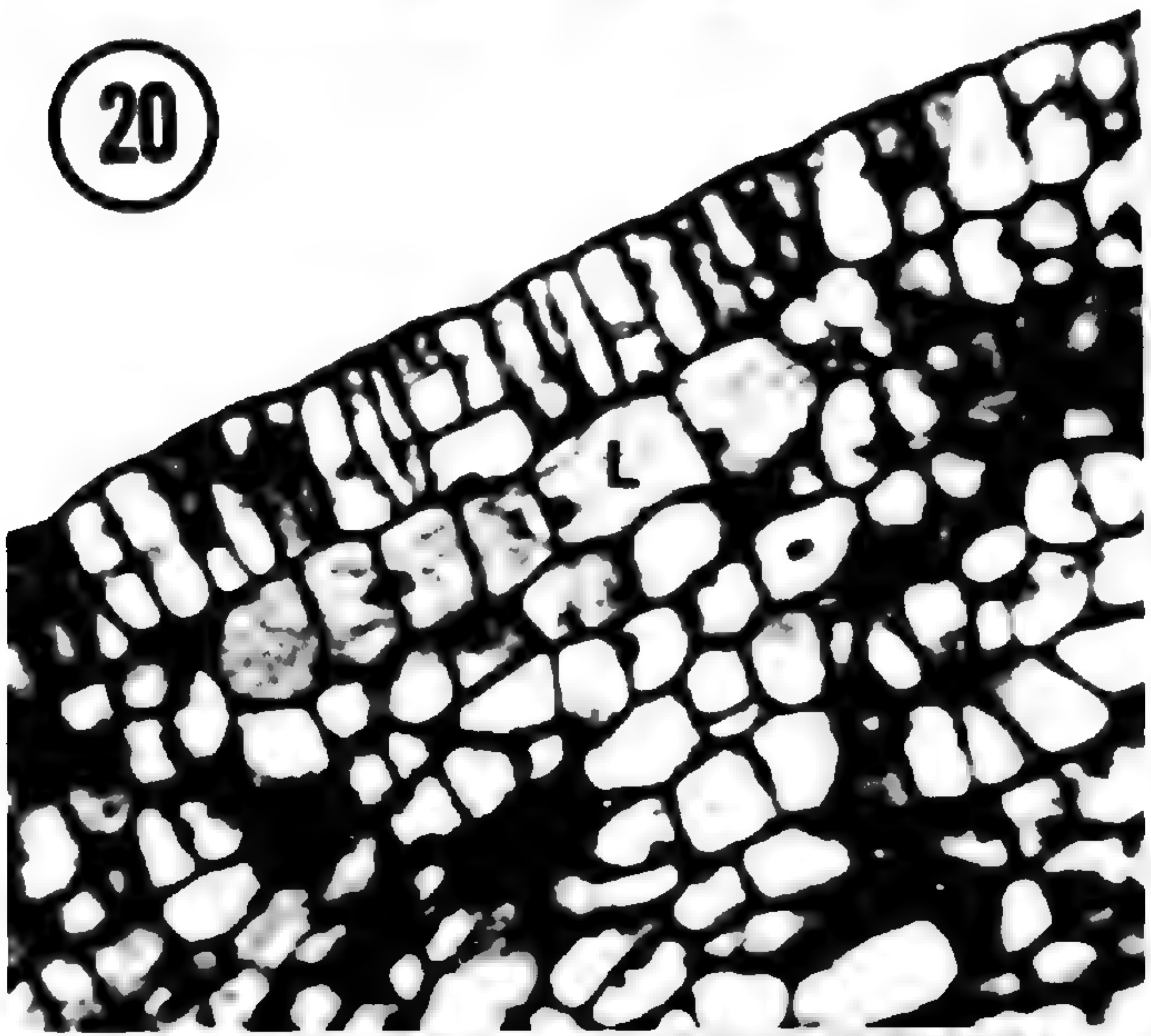
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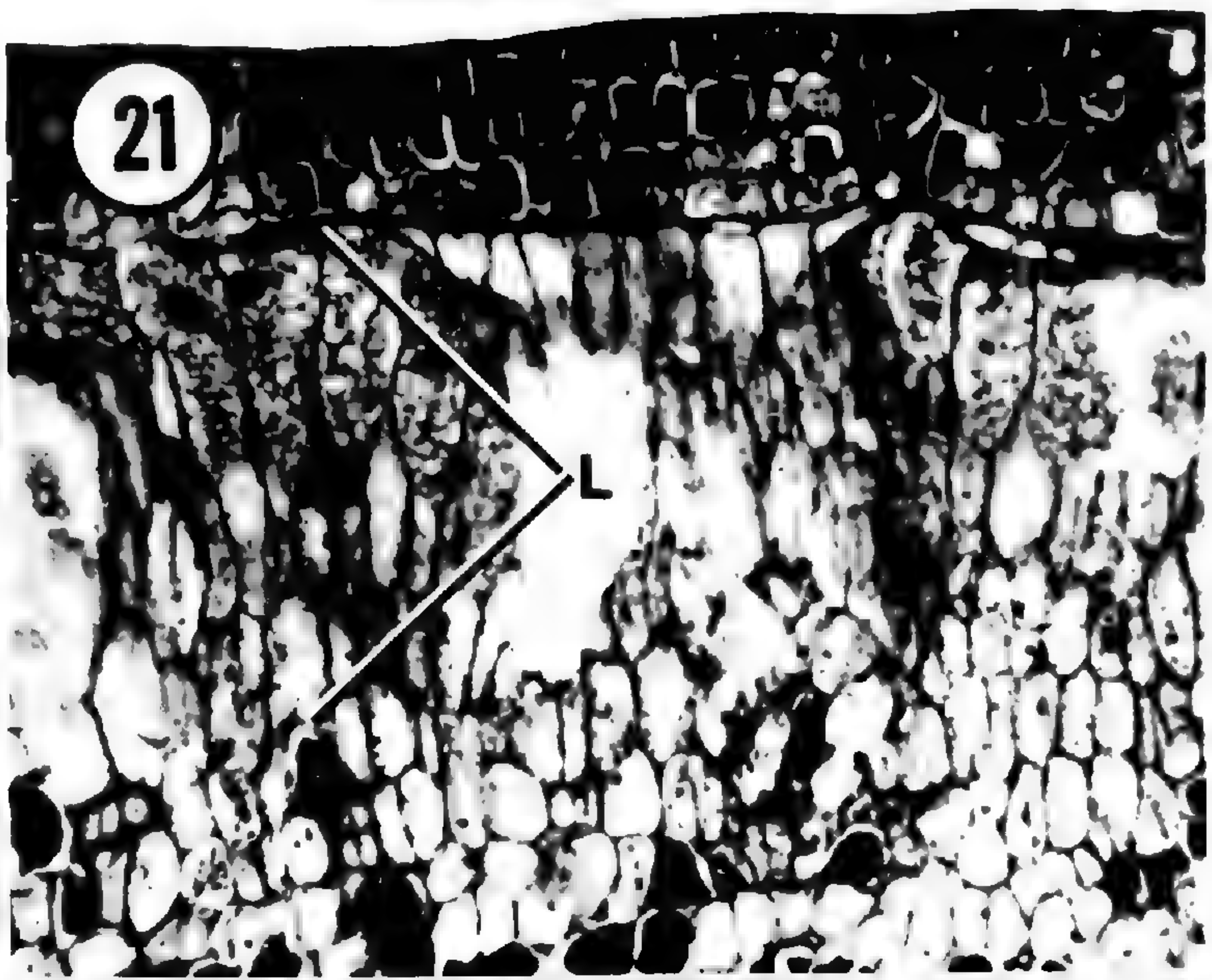
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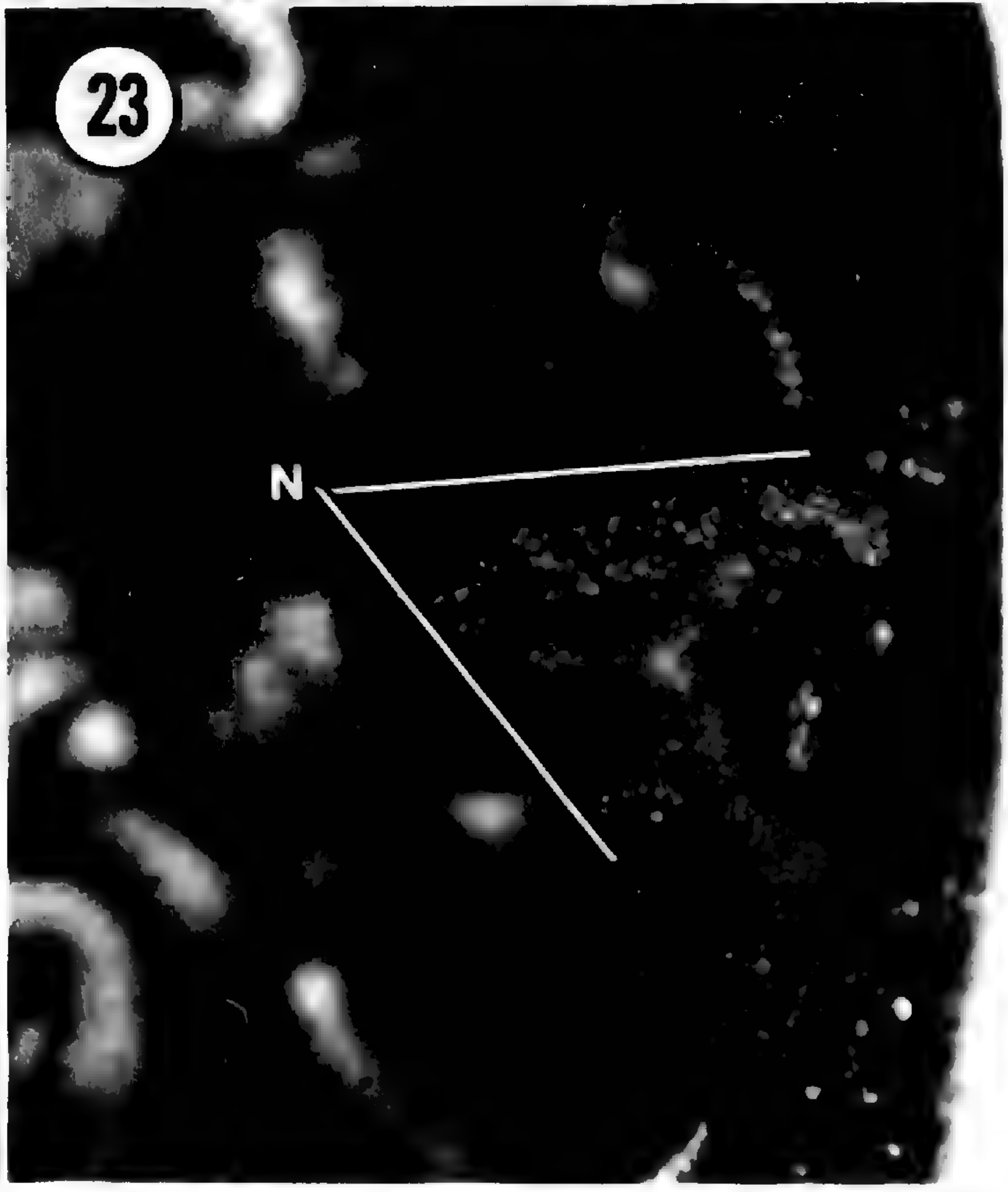
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petals still bear a terminal arista and enclose individual stamens. Although fringed petals are found in a number of other families, including Anisophylleaceae, their mature morphology and probably also early development do not resemble those of petals of Rhizophoraceae.

Another distinctive characteristic of rhizophoraceous flowers is the presence of a layer of laticiferous cells in the ovary and calyx. These cells may form a more or less continuous layer (*Cassipourea* and Rhizophoreae; Fig. 20) or may grow radially, usually dividing periclinally (*Crossostylis* and *Carallia*; Fig. 21). In *Gynotroches* and *Pellacalyx*, the laticifers are further modified into disconnected canals or idioblastic cells. In most genera, the epidermis surrounding the laticiferous layer divides periclinally, becoming 5–7-seriate.

The androecium in most Rhizophoraceae is diplostemonous, and the antisepalous whorl of stamens is ordinarily initiated earlier than the antipetalous whorl. Nearly all Macarisieae and at least one genus in each of the other two tribes exhibit this basic floral pattern, which we believe to be ancestral for the family. However, significant modifications have arisen in parallel in all three tribes. For example, in *Carallia* and *Pellacalyx* (Gynotrocheae), the antipetalous stamens are initiated earlier than the antisepalous stamens (Juncosa, in press). Also, one genus in each of the three tribes has polyandrous flowers, probably a homoplasy (see Fig. 27). This indirect conclusion, based upon the likely cladistic relationship of the genera, is also supported by the diversity of developmental pathways that give rise to the numerous stamens in these three genera. In *Kandelia*, the polyandrous mangrove genus, the supernumerary stamens result from the initiation of about five stamens on a large common primordium that also produces a petal (Juncosa & Tomlinson, 1987). In the distantly related inland genus *Cassipourea* (Macarisieae), additional stamens are not initiated together with the petals, but the vasculature of each petal is closely associated with that of several nearby stamens. In several species of *Crossostylis*, the groups of stamens are found opposite the sepals instead of the petals (Smith, 1981).

All Rhizophoraceae have a single style and stigma, although in *Gynotroches* the stigmatic lobes may be rather long. The separate stigmatic lobes may be discernable at gynoecial initiation (e.g., *Gynotroches, Pellacalyx*), or the gynoecium may arise as a single toroidal primordium (e.g., *Carallia, Bruguiera*). Most Macarisieae have fully superior ovaries, but two genera of this tribe and most other genera in the family have half-inferior or completely inferior ovaries. Details of the development and vasculature of the ovary appear in Juncosa (in press). The occurrence of a superior ovary in female flowers of *Gynotroches* is probably a reversion from the half-inferior condition, which occurs in the functionally male flowers of the same genus. (As detailed above, unisexuality occurs in this genus by very late-developmental changes; the basic morphology of the two kinds of flowers is quite similar.) Additional support for this hypothesis comes from the diversity of placentation types in *Gynotroches* (Ding Hou, 1958); placentation in all other genera of Rhizophoraceae is invariably apical-axile.

Rhizophoraceae typically have 3–5 carpels (whether the locules are completely separate or not) and only two ovules per carpel, but an increase in the total number of ovules and seeds has evolved in several ways. In *Crossostylis*, this is achieved by multiplication in the number of carpels, up to as many as 20. In *Gynotroches* there are only five carpels, but each contains up to eight ovules. In *Pellacalyx* both the number of carpels and the number of ovules in each is increased.

The presence of a floral disc is often used as a systematic character, but an imprecise understanding of the initiation and development of this organ

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FIGURES 18–23. *Floral morphology and anatomy of Rhizophoraceae and* Anisophyllea.—*18. Transverse section of flower bud of* Cassipourea elliptica; *a petal, largely represented by its filamentous appendages, and the small group of stamens that it encloses are indicated by a bracket. Note that antisepalous stamens are not enclosed by petals but stand between their lateral abaxial sides (arrows).—19. SEM of petal of* Pellacalyx cristatus *at an early developmental stage, showing filamentous appendages (Ap) and terminal arista (Ar).—20. Continuous uniseriate laticifer of* Bruguiera exaristata *at an early stage of development. Periclinal divisions are beginning in the epidermis, which will become 5–7-seriate, but laticifer cells seem only to expand somewhat periclinally, not to divide.—21. Longitudinal section of flower of* Crossostylis biflora, *showing anticlinally expanded laticiferous cells (L); these seem also to divide periclinally, but this is difficult to establish.—22. Medial longitudinal section of flower of* Carallia borneensis, *showing that the putative nectary (N) is strictly intrastaminal. St, stamen; P, petal.—23. Epi-illumination light micrograph of crenate nectary (N) of* Anisophyllea obtusifolia. *Divisions extend to the base of the nectary. (Material courtesy of Hiroshi Tobe.)*

may have led to considerable confusion and misinterpretation in the study of angiosperm phylogeny. In Rhizophoraceae, a nectarial ring arises inside the androecium late in floral development (Juncosa & Tomlinson, 1987). Thus, the stamens are not inserted on this ring, nor is it part of the androecium (Fig. 22). This important distinction is clearly illustrated by the genus *Bruguiera*, in which the androecium is initiated as a toroidal primordium, upon which separate stamen primordia later develop. Later, a separate toroidal primordium is initiated internally (centripetally) to the androecium and ultimately develops into the nectary. Some significant modifications to this basic pattern occur in certain inland genera in tribe Gynotrocheae, but the oft-cited character state "stamens inserted on a disc" is certainly incorrect for nearly all Rhizophoraceae.

Unfortunately, detailed information on development of flowers of Anisophylleaceae is not available, but descriptions of their mature morphology (Ding Hou, 1958; Tobe & Raven, 1987b) reveal several major differences from Rhizophoraceae. Petals of several genera of Anisophylleaceae are fringed (*Poga*, *Anisophyllea*) or weakly divided (*Combretocarpus*), but the distinctive morphology described above for Rhizophoraceae does not occur here. In particular, the prominent terminal arista is absent, and even in the few cases where the petals are bifid (some species of *Anisophyllea*), they do not individually enclose one or more stamens. Other floral differences are seen in gynoecial morphology. The several styles are separate all the way to their bases in all Anisophylleaceae. The inferior ovary is evidently ancestral for the family (not superior, as in Rhizophoraceae). The morphology of the nectary in Anisophylleaceae is unusual. The mature nectary is both inter- and intrastaminal and is cleft to its base in many places (Fig. 23). Information on its development is lacking, but it is safe to speculate that it is likely to be very different from that of nectaries of Rhizophoraceae.

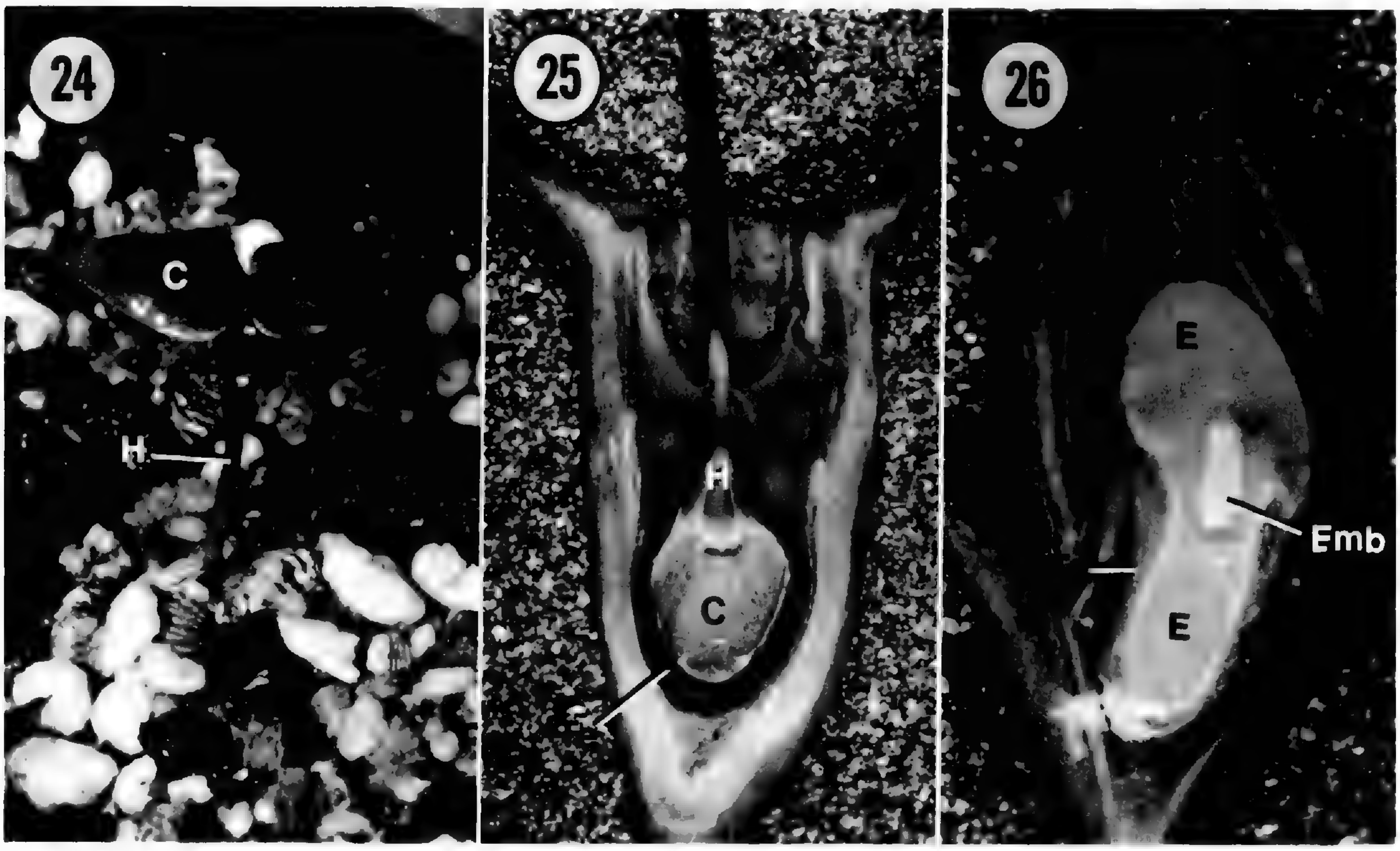
FRUIT AND SEED

Within the Rhizophoraceae, a clear evolutionary trend can be seen in fruit structure. All Macarisieae have capsular fruits, although these vary in their degree of sclerification and in how readily they dehisce. The tough-fleshy capsules of *Cassipourea elliptica* (Sw.) Poir., for example, often (always?) drop from the trees unopened, dehiscing on the ground as they dry slightly; the arillate seeds are then carried off in great numbers by leaf-cutter ants. Field observation on the Osa Peninsula of Costa Rica revealed that the ants carry the seeds into the nest, remove the arils, and discard the stripped seeds (Juncosa, pers. obs.). This may seem an unadaptive destination, but Prance (pers. comm.) correctly pointed out that the dispersal function is satisfied by those seeds dropped along the way by accident or as a result of such common disturbances as rain showers. In *Cassipourea*, presence of the aril does not inhibit germination. The comparatively large (3.5 cm), woody capsules of *Anopyxis* have been described as indehiscent, but we imagine that the description was based on immature fruits; it seems overwhelmingly likely that a canopy tree with winged seeds would also have dehiscent fruits. Consideration of the probable cladistic relationship of genera yields the interesting conclusion that some or all of the arillate-seeded genera were derived from winged-seeded ancestors. The homology of wing and aril is established by Tobe & Raven (this volume) on the basis of comparative morphology of mature seeds; these authors consider the aril to represent the ancestral condition, primarily because of its strong correlation with a superior ovary. Fruits of *Crossostylis* (Gynotrocheae) are also capsular, often only partly dehiscent, the small seeds falling out through the slots.

Fruits of all Gynotrocheae other than *Crossostylis* and those of all Rhizophoreae are baccate, and the seeds are naked. In *Gynotroches* and *Pellacalyx*, the many small seeds are embedded in a nearly homogeneous juicy berry. In *Carallia* and in Rhizophoreae, a distinctive loose spongy region develops below the ovules, allowing for the rapid early expansion of the seed(s). In *Ceriops*, *Kandelia*, and *Rhizophora* the superior portion of the ovary develops greatly in fruit.

The seed coats of all Macarisieae and most Gynotrocheae are characterized by a sclerified exotegmen (Corner, 1976; Juncosa, 1984a and unpubl.; Tobe & Raven, 1987b), but this structure is absent from seeds of *Carallia* and the Rhizophoreae. That this absence probably represents an evolutionary loss is supported by developmental evidence: the outer epidermis of the inner integument of *Carallia* ovules is histologically distinctive, as in other inland genera, but the cells fail to expand and sclerify.

Fruits of most Anisophylleaceae are drupaceous, unlike those of any Rhizophoraceae. The fruit of *Combretocarpus* is light and three-winged, so it is not surprising that the development of a heavily sclerified endocarp is suppressed. The seed coats of Anisophylleaceae lack a sclerified exotegmen and differ in other respects from those of Rhizo-



FIGURES 24–26. *Seedling germination in Rhizophoraceae.—24. Epigeal germination in* Cassipourea elliptica.—*25. Viviparous germination by growth of hypocotyl in* Bruguiera exaristata.—*26. Viviparous germination by expansion of endosperm in* Rhizophora mangle. *C, cotyledon; E, endosperm; Emb, embryo; H, hypocotyl; Te, testa or seed coat.*

phoraceae (Tobe & Raven, 1987a). Seeds of Anisophylleaceae also lack endosperm (Floret, 1979), which is present in all Rhizophoraceae.

EMBRYO AND GERMINATION

As far as is known, all inland Rhizophoraceae have epigeal germination and foliaceous cotyledons (Fig. 24) (*Cassipourea*: Juncosa, 1982a, b, 1984a; *Carallia, Pellacalyx,* and *Gynotroches*: Geh & Keng, 1974; Ng, 1980; Ng & Sanah, 1979; Ng, pers. comm.). Development of the embryo to a large seedling while still attached to the parent plant (vivipary) characterizes the Rhizophoreae and offers interesting material for comparative study. Germination morphology in these (mangrove) genera has been classified as "Durian-germination," in which the hypocotyl elongates, but the cotyledons remain hidden (Ng, 1978). Both outgroup comparison (with all inland Rhizophoraceae) and comparative developmental morphology indicate that this is a modification of ancestral epigeal germination.

Among the Rhizophoreae, cotyledonary morphology varies. *Bruguiera* species have two or three cotyledons, which are thick and fleshy and remain permanently within the seed coat throughout the viviparous seedling development. The development of these cotyledons and their median-plus-split-laterals vasculature reveals their foliaceous ancestry; they also subtend axillary buds (Juncosa, 1984b). In the more advanced Rhizophoreae, however, the cotyledons arise as a single toroidal primordium and form a solid cylindrical body, sometimes becoming 2–3-lobed distally; it is vascularized by many separate traces, evenly spaced. Vasculature of the cotyledonary body of *Kandelia* is intermediate between that of *Bruguiera* and that of *Ceriops* and *Rhizophora.*

In addition to being the only genus in the tribe with separate cotyledons, *Bruguiera* also exhibits the intermediate condition in the evolution of vivipary: the embryo grows to fill the seed completely, then germination occurs by elongation of the hypocotyl, much as in the nonviviparous inland genera (Fig. 25). Endosperm is not involved in viviparous germination. However, in *Ceriops, Kandelia* and *Rhizophora,* the micropyle is forced open by growth of the endosperm, which in *Rhizophora* may even carry the undifferentiated proembryo partially or entirely out of the seed (Fig. 26). In all genera, the cotyledonary body subsequently grows to fill the seed coat, with only a thin layer (usually one cell thick) of intervening endosperm. This persistent endosperm forms transfer cells (Juncosa, 1982a, b). A considerable amount

TABLE 1. *Summary comparison of Rhizophoraceae and Anisophylleaceae. Refer to text for important details and exceptions.*

	Rhizophoraceae (14 genera)	Anisophylleaceae (4 genera)
Growth	continuous	rhythmic
Branch differentiation	minimal	extreme
Wood	very heterogeneous	large vessels, alternate pitting with coalescent apertures
Aerial stilt roots	formed in Gynotrocheae and Rhizophoreae	not formed
Phyllotaxis	leaves opposite (bijugate or decussate)	leaves alternate (distichous or tetrastichous)
Stipules	present, interpetiolar	vestigial or absent
Leaf morphology	toothed margins in inland genera	entire margins
Nodal anatomy	tri- or multilacunar, split laterals	unilacunar
Inflorescences	cymose (dichasial changing to monochasial)	racemose (to paniculate)
Floral histology	subepidermal laticifers	no laticifers
Petals	bifid, fringed, with terminal aristata, convolute	sometimes fringed or divided, not folded
Ovary	superior to inferior	inferior
Fruit	capsular to baccate	drupaceous or winged
Seed coat	sclerified exotegmen in most inland genera	sclerified exotegmen absent
Seed	albuminous	exalbuminous
Cotyledons	laminar (modified in mangroves)	minute or absent
Germination	epigeal or viviparous	hypogeal
Sieve-tube plastids	Pv-type	S-type
Chromosome number	$n = 14, 18, 21, 32$	$n = 7, 8$

of endosperm emerges from the seed coat in all three genera. In *Rhizophora,* this endosperm merely forms a collar around the (intercalary) meristematic upper portion of the hypocotyl (Juncosa, 1982a), but in *Ceriops* and *Kandelia* it grows invasively into the ovary wall, forming an irregularly branched haustorium.

Embryo anatomy and germination in Anisophylleaceae differ sharply from that of any Rhizophoraceae. The embryo in Anisophylleaceae has a massive hypocotyl, with the cotyledons represented by minute scales (*Anisophyllea*) or even entirely absent, not even detectable under microscopic examination (*Poga*; Floret, 1979). Germination is hypogeal, with all of the morphological characteristics associated with that growth habit (e.g., earliest epicotyledonary leaves cataphylls, not foliaceous as in epigeal germination). In *Anisophyllea disticha,* shoots may arise from both ends of the seed (Geh & Keng, 1974). Regrettably, anatomical information is lacking.

CYTOLOGY

Chromosome numbers are often regarded as systematically important, but only a few genera of these two families have been counted. Rhizophoreae uniformly have $n = 18$ (Sidhu, 1968; Yoshioka et al., 1984). *Crossostylis* has $n = 14$ (Tobe & Raven, pers. comm.); *Anopyxis,* $n = 32$ (Mangenot & Mangenot, 1958). Counts of $n = 18$ and $n = 21$ have been reported in *Cassipourea* (Weiss, 1973; Juncosa, unpubl.); further data from this large genus are urgently needed. Chromosomes throughout Rhizophoraceae are extremely small, most of them being about 1 μm long.

Chromosome numbers in Anisophylleaceae have been counted only in sectioned material (Tobe & Raven, 1987a) but show quite different numbers ($n = 7, 8$), which have not yet been observed in Rhizophoraceae.

Other systematic characters that have recently proved revealing include sieve-tube plastids. Behnke (1982) found that Anisophylleaceae have S-type (starch-containing) plastids, whereas Rhizophoraceae have the rare PVc-type, in which crystalline protein inclusions are found. Further discussion of this and several important chemical characters appear in Dahlgren (this volume).

SYSTEMATIC CONCLUSIONS

A summary of the systematic characters of Anisophylleaceae and Rhizophoraceae (Table 1) re-

TABLE 2. *Characters used in cladistic analysis (Fig. 27). See text for full descriptions of many of the one-word character states.*

	Condition		
Character	Ancestral (00)	Derived (01/10)	More Derived (11)
1. Stilt roots	absent	present	
2. Root hairs	present	absent	
3. Phyllotaxy	decussate	bijugate	
4. Stipule vernation	valvate	imbricate	
5. Leaf margin	serrate	entire	
6. Hypodermis	absent	present	
7. Salt-tolerant?	no	yes	
8. Inflorescence	open-branched	fasciculate	
9. Terminal flower	present	absent	
10. Breeding system	hermaphroditic or monoecious	dioecious	
11. Floral laticifers	one layer	radially expanded	idioblastic[1]
12. Petal arista	as laterals	differentiated	
13. Lateral appendages	present	abort	never initiated
14. Petal orientation	reflexed	erect	
15. Androecium	diplostemonous	polyandrous	
16. Hypanthium[2]	absent	present	
17. Ovary position	superior	half-inferior	inferior
18. Locule formation	enclosure	schizogeny	
19. Carpels	5	3/many	2
20. Ovules per locule	2	5–8	
21. Receptacle	solid	spongy	
22. Exotegmen	present	vestigial	absent
23. Nucellus	crassinucellate	tenuinucellate	
24. Integument	not vascularized	vascularized	
25. Seed appendage	wing[3]	aril[3]	none
26. Seeds per fruit	several to many	1	
27. Fruit	dehiscent	baccate	
28. Cotyledons	separate	connate	
29. Cotyledonary node	unilacunar	trilacunar	multilacunar
30. Extra-ovular endosperm	absent	present	
31. Endosperm transfer cells	absent	present	
32. Viviparous?	no	yes	
33. Germination process	by hypocotyl	by endosperm expansion	
34. Seedling establishment	by radicle	by lateral roots	

Autapomorphy	Genus
35. Multimery	*Bruguiera*
36. Explosive pollination system[4]	*Bruguiera*
37. Cotyledonary axillary buds	*Bruguiera*
38. Coleorhiza	*Bruguiera*
39. Extrastipular glands	*Carallia*
40. Androecial appendages	*Crossostylis*
41. Stellate pubescence	*Pellacalyx*
42. Trichosclereids	*Rhizophora*
43. Anemophily	*Rhizophora*
44. Multilocellate anthers	*Rhizophora*
45. Abortion of first epicotyledonary leaves	*Rhizophora*

[1] The idioblastic laticifers or mucilage cells of *Gynotroches* and *Pellacalyx* are here interpreted as derived from the radially expanded ones of other Gynotrocheae. They may actually be instead a cell type *sui generis* within the family, but this has no effect whatever on the cladogram.

[2] Used here as a perianth/androecium character, independent of ovary position.

[3] Separate analyses were carried out with the aril as the ancestral condition, but the resulting trees were essentially topologically equivalent and equally (not more) parsimonious.

[4] Evolved independently in *Ceriops tagal*; not present in *C. decandra*.

veals virtually no points of agreement. The very few points of vegetative similarity are clearly homoplasies—for example, entire leaves in tribe Rhizophoreae and in Anisophylleaceae. The most frequently cited floral character state common to both families is fimbriate petals (e.g., Tobe & Raven, 1987a), but this also occurs in many dicotyledonous families and is even a diagnostic character of several of these (e.g., Cunoniaceae, Elaeocarpaceae). Moreover, as emphasized above, the petals of Rhizophoraceae have a unique pattern of development and mature morphology and vernation. The ancestral androecial condition in both Rhizophoraceae and Anisophylleaceae is diplostemonous, but this can hardly be regarded as a synapomorphy, as it is found in many other apopetalous dicotyledons. We feel that the overwhelming number of differences in all aspects of growth, anatomy, and reproductive cycle of Rhizophoraceae and Anisophylleaceae make it clear that these two families are not at all closely related. It is to be hoped that the data assembled in addressing this question will also aid in assigning them to their correct phylogenetic positions.

Although more information about the poorly known African genera of Macarisieae will be required before the family can be rigorously revised, a well-supported cladogram (Fig. 27) has been derived from analysis of the 45 characters listed in Table 2. Many other characters that we were unable to study in crucial taxa, or the coding of which could not be satisfactorily resolved, or whose states were unknown in as many as half of the genera, were not included in this preliminary analysis. For the sake of consistency, all anatomical character states noted were derived from our own observations. Computer analysis was carried out using the Phylogeny Inference Package (PHYLIP; Felsenstein, 1985); the PENNY branch-and-bound algorithm was utilized to ensure that all most parsimonious trees were found. Characters were weighted equally and all reversals were permitted. Primarily due to the paucity of characters distinguishing genera of Macarisieae, numerous alternative most-parsimonious trees were found, but all were essentially topologically equivalent and reflected only different placements of the clades and genera of this tribe. Specifying the ancestral condition of the seed appendage as arillate, as would be indicated by comparison with the hypothetical out-groups (Dahlgren, this volume), neither resolves this point nor results in a more parsimonious tree. We emphasize again that more characters from a variety of aspects of the plants are required in order to elucidate the relationships of the Macarisieae.

A complete character analysis and discussion of generic relationships will be presented elsewhere, but several comments are appropriate here. Tribe Gynotrocheae is clearly paraphyletic and is maintained here and in our synopsis (Juncosa & Tomlinson, this volume) merely for convenience. Despite the occurrence of arils in *Crossostylis*, a character traditionally given much weight, it is clear that this genus is much more closely related to other Gynotrocheae than it is to Macarisieae. It is also evident that *Carallia* is more closely allied to the mangroves than is any other inland genus. In fact, *C. borneensis* shares several additional characters with the mangroves (vascularized integument, frequently single-seeded fruits, complete disappearance of exotegmic cell layer, etc.) that we have conservatively regarded as homoplasies at present. If the extra-stipular glands, the only apomorphy distinguishing the genus, do not occur in all species, then the genus may have to be regarded as paraphyletic, with *C. borneensis* and possibly other species placed further up on the clade leading to Rhizophoreae.

It is instructive to note which characters are homoplastic in Rhizophoraceae. Polyandry occurs in *Kandelia*, *Crossostylis*, and in two subgenera of *Cassipourea*, all independent origins of this character. As described above, this is also reflected in the different modes of development of the additional stamens or, in the case of species of *Crossostylis* not yet studied developmentally, in the positions of those stamens. Condensation of inflorescences also arose at least three times, as did the suppression of later development of the lateral appendages of the petals; this is hardly surprising, considering the minor developmental changes that are involved. Traditionally, the number of carpels or locules and the position of the ovary have been regarded as systematically important, but it is clear that substantial changes in both of these characters have occurred within the Rhizophoraceae. However, the trend from a superior ovary to half-inferior to inferior is reversed only once, in the female flowers of *Gynotroches*. In these, a secondary expansion of the superior portion of the ovary occurs, accommodating the increased number of ovules. Male flowers of the genus also form an ovary and (slightly fewer) ovules, but the ovary is half-inferior. In our judgment, the agreement between the unbiased cladistic analysis and the developmental evidence strongly supports our systematic conclusions.

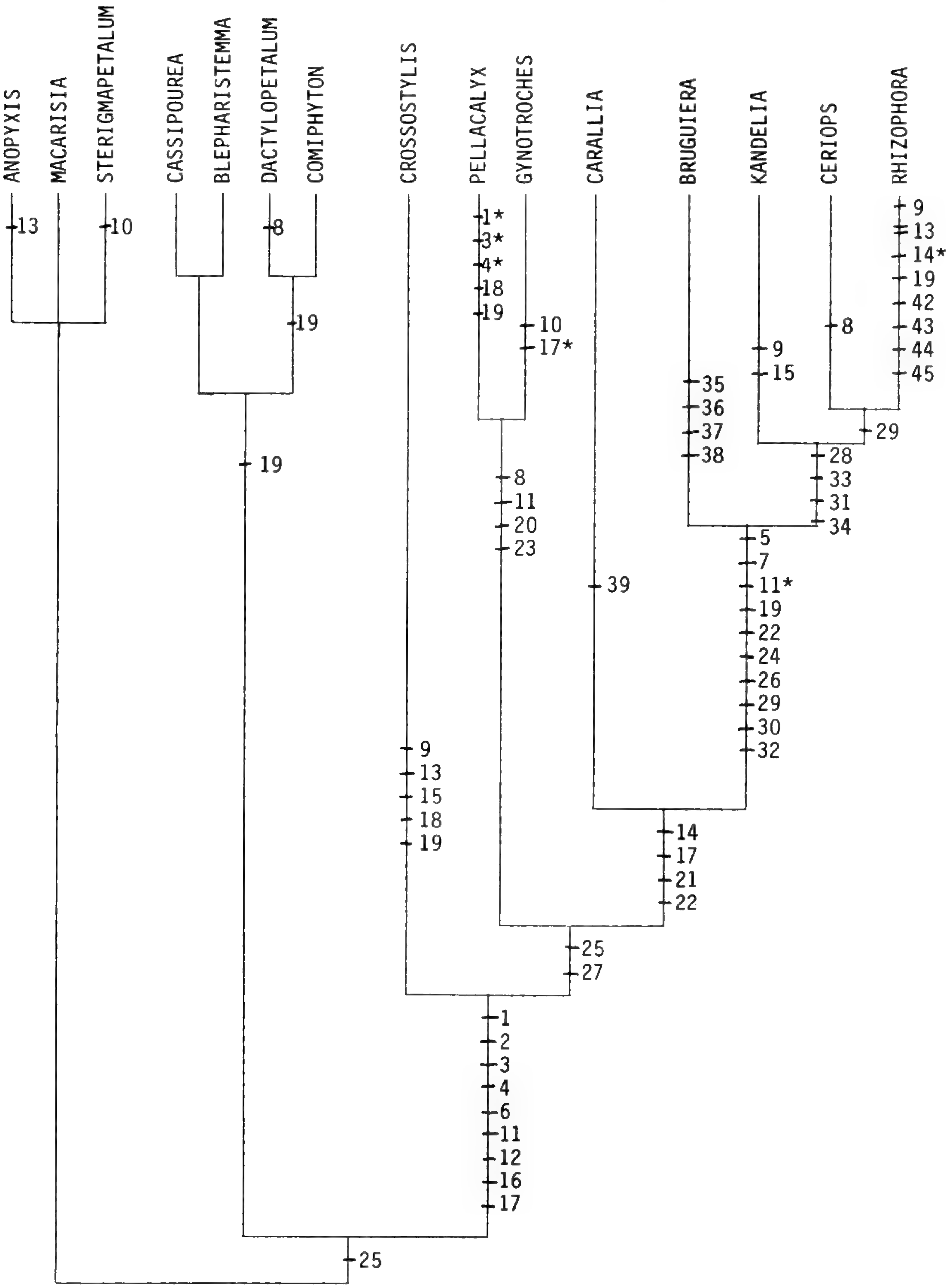


FIGURE 27. *Probable phylogenetic relationships of genera of Rhizophoraceae, a most-parsimonious cladogram resulting from analysis of the characters listed in Table 2 by PHYLIP (see text). Alternative equally parsimonious trees reverse the positions of the two basal clades and the genera that terminate them; all these nodes basically represent trichotomies. On the diagram, each mark indicates a one-step change in character state (thus two marks for the exappendiculate petals of* Rhizophora*); characters noted as changing in more than one place may be multistate or homoplastic or both. Asterisks indicate reversals.*

ECOLOGY AND BIOLOGY

The ecological status of mangroves is presented by Tomlinson (1986: 23) as that of species combining the attributes of pioneer species (e.g., early flowering, wide distribution, extended or even continuous flowering and fruiting, short period of dormancy) with attributes of mature-phase species (dense wood, slow growth, large seeds). It is suggested that this is because there is no real succession in the community (although zonation is pronounced) so that individuals have to be both pioneers and climax constituents at different stages in their life span within communities that are inherently unstable. The vegetation itself (mangal) largely shows the characteristics of a pioneer community.

Little is known about the ecology of terrestrial taxa in both families; this makes difficult the search for possible ancestral traits of mangrove taxa within extant rain forest plants.

The following paragraphs outline some of these morphological and biological features, with inevitable emphasis on mangrove taxa, which have been most extensively studied. These plants are unusual in the possibilities they offer, not only for systematic out-group comparison, but for *ecological* out-group comparison, since it is useful to establish those features that occur in unrelated mangrove taxa, i.e., in mangrove members of other families, and which may suggest themselves as features of direct functional significance, and therefore of limited systematic and phyletic value. Aerial roots are an obvious example. In contrast, some features occur in mangrove taxa but not in their terrestrial or ecological relatives.

AERIAL ROOTS

The aerial roots of *Rhizophora* are all initiated from above-ground parts and develop as a series of sympodial loops, which branch aerially only when they are damaged or when the root apex becomes anchored at the end of a loop (Fig. 28). Sympodial branching is adventitious and is of two contrasted kinds. After damage it is distal, i.e., immediately behind the damaged portion, but after anchoring it is proximal, i.e., some distance behind the point of anchorage. A remarkable anatomical transformation occurs in aerial roots as they become submerged distally. Aerial roots have extensive development of trichosclereids, lack aerenchyma, develop secondary xylem, and branch infrequently and adventitiously. Submerged roots lack trichosclereids and other mechanical tissues, develop a lacunose aerenchymatous cortex, have little secondary xylem, and branch abundantly and nonadventitiously. This kind of root system seems unique to *Rhizophora.* On old trees the trunk-borne roots develop as massive flying buttresses, the trunk base itself being obconical (Fig. 1).

As described in the previous section, *Ceriops tagal* and *Bruguiera sexangula* develop a fluted base formed by the coalescence of clusters of stilt roots that are initiated on the hypocotyl after the seedling has taken root (Fig. 2). This kind of development is also found in the quite unrelated New World mangrove *Pelliciera rhizophorae* (Pelliceraceae) (Tomlinson, 1986). Flutings of this kind seem also to be the maximum extent of aerial root development in *Kandelia.* However, in *Ceriops* and some species of *Bruguiera* an emergent portion of the subterranean root system further develops by the periodic looping of the major horizontal roots, each loop becoming the site of a woody pneumatophore from which branch roots subsequently arise (Fig. 29).

Aerial roots in tropical woody plants have a specific function in supplying oxygen to the submerged roots by the shortest possible pathway in anaerobic, waterlogged substrates. Consequently, such structural variations can be seen as convergences in which developmental modifications result in an identical suite of clearly nonhomologous functional components (Gill & Tomlinson, 1975; Tomlinson, 1986). The functional components always include anchoring and absorption, connecting the separate units horizontally (cable component), and providing for aeration. Consequently, we are provided with a clear picture of the limited value of aerial roots in phyletic analysis. At the same time, this aspect of functional morphology could be a necessary preadaptation in a hypothetical ancestor for the Rhizophoreae. *Kandelia,* which lacks pneumatophores, makes implausible any direct statement about the root system of ancestral mangrove Rhizophoraceae, since it could represent either an ancestral or a derived state. Troll & Dragendorff (1931) denied that aerial roots have a respiratory function and preferred to see them as allowing the trees to root in sediments whose level may fluctuate. The aerating and layering functions are, of course, not mutually exclusive.

WOOD ANATOMY

The relevance of wood anatomy to ecological as distinct from phyletic considerations is again well borne out by a comparison between the mangrove and nonmangrove Rhizophoraceae. The former are uniformly characterized by relatively narrow vessels with scalariform perforation plates, the latter by wider vessels with partly or exclusively simple perforation plates. One can ascribe the differences in vessel diameters to direct ecological causes because they render the wood of mangroves safer in environments where vessel embolisms are likely to be more frequent as tensions are increased because of the low water potential of sea water (Scholander et al., 1965). Safety is maximized by the production of large numbers of narrow elements (Tomlinson, 1986; Zimmerman, 1983). On the other hand, scalariform perforation plates, whose function is quite unknown, do not seem to have any necessary significance in relation to water stress as suggested by "ecological out-group comparison." Vessel elements in all other true mangroves have simple perforation plates (Janssonius, 1950; Panshin, 1932). Significantly, Sperry (1985) provided experimental evidence that scalariform perforation plates in the palm *Rhapis excelsa* restrict the size of bubbles in recently embolized vessels as they refill with water under positive pressures. Restricting bubble size may facilitate recovery of vessels after water columns are broken during exceptional water stress in any plant. Mangrove Rhizophoraceae could then have a functional advantage not found in their ecological associates from other families.

ARCHITECTURE

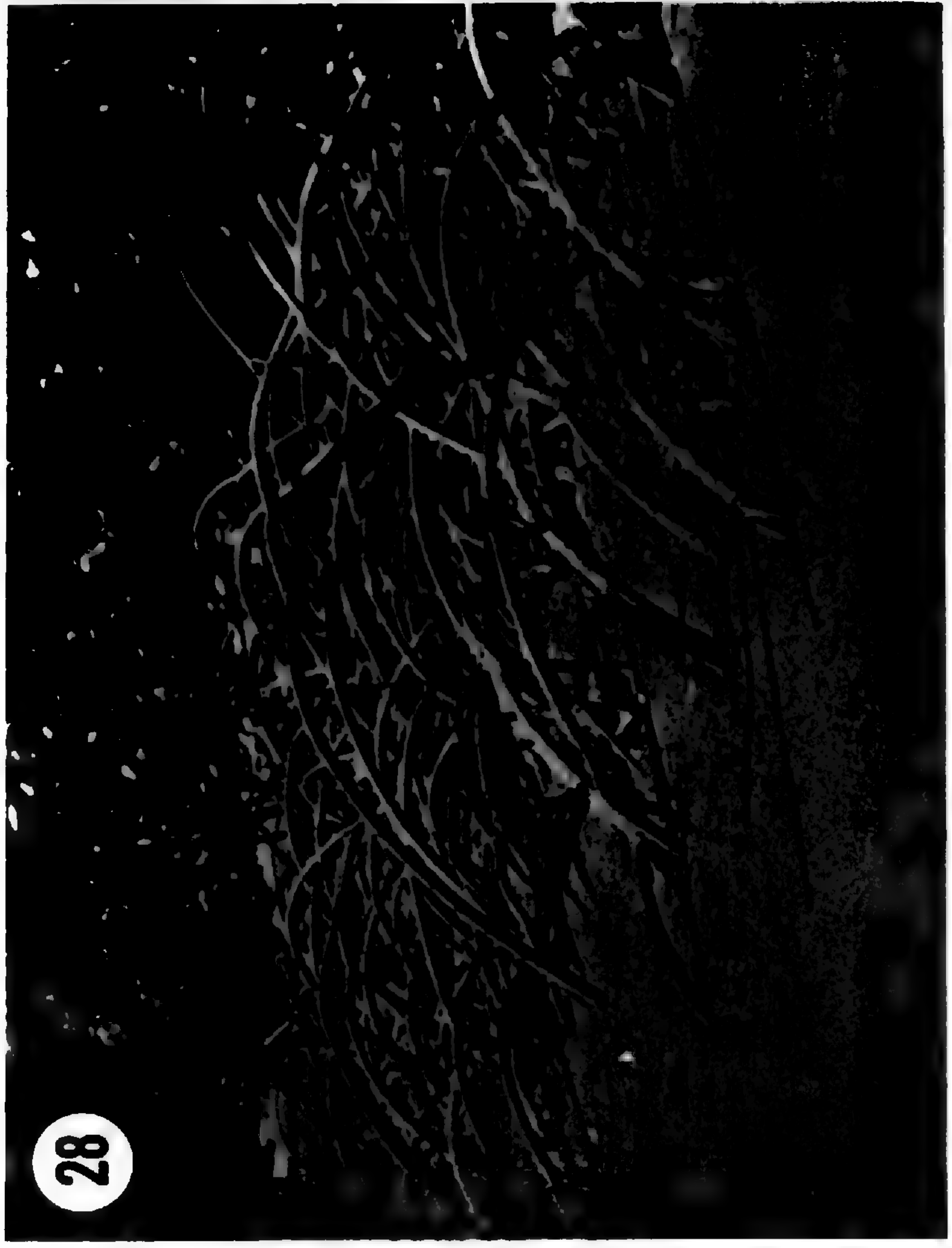
Phyllotactic differences between Rhizophoraceae and Anisophylleaceae, so far as they are understood, are but one of a suite of characters that lead to architectural differences of quite a fundamental nature. In the Rhizophoraceae there is a strong tendency toward continuous growth and the expression of Attims's model, whereas *Anisophyllea* suggests rhythmic growth and Massart's model. Continuous growth has been suggested as an adaptive feature in mangrove taxa simply because the tree must remain permanently active metabolically in order to maintain its salt balance (Scholander, 1968; Hallé et al., 1978; Tomlinson, 1986). Trunk axes are therefore monopodial, although they may branch continuously or diffusely. Branching seems always to be by syllepsis (Fig. 31; cf. Wheat, 1981). The branches themselves may then repeat the structure of the parent axis (Attims's model, as in *Rhizophora*) but progressively become plagiotropic by apposition (Fig. 30). Their incipient orthotropy is, however, demonstrated when they are released from apical control; reiteration in *Rhizophora* occurs chiefly by dedifferentiation of existing sylleptic branches.

Species of *Bruguiera*, notably *B. gymnorrhiza*, more nearly conform to Aubréville's model, since from inception the branches are plagiotropic by apposition. Dedifferentiation of axes is less common. Although distal branches in trees belonging to these contrasted models all become superficially similar, there is a strong underlying difference: *Bruguiera* tends to remain narrow-crowned, while *Rhizophora* is very plastic in its crown form, especially as lower branches are readily supported by aerial roots. Very likely part of the ecological success of *Rhizophora* as compared with *Bruguiera* lies in this greater plasticity of form. Little is known about the architecture of inland Rhizophoraceae, but superficial study suggests a limited range of crown form comparable to that in *Bruguiera*. *Carallia* and *Gynotroches* seem to conform to Attims's model.

Anisophyllea, in contrast, provides an extreme example of Massart's model (Vincent & Tomlinson, 1983), since the trunk grows episodically, producing pronounced tiers of branches, which are themselves strongly plagiotropic. The trunk axis supports only scale leaves. The differences in phyllotaxis that underlie this contrast have already been mentioned.

Multiple serial buds occur in *Anisophyllea* spp. and some other Anisophylleaceae. The extent to which these are committed at inception to become either reproductive or vegetative branches is unknown. Serial buds also occur in Rhizophoraceae but are more strictly committed at the inception of the first primordia on the axillary apex; the pair of bracteole primordia that form on a future inflorescence apex can be distinguished from leaf primordia that form on a future vegetative apex. It should be emphasized that in most Rhizophoraceae that we have studied, vegetative branching is by syllepsis, additional vegetative "reserve" buds may be formed as part of a primary branch complex, but their further development is very limited (Wheat, 1981). In both inland and mangrove genera, when the plant is in reproductive condition, an inflorescence develops in the axil of each leaf of a pair, and, at least on vigorously growing shoots, a single vegetative bud develops above this, although it is often not evident even with a hand lens. In adult *Rhizophora*, reiteration can occur from these residual buds, but more usually reiteration is the result of dedifferentiation of existing branches. Adventitious buds, however, do occur on the hypocotyl of damaged seedlings (Larue & Muzik, 1954; Gill & Tomlinson, 1969).

In summary, we recognize that Rhizophoraceae and Anisophylleaceae differ in architecture and reiterative ability in ways that support their seg-



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FIGURES 32, 33. *Floral mechanism in* Bruguiera gymnorrhiza.—*32. Flower before being tripped; stamens are enclosed under tension by the petals.—33. Similar flower after being tripped; petals spring open, releasing the stamens and pollen explosively. Stamens are now visible at center of flower.*

regation as two families. If this discussion seems imperfectly formulated, it is simply because the problem of morphological plasticity in woody plants of the tropics itself is a subject that remains little understood, despite its considerable ecological importance.

FLORAL MECHANISMS

Understanding of floral structure and development stands in an interesting relationship to our knowledge of floral mechanism, which is fairly complete for the mangrove taxa, from the work of Tomlinson et al. (1979) and Kondo et al. (1987), but is scarcely investigated for either terrestrial Rhizophoraceae or Anisophylleaceae. In the Rhizophoreae there is an initial contrast between *Rhizophora*, which is wind-pollinated, and the other genera, which are animal-pollinated. Evidence for wind pollination comes from floral mechanism, pollen–ovule ratios, dispersibility of pollen, and infrequency of insect visitors, even though the flowers do not display a conspicuous wind-pollination syndrome as it is familiarly understood for temperate trees. Animal pollinators of other genera include birds, bees, moths, and butterflies, at least, with each species or group of species visited by a particular type of flower visitor. Floral specialization involves a very distinctive explosive mechanism that physically projects the light pollen onto the visitor but only when the mechanism is tripped by the visitor (cf. Figs. 32, 33). Differences in the biotic interaction relate to differences in flower size, orientation, and attractant (nectar and odor). *Ceriops decandra* and *Kandelia* lack any specialized mechanism and seem to be pollinated by rather generalized visitors. Of interest is that *Ceriops tagal* and *C. decandra* are strongly contrasted in their floral mechanism. The existence of light powdery pollen in the taxa with animal pollination is an example of the way in which pollen characteristics may be misleading about the method of pollination; most animal-pollinated plants have heavy, sticky pollen. In the Rhizophoreae one may speculate that this pollen type is a preadaptation for wind pollination in *Rhizophora*, which represents

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FIGURES 28–31. *Root and branch development in Rhizophoreae.—28. Development of aerial root system of* Rhizophora; *branch roots arise from the arches after the main apex enters the substrate (Queensland, from a transparency by A. M. Gill).—29. Development of knee roots in* Ceriops tagal *(Philippines, from a transparency by A. M. Gill). Successive stages are indicated A–D. Similar development occurs in* Bruguiera *(see Fig. 2).—30. Older branch of* Rhizophora mangle, *which has become plagiotropic by apposition.—31. Sylleptic branching (arrows) in* Ceriops tagal; *branches are elongating even before stipule has fallen from the node.*

a derived condition, and is itself an adaptation to animal pollination by the distinctive explosive projection of pollen. Flower orientation itself provides contrast with reference to classes of visitor. Small-flowered species of *Bruguiera* have erect flowers, suitable for the approach from above of small, delicate-winged visitors, such as butterflies; large-flowered species of *Bruguiera* have pendulous flowers on recurved pedicels and are approached from below by large visitors like birds. There is evidence that pollination can occur in conditions of autogamy, allogamy, and gectonogamy, but none for apomixis (Kondo et al., 1987).

The general ecological conclusion is that this group of related mangrove plants partitions the available pollinator resource by adopting either different mechanisms, or, where there is a common mechanism, by varying it to suit different types of pollinator.

CONCLUSIONS

The phyletic and systematic conclusions of the various contributors to this symposium are drawn from an examination of a remarkable diversity of characters, ranging from features of gross morphology to ultrastructural details of sieve-tube plastids. Consciously or unconsciously there is a good deal of weighting of these characters; consciously because there can be bias towards acceptance of a character state if it agrees with a pre-existing position, unconsciously because a single biological character (e.g., wind-dispersed seeds) may be reflected in several morphological characters (dehiscent fruits, winged seeds, thin seed coat). Rarely is a character sufficiently understood at a functional level for the bias to be rational. The taxonomist will emphasize that it is impractical to consider the possible biological significance of all attributes of a character in making systematic hypotheses, but the consequences of this restriction should at least be understood. The more information one has about a feature used in systematic analysis, the more likely that its systematic or phyletic significance can be correctly assessed. Subjectivity is an inevitable consequence of the empiricism of systematic methodology—the papers in this symposium are replete with examples—and any claim of objective neutrality is particularly inappropriate where the evolutionary polarity of character states is continually invoked. There should be some appreciation of what may be termed "biological" attributes of characters if they are to be manipulated successfully.

Within this broad spectrum of attributes, specific attention needs to be given to three classes of information: correlation among characters; functional aspects of characters; developmental history of characters, particularly at the primordial level.

An understanding of the way in which seemingly different characters are correlated is necessary since an apparent complex that may or may not be structurally connected may all be subsumed as a single character if the interdependence is appreciated. For example, phyllotaxis, stipular morphology and nodal anatomy are interlinked; thus, aspects of nodal vasculature may be a direct expression of phyllotaxis, as in the presence or absence of split laterals, distinguishing Rhizophoraceae from Anisophylleaceae. More subtle physiological connections need to be sought, as in the relation between leaf succulence and salt-excluding mechanisms in Rhizophoraceae.

The contrast between mangrove and terrestrial taxa in such features as root morphology, leaf anatomy, wood structure, and embryo development could well be cited as characters with little systematic weight because their functional attributes are at least perceived, if not totally understood—they are the "Anpassungsmerkmal" of Schimper. It is well established that the tribe Rhizophoreae is an advanced group, even though a diagnostic feature is the presence of scalariform perforation plates in its wood. An evolutionary scenario sees this simply as the retention of a putatively primitive character. If this is true, it is surely helpful to know why it has been retained. If the preferred explanation of the function of scalariform plates in restricted air-bubble size in embolized vessels is accepted, we can appreciate its occurrence in a more informed way.

Developmental information may simply add to the range of characters made available, an attribute that strongly justifies embryological study (cf. Tobe & Raven, 1987a, b), but it can also clarify structural, functional, and correlative attributes; for example, floral development suggests that pleiomery is derived in the Rhizophoraceae. The best example is provided by *Kandelia*. Here the feature is related to a rather unspecialized floral mechanism that may be derived, not an ancestral feature. Currently we have no evidence for a specialized pollinator group in this genus. Comparative study of embryo development shows a trend of modification leading from epigeal germination to vivipary, with *Bruguiera* the least specialized within the viviparous group. "Vivipary" becomes more useful as a systematic character when viewed developmentally, even though we do not understand its functional significance. Developmental study may also reveal the extent of convergence, in which superficially similar structures show contrasted developmental pathways; the diversity of root systems is a very gross example.

These examples relate to "primordial development" (Tomlinson, 1982); "ontogenetic development" provides an independent set of attributes. The distribution of axes with contrasted kinds of phyllotaxis in Anisophylleaceae clearly has an ontogenetic component that is still incompletely explored. Once it has been done and its correlation with stem vasculature worked out, we are likely to be in a position to make evolutionary statements, because some of the phyllotactic patterns in this species are clearly derived, as indicated by their uniqueness.

Inevitably these considerations of "character analysis" to which we have drawn attention may lie in the realm of "consummations devoutly to be wished" as far as practicing systematists are concerned. Nevertheless we hope that investigations of functional, developmental, and correlative attributes can be seen to play a central role in systematics.

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SEED MORPHOLOGY AND ANATOMY OF RHIZOPHORACEAE, INTER- AND INFRAFAMILIAL RELATIONSHIPS[1]

Hiroshi Tobe[2] *and Peter H. Raven*[3]

ABSTRACT

We present an overall study of the seed morphology and anatomy of all Rhizophoraceae (10 inland and 4 mangrove genera). Morphologically seeds are arillate, winged or nonappendaged; both arillate and winged seeds are borne in capsular fruits, and nonappendaged seeds in baccate or indehiscent hard-walled capsules. Seed coat anatomy is diversified in correlation with the seed and fruit morphology, but a well-developed exotesta and a fibrous exotegmen are common to all inland genera. Despite certain minor divergences, the seed coat of different genera of Rhizophoraceae is defined as exotestal, exotestal-exotegmic, or undifferentiated. Different combinations of seed morphological and anatomical features characterize different genera or groups of genera. An overall comparison of seeds and other reproductive characters confirms that in Rhizophoraceae arillate seeds and the presence of a fibrous exotegmen are plesiomorphic features that can be used in searching for related families. Seed morphology and anatomy also support grouping Rhizophoraceae with Elaeocarpaceae and Celastraceae, and the exclusion of Elaeocarpaceae from Malvales. Our comparison further suggests that the seed morphology and anatomy of Rhizophoraceae have evolved as the result of adaptation to different methods of seed dispersal from ant dispersal to dispersal by wind, bird, mammal, or water. We carried out a cladistic analysis of the genera of Rhizophoraceae on the basis of 16 reproductive characters (including those of seed morphology and anatomy). Blepharistemma, Cassipourea, Comiphyton, Anopyxis, Macarisia, *and* Sterigmapetalum, *all inland genera that have been assigned to Macarisieae, are characterized by having many plesiomorphies (particularly a superior ovary). The last three genera have winged seeds and a thinner seed coat (apomorphies), whereas the first three have arillate seeds. Among the four remaining inland genera, which have been assigned to Gynotrocheae,* Crossostylis *(with arillate seeds) differs greatly from the others in having only one apomorphy (i.e., an inferior ovary); it retains many plesiomorphies. In contrast,* Carallia, Gynotroches, *and* Pellacalyx *share a nonappendaged seed and a persistent meso- and endotegmen, both clearly synapomorphies, and* Gynotroches *and* Pellacalyx *further share some distinct synapomorphies, suggesting their close affinities. The four mangrove genera—*Bruguiera, Ceriops, Kandelia, *and* Rhizophora*—which have been segregated as Rhizophoreae, share many synapomorphies (e.g., an undifferentiated seed coat and the complete lack of the tegmen), and therefore the coherence of Rhizophoreae is not in doubt. Cladistically the mangrove genera are more closely related to* Carallia, Gynotroches, *and* Pellacalyx *than to Macarisieae. Based on our cladistic analysis, the traditional infrafamilial classification is revised, and a new tribe Crossostylideae, which consists of* Crossostylis *only, is proposed.*

Traditionally, Rhizophoraceae have been broadly defined to contain one mangrove tribe Rhizophoreae (4 genera) and three inland tribes: Macarisieae (6 genera), Gynotrocheae (4 genera), and Anisophylleae (4 genera) (e.g., Melchior, 1964). The comparative study of wood anatomy (van Vliet, 1976) and leaf architecture and anatomy (Keating & Randrianasolo, this volume; Baas, pers. comm.) has supported this broad definition of the family. In contrast, embryological evidence (Tobe & Raven, 1983), as well as an overall comparison based on various systematic characters (Dahlgren & Thorne, 1984), strongly suggested that the overall group was heterogeneous and indicated the need for further embryological studies of the constituent genera and tribes as an important key to their

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relationship. Earlier embryological studies were limited to 9 of 18 genera: *Bruguiera, Ceriops,* and *Rhizophora* of Rhizophoreae (Karsten, 1891; Cook, 1907; Carey, 1934; Mauritzon, 1939; Juncosa, 1982, 1984b); *Cassipourea* of Macarisieae (Juncosa, 1984a); *Carallia* and *Gynotroches* of Gynotrocheae (Karsten, 1891; Haberlandt, 1895; Mauritzon, 1939; Corner, 1976); and *Anisophyllea, Combretocarpus,* and *Poga* of Anisophylleae (Karsten, 1891; Hou, 1958; Vaughan, 1970; Geh & Keng, 1974). Most of these studies were concerned with relatively few embryological features.

Thus we recently presented an overall embryological study of "Anisophylleae" (Tobe & Raven, 1987b) and, with support of evidence from other sources, justified the separation of Anisophylleaceae as a distinct family from the rest of Rhizophoraceae, as proposed earlier by several authors (e.g., Ridley, 1922; Cronquist, 1981, 1983; Dahlgren, 1983). Subsequently, we presented the first comprehensive embryological study on two inland genera, *Cassipourea* and *Sterigmapetalum* of Macarisieae (Tobe & Raven, 1987a), which were recently separated from Macarisieae as constituting a new tribe Hypogyneae (Steyermark & Leisner, 1983), and we provided some discussion on infrafamilial relationships based on data available. Juncosa (pers. comm.) has surveyed the respective embryological features of the remaining tribes, Gynotrocheae and Rhizophoreae. Consequently, Rhizophoraceae are becoming one of the most well-known families with respect to their embryological characters.

Previous embryological studies of Rhizophoraceae have lacked comprehensive, comparative information on the seed morphology and anatomy of the whole family. Concerning the seed morphology, Schimper (1893), Hou (1958, 1968), Floret (1974, 1976), and Tobe & Raven (1987a) described some of the constituent genera and suggested that Rhizophoraceae are diverse in this feature. However, no overall studies, except for the preliminary discussions in our previous paper (Tobe & Raven, 1987a), have been made.

Carey (1934) provided fragmentary descriptions on the seed coat anatomy of *Rhizophora* and *Ceriops* of Rhizophoreae. Later, Corner (1976) described some details of the seed coat anatomy of *Carallia, Gynotroches,* and *Pellacalyx* (all Gynotrocheae); Tobe & Raven (1987a) described those of *Cassipourea* and *Sterigmapetalum* of Macarisieae; and Juncosa studied those of *Carallia* and *Gynotroches.* These works contained important suggestions inducing further studies. For example, Corner (1976, 1: 161) defined the seed coat of both *Gynotroches* and *Pellacalyx* as "exotegmic," with the exotegmen fibrous and, on the basis of seed coat anatomy, transferred the two genera into Legnotidaceae, a family first described by Endlicher (1840) as "Legnotidae" to comprise *Cassipourea* and *Gynotroches.* Tobe & Raven (1987a) showed that *Cassipourea* and *Sterigmapetalum* (Macarisieae) have a thick and a thin testa, respectively, and are clearly distinct from each other based on seed coat anatomy. Juncosa (pers. comm.) reports that the seed coat of *Carallia borneensis* differs from those of other inland genera in having no persistent tegmen and a vascularized testa. Thus, the works of Corner (1976), Tobe & Raven (1987a), and Juncosa strongly suggested the utility of seed coat anatomy in considering relationships of genera in Rhizophoraceae and indicated that an overall study of seed coat anatomy was needed for further understanding of infrafamilial relationships. The utility of the seed morphology and anatomy in such considerations has already been demonstrated in studies on several unrelated families (e.g., Cruciferae—Vaughan & Whitehouse, 1971; Polygalaceae—Verkerke, 1985), leading to a revision of conventional tribal classifications in each case.

This paper presents the features of seed morphology and anatomy for the whole family Rhizophoraceae, which consists of 14 genera (excluding the genera of Anisophylleaceae). These results, which have revealed a considerable degree of diversity in these features, are then used together with other evidence to clarify infrafamilial phylogenetic relationships. Dahlgren (this volume) has used these features extensively in searching for relatives, and this analysis is of fundamental importance for such comparisons.

Materials and Methods

Twenty-one species representing all 14 genera of Rhizophoraceae were investigated. Collection data are provided in Table 1. For microscopic observations mature and immature seeds were microtome sectioned following standard paraffin methods described elsewhere (Tobe & Raven, 1987b). Some hard specimens, like those of *Ceriops,* were embedded in glycol methacrylate, sectioned with glass knives, and stained with 0.1% Toluidine Blue (e.g., Figs. 28, 29). Scanning electron micrographs were also used in observing seeds of *Gynotroches* and *Pellacalyx,* and they were prepared following the standard method using a JEOL 25S instrument

TABLE 1. *Studied taxa, collections, and materials. Asterisk (*) indicates that dry herbarium materials were investigated. Tribal positions of genera follow Melchior (1964) and Floret (1976).*

Taxa	Collections and Materials
Macarisieae	
Anopyxis klaineana (Pierre) Engl.	Cameroon. *D. Thomas 3464* (MO)—buds & fruits
Blepharistemma membranifolia (Miq.) Ding Hou	India. Quilon, Kerala, *K. Manilal s.n. in 1984* (MO)—female buds India. Grichur District, Kerala, *N. Sasidharan s.n. in 1986* (MO)—fruits
Cassipourea gummiflua Tul. var. *verticillata* (N. E. Br.) J. Lewis	Zimbabwe. Cultivated, National Botanic Garden, Harare, *Th. Müller 3558* (SRGH); original collection: Mt. Inyangani, *Th. Müller 698* (SRGH)—buds and fruits
C. guianensis Aubl.	Brazil. Manaus, *B. Nelson 1324* (MO, NY)—buds & fruits
C. malosana (Bak.) Alston	Zimbabwe. Cultivated, National Botanic Garden, Harare, *Th. Müller 3557* (SRGH); original collection: Chirinda Forest, Mt. Selinda, *B. Goldsmith*—buds & fruits
**Comiphyton gabonense* (J.-J. Floret	Zaire. Mt. Homas, Irumu, *Germain 5213* (BR)—fruits
Macarisia pyramidata Thou.	Madagascar. *L. Dorr 4392* (MO)—fruits
Sterigmapetalum heterodoxum Steyermark & Liesner	Venezuela. Sierra de San Luis, Falcón, *R. Wingfield 13692* (MO)—female buds, *13696* (MO)—fruits
Gynotrocheae	
Carallia brachiata (Lour.) Merr.	Australia. Jourama Falls National Park, North Queensland, *B. Jackes s.n. in 1983* (JCT)—buds & fruits
C. eugenioidea King.	Malasia. Selangor, *B. Stone 15114* (KLU)—buds & fruits
**Crossostylis biflora* Forst.	Society Islands. Tahaa, Mt. Purauti, *H. St. John 17346* (MO)—fruits
C. grandiflora Brongn. & Gris	New Caledonia. *G. McPherson 6331* (MO)—buds & fruits
**C. multiflora* Brongn. & Gris	New Caledonia. Thy River valley, ca. 12 km NE Noumea, *G. McPherson 1617* (MO)—fruits
Gynotroches axillaris Bl.	Malaysia. Maxwell Hill, Perak, *B. Stone 15397* (KLU)—buds & fruits
Pellacalyx lobbii (Hook. f.) Schimp.	Malaysia. Sarawak, *P. Chai s.n. in 1986*, no voucher—fruits
P. cf. *saccardianus* Scort.	Malaysia. Maxwell Hill, Perak, *B. Stone 15396* (KLU)—buds & fruits
Rhizophoreae	
Bruguiera gymnorrhiza (L.) Lam.	Mozambique. Maputo, Costa do Sol, *J. de Koning & M. C. Groenaedyk 9243* (LMU)—buds & fruits
Ceriops tagal (Perr.) C. B. Rob.	Malaysia. Port Klang, Selangor, *Mahmud Sider s.n. in 1983*, no voucher—buds & fruits Philippines. Dagbilao, Quezon, Luzon, *Hernaez CA 29249* (CAHUP)—buds
Kandelia candel (L.) Druce	Republic of China (Taiwan). Tanshuei, Taipei Co., *C. Peng 4504* (HAST)—buds & fruits
Rhizophora mangle L.	U.S.A. Cultivated, Fairchild Tropical Garden, Florida. *H. Tobe s.n. in 1981*, no voucher—buds & fruits
R. stylosa Griff.	U.S.A. Cultivated, Fairchild Tropical Garden, Florida. *FG 69-111. H. Tobe s.n. in 1981*, no voucher—buds; *A. Bird s.n. in 1983*, no voucher—fruits

(Tobe & Raven, 1987b). Comparisons among genera were made on the basis of mature seeds, and when materials were available, seed coat ontogeny was investigated to understand the mature structure more completely. The terminology on seeds and seed coat anatomy follows Corner (1976) and Schmid (1986); Schmid elaborated Corner's terminology.

OBSERVATIONS

The seeds of rhizophoraceous genera have either an aril or a wing, or they lack appendages. Arillate seeds occur in *Blepharistemma*, *Cassipourea*, and *Comiphyton* (all in Macarisieae), which have loculicidally (?) or septicidally dehiscent or indeshiscent capsular fruits (Floret, 1976), and in *Cros-*

sostylis (Gynotrocheae), which has capsular fruits of unknown dehiscence mode. Winged seeds occur in *Anopyxis*, *Macarisia*, and *Sterigmapetalum* (all in Macarisieae), which have septicidally dehiscent capsular fruits (Floret, 1976; contrary to Floret, Arênes (1954) described fruit dehiscence in *Macarisia* as loculicidal, but we confirmed septicidal dehiscence in *M. pyramidata*). Nonappendaged seeds occur in *Carallia*, *Gynotroches*, and *Pellacalyx* (all in Gynotrocheae), which have baccate fruits, and in *Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora* (all in Rhizophoreae), which have indehiscent hard-walled fruits. Both the aril and the wing develop as an outgrowth of the exostome: compare the young arillate seed of *Cassipourea malosana* (Figs. 1, 2) with the young winged seed of *Anopyxis klaineana* (Figs. 3, 4). In the case of the aril, a raphal tissue, which continues from the outer integument, may also join the aril formation; however, a funicular or hilar tissue never joins there. Therefore, as discussed in a previous paper (Tobe & Raven, 1987a), the aril and the wing are homologous to each other, and the histogenetic origin of both structures are regarded substantially as exostomal.

We have also confirmed that the seed coat anatomy correlates with the external seed morphology type (i.e., arillate, winged, and nonappendaged) and, in addition, that within the nonappendaged seed category the seeds of *Gynotroches* and *Pellacalyx* are distinct from those of *Carallia*, as already described by Corner (1976) to some degree. The details are documented below.

ARILLATE SEEDS

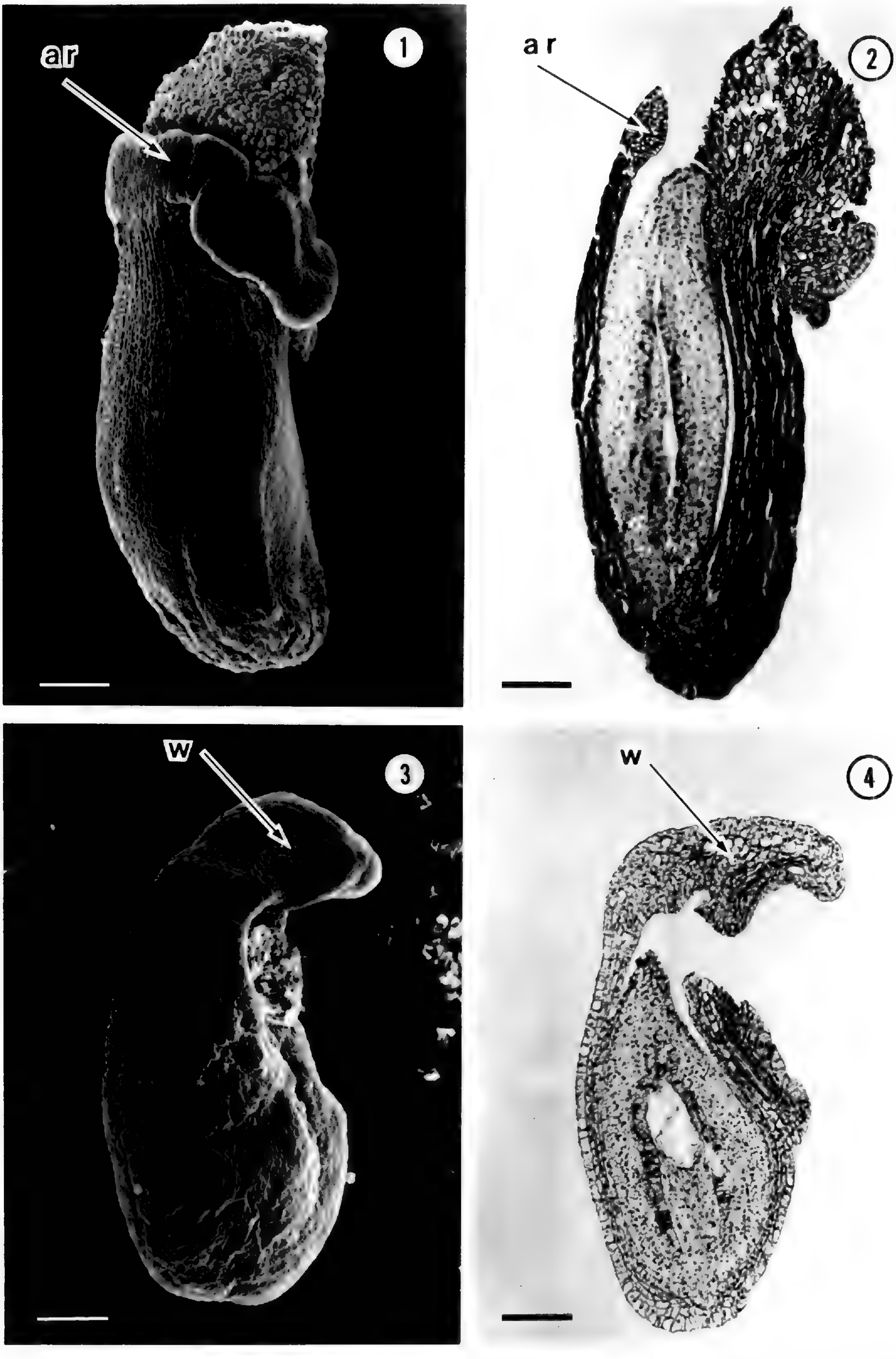
Blepharistemma. It has been previously uncertain whether *Blepharistemma* has an aril, a wing, or neither, because fruits and seeds of this genus are undescribed. We found for the first time that *B. membranifolia*, the only species of the genus, has a fleshy aril (Fig. 5), which covers nearly the upper half of the seed. The mature seed is ellipsoid, with a somewhat conspicuous raphe, and very slightly depressed toward the lateral side; it is 4.3–4.5 mm long and 2.4–2.5 mm thick, as measured from the raphe to antiraphe (R–A), and 2.2–2.3 mm thick from side to side (L–L) (see Tobe & Raven, 1987a, fig. 14, for directions of width measurement).

The oldest seed coat available is 0.20–0.22 mm thick in total, comprising the testa 135–142 μm thick and the tegmen about 50 μm thick. When the embryo sac is mature, the outer and inner integuments are 3–4 cells and 4–5 cells thick, respectively. The outer integument increases its thickness in postfertilization stages and eventually differentiates into a 1-cell-layered exotesta, a 3–6-cell-layered mesotesta, and a 1-cell-layered endotesta (Fig. 6). There is no clear histological difference between the mesotesta and the endotesta. Exotestal cells are radially enlarged, thick-walled, and tanniferous, forming a palisade (Fig. 6). Meso- and endotestal cells are much smaller than the exotestal cells, but also somewhat thick-walled and tanniferous. The endotestal cells often contain crystals. On the other hand, the inner integument develops into a 1-cell-layered fibrous exotegmen and 2 or 3 underlying unspecialized cell layers, the latter of which apparently disintegrates further. (The seeds investigated in this study seem still somewhat immature, and we believe that the underlying cell layers below the exotegmen eventually disappear completely.) Of the constituent cell layers, the exotesta is the most conspicuously developed as a mechanical structure; therefore, the seed coat of *Blepharistemma* is exotestal.

Cassipourea. Cassipourea is a large and variable genus (4 subgenera and 80 species (Alston, 1925; Airy Shaw, 1973)), which shows a range of variation in seed size and anatomical structure. We described some details of seed size and seed anatomy earlier (Tobe & Raven, 1987a), and therefore these are only briefly summarized here. Only data on the total thickness of the mature seed coat were added.

The mature seed is ellipsoid (*Cassipourea guianensis* and *C. gummiflua* var. *verticillata*) to broad ellipsoid (*C. malosana*) and slightly depressed to the raphe. In *C. guianensis*, the seed is 8.9–9.2 mm long and 2.6–2.8 mm thick (R–A) to 3.3–3.6 mm thick (L–L); in *C. gummiflua* var. *verticillata* it is 4.2–4.4 mm long and 1.6–1.8 mm thick (R–A) to 2.2–2.4 mm thick (L–L); in *C. malosana* it is 5.0–5.2 mm long and 2.8–3.1 mm thick (R–A) to 4.5–4.8 mm thick (L–L). The aril is fleshy and wholly covers the seed except on the chalazal and antiraphe side.

In the three examined species, the mature seed coat is 0.16–0.22 mm thick in total and is composed of a 1-cell-layered exotesta, a 2–6-cell-layered mesotesta, a 1-cell-layered endotesta, and a 1-cell-layered exotegmen; all other cell layers of the tegmen are crushed and disappear, although both the outer and the inner integuments are multiple cell-layered at the mature embryo sac stage. The exotesta comprises enlarged cuboid, thick-walled cells; the meso- and endotesta are composed of much smaller cells, and endotestal cells may



FIGURES 1–4. —*1, 2. Scanning electron micrograph (SEM) and longitudinal section (LS) of a mature ovule of* Cassipourea malosana *showing the early development of an aril.—3, 4. SEM and LS of a mature ovule of* Anopyxis klaineana *showing early development of a wing. All scales = 100 µm. ar, aril; w, wing.*

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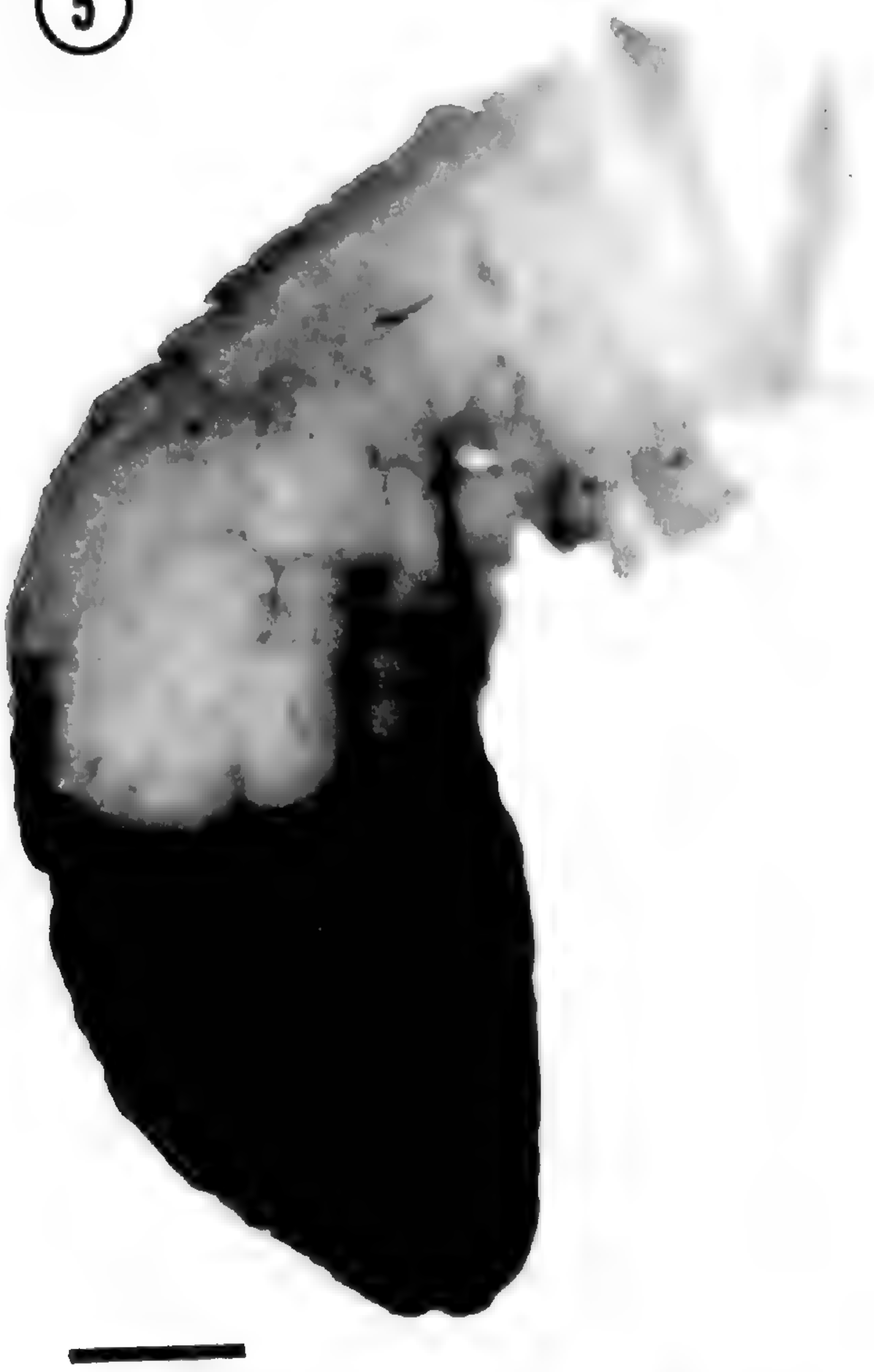

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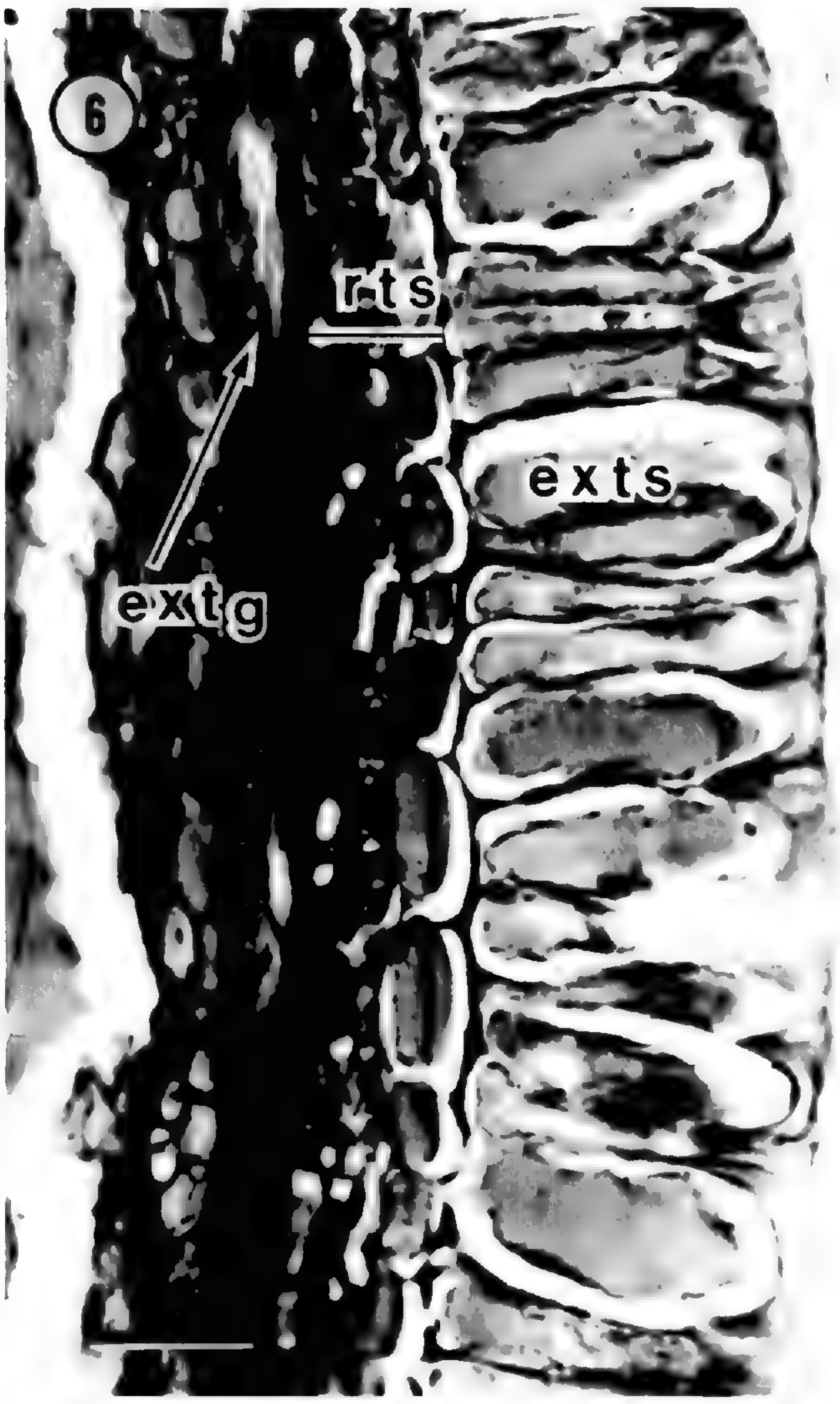

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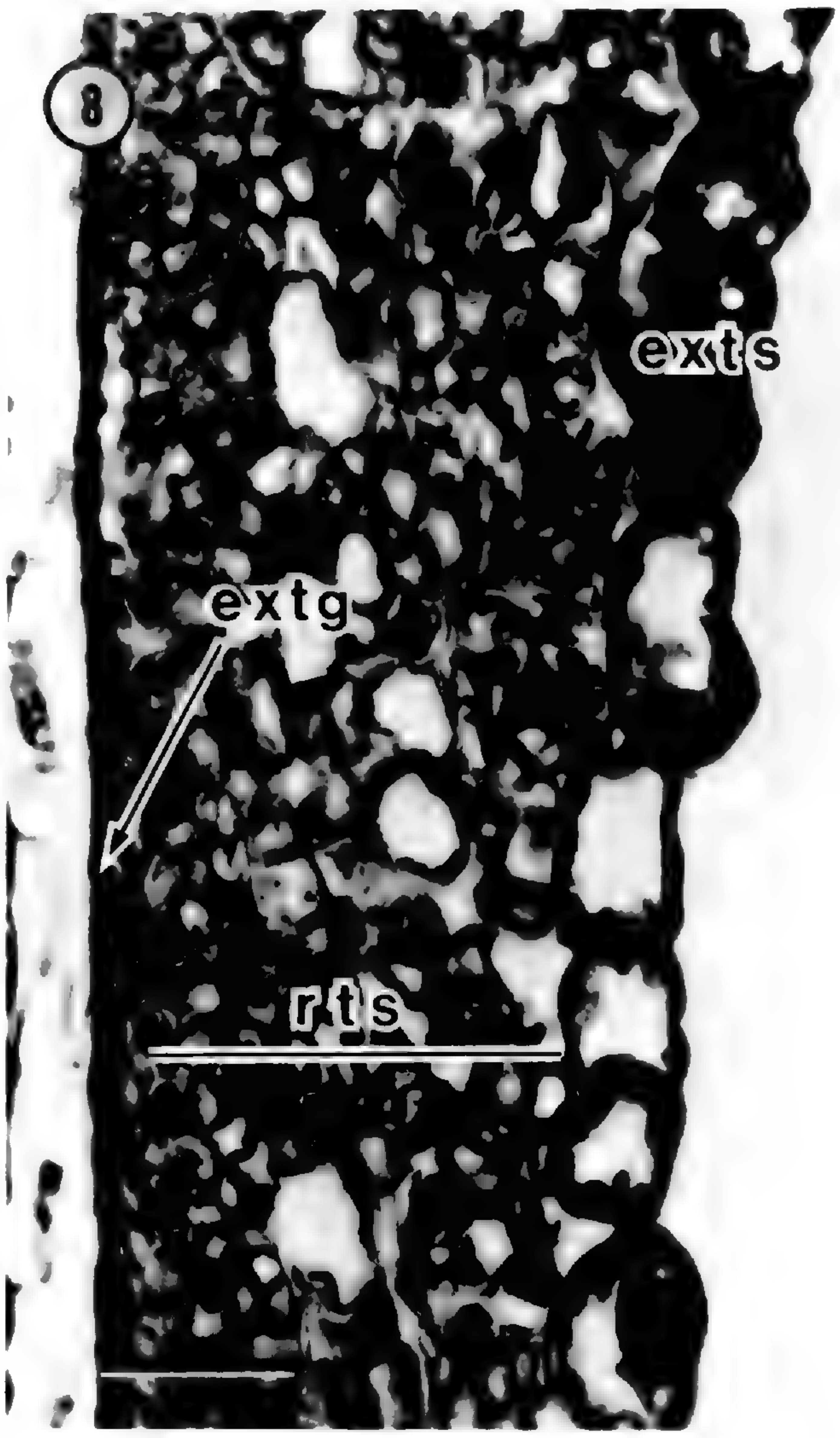

contain crystals; the exotegmen is composed of longitudinally elongate, thick-walled fibrous cells. Testal cells are mostly tanniferous. In all three species, the exotesta is most conspicuously developed as a mechanical structure, and therefore the seed coat of *Cassipourea* is exotestal.

Comiphyton. The mature seed of the only species of the genus, *C. gabonense*, is narrowly ellipsoid (Fig. 7) and nearly circular in cross section; it is 7.0–7.5 mm long and 2.0–2.8 mm in diameter. The aril is restricted to a micropylar top, and its tissue is apparently irregularly folded (Fig. 7). Compared with those of the species examined of *Cassipourea*, the seed coat surface of *Comiphyton* is more undulated, although it is uncertain whether this difference distinguishes *Comiphyton* from all species of *Cassipourea.*

The mature seed coat is 0.14–0.18 mm thick in total and is composed of a 1-cell-layered exotesta, an 8–10-cell-layered mesotesta, a 1-cell-layered endotesta, and a 1-cell-layered exotegmen (Fig. 8). There is no clear difference between the mesotesta and the endotesta. The exotesta is composed of somewhat enlarged, thick-walled tanniferous cells; the meso- and endotesta comprise much smaller cells, and they do not contain crystals; the exotegmen is composed of longitudinally very narrow, fibrous cells. No other cell layers of the tegmen persist. Considering the structure of the entire seed coat, only the exotesta is relatively well developed as a mechanical structure. Therefore, the seed coat of *Comiphyton* is exotestal.

Crossostylis. The mature seeds of the three examined species, *C. biflora*, *C. grandiflora* (Fig. 9), and *C. multiflora*, are ellipsoid, bearing a raphe as a very narrow longitudinal ridge. The mature seed is 2.1–2.3 mm long and 1.4–1.6 mm in diameter in *C. biflora*; 3.6–3.8 mm long and 1.8–2.0 mm in diameter in *C. grandiflora*; and 1.8–1.9 mm long and 1.0–1.2 mm in diameter in *C. multiflora*. The aril is membranous, and its tissue is irregularly folded. The aril spreads over the micropylar top and does not tightly cover the seed proper.

The mature seed coat structure differs from species to species. In *Crossostylis grandiflora*, the mature seed coat is relatively thick—0.19–0.20 mm in total—and is composed of a 1-cell-layered exotesta, a 2–3-cell-layered mesotesta, a 1-cell-layered endotesta, and a 1-cell-layered exotegmen (Fig. 10). There is no histological difference between the mesotesta and the endotesta. At the mature embryo sac stage, the outer and the inner integuments are 4–5 cells thick and 9–11 cells thick, respectively. As the seed matures, therefore, the inner integument completely disappears except for the outer epidermis—i.e., exotegmen—while the outer integument remains nearly persistent. The exotesta comprises enlarged, extremely thick-walled, tanniferous cuboidal cells; the meso- and endotesta are formed by unspecialized smaller cells; and the exotegmen is composed of longitudinally elongate, thick-walled, fibrous cells. Since the exotesta is most conspicuous as a mechanical structure, the seed coat of *C. grandiflora* is exotestal.

The mature seed coat structures of *Crossostylis biflora* (Fig. 13) and *C. multiflora* (Figs. 11, 12) are very similar. The total thickness is about 0.09 mm (*C. biflora*) or 0.06–0.07 mm (*C. multiflora*). The mature seed coat is basically composed of a 1-cell-layered exotesta, a 1-cell-layered mesotesta, a 1-cell-layered endotesta, and a 1-cell-layered exotegmen; however, the mesotesta and even the endotesta may be lacking in *C. multiflora* (Figs. 11, 12). Although we did not confirm the thickness of the integuments, they seem to be multiplicative, as we saw more clearly in our sample of *C. grandiflora*. The exotesta is covered with a thick cuticle; its cells are longitudinally elongate and contain tanninlike pigments. The meso- and endotestal cells are much smaller than those of the exotesta and contain crystals. The exotegmen is composed of extremely sclerotic, longitudinally elongate, fibrous cells. Compared with that of *C. grandiflora*, the exotegmen of these species is much more conspicuously developed as a mechanical structure. Therefore, the seed coat of *C. biflora* and *C. multiflora* is exotestal-exotegmic.

WINGED SEEDS

Anopyxis. The species examined, *A. klaineana*, has a large mature seed; it comprises the seed proper and a membranous wing (Fig. 14). The seed proper is oblanceoloid but extremely depressed laterally, and it is 13.4–13.7 mm long and 5.2–5.7 mm thick (R–A) to 1.6–2.1 mm thick (L–L). The

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FIGURES 5–8.—*5, 6. Oldest arillate seed available of* Blepharistemma membranifolia *and longitudinal section (LS) of its seed coat.—7, 8. Mature arillate seed of* Comiphyton gabonense *and LS of its seed coat. Scales = 1 mm (Figs. 5, 7) and 50 μm (Figs. 6, 8). exts, exotesta; rts, meso- and endotesta; extg, exotegmen.*

wing is always larger than the seed proper and is 23.9–25.0 mm long and 10.6–11.4 mm wide.

The mature seed coat is thin and 0.09–0.11 mm thick; for the most part it is apparently composed largely of a 1-cell-layered exotesta and a 1-cell-layered exotegmen (Fig. 15). In the mature embryo sac stage, however, the outer and the inner integuments are 4–5 cells thick and 6–7 cells thick, respectively. As the seed matures, therefore, all integumentary cell layers except for the outer epidermis of both integuments seem to degenerate or collapse. The exotesta is composed of enlarged, thick-walled, tanniferous cells, and the exotegmen of longitudinally elongate, thick-walled, fibrous cells. Both the exotesta and exotegmen are conspicuous as mechanical layers, and therefore the seed coat of *Anopyxis* is exotestal-exotegmic.

Macarisia. The mature seed of this genus, like that of *Anopyxis,* comprises a seed proper and a membranous wing (Fig. 16). The size of seed varies within the genus; the species examined, *M. pyramidata,* is known to have the largest seeds in the genus (Arènes, 1954), which, however, are much smaller than those of *Anopyxis.* In *M. pyramidata,* the seed proper is ellipsoid but extremely depressed laterally as in other species of the genus; it is 3.5–3.9 mm long and 2.1–2.5 mm thick (R–A) to 0.4 mm thick (L–L). The wing is always larger than the seed proper and is 8.5–9.1 mm long and 3.6–4.2 mm wide.

The mature seed coat of *Macarisia pyramidata* is 0.05–0.07 mm thick in total, and it comprises mainly a 1-cell-layered exotesta and a 1-cell-layered exotegmen (Fig. 17). Crystalliferous (endotestal) cells may remain at places between the exotesta and the exotegmen (Fig. 17). We did not examine the thickness of integuments because we lacked material. The exotesta is composed of enlarged, thick-walled, and tanniferous cells; the exotegmen comprises longitudinally elongate, thick-walled, fibrous cells. Based on *M. pyramidata,* the seed coat of *Macarisia* is exotestal-exotegmic.

Sterigmapetalum. Although the seed structure of this genus (consisting of seven species according to Steyermark & Liesner, 1983) has not been emphasized as a systematic character, it agrees with those of *Anopyxis* and *Macarisia* in having a seed proper and a membranous wing on the micropylar top. The morphology and anatomy of the mature seed of *S. heterodoxum* were discussed by Tobe & Raven (1987a). In this paper, only characteristic features of the species are briefly summarized, and data on the total thickness are added.

The seed proper is oblanceoloid and extremely depressed laterally; it is 5.0–6.0 mm long and 1.6–2.0 mm thick (R–A) to 0.8–1.0 mm thick (L–L). The wing is 7.4–10.2 mm long and 3.9–5.0 mm wide. (For other species of the genus, Steyermark & Liesner (1983) described the seeds of *S. obovatum* as oblong, plano-convex, 8 mm long and 3.5–4 mm wide.)

The mature seed coat is 0.08–0.10 mm thick in total and is composed only of a 1-cell-layered exotesta and a 1-cell-layered exotegmen, although the outer and the inner integuments were originally 2–4 cells thick and 8–10 cells thick, respectively. The exotesta comprises enlarged, somewhat radially elongate, thick-walled, tanniferous cells; the exotegmen is composed of longitudinally elongate, thick-walled, fibrous cells. The seed coat of *Sterigmapetalum* is exotestal-exotegmic.

NONAPPENDAGED SEEDS

Gynotroches. The mature seeds of the only species of the genus, *G. axillaris,* are ellipsoid and small with an areolate surface (Fig. 18). They are

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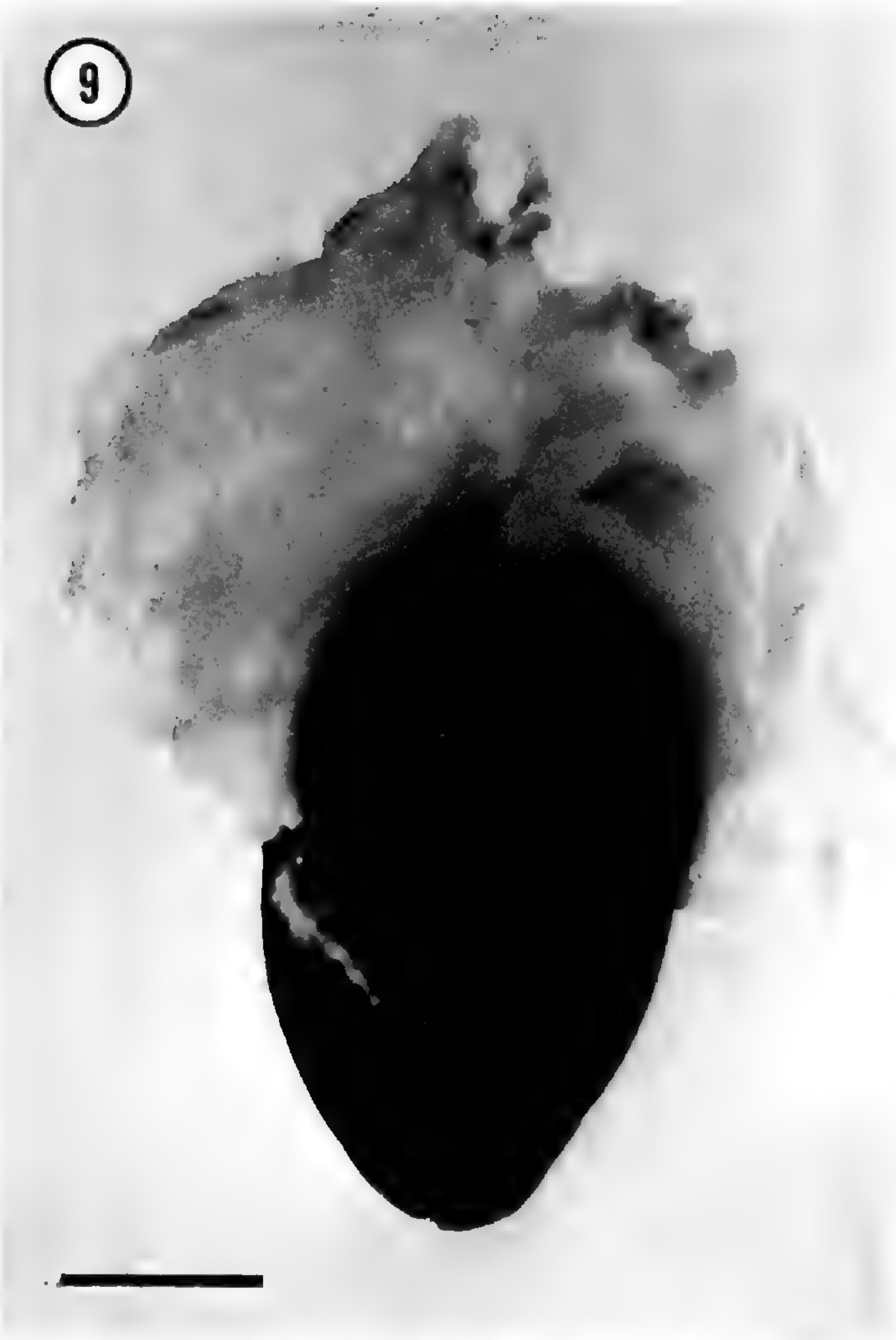
FIGURES 9–13.—*9, 10. Mature arillate seed of* Crossostylis grandiflora *and longitudinal section (LS) of its seed coat.—11, 12. LS and transverse section of mature seed coat of* C. multiflora.—*13. LS of mature seed coat of* C. biflora. *Scales = 1 mm (Fig. 9) and 50 µm (Figs. 10–13). exts, exotesta; rts, meso- and endotesta; extg, exotegmen; cr, crystal.*

FIGURES 14–17.—*14, 15. Mature winged seed of* Anopyxis klaineana *and longitudinal section (LS) of its seed coat.—16, 17. Mature winged seed of* Macarisia pyramidata *and LS of its seed coat. Scales = 1 mm (Figs. 14, 16) and 50 µm (Figs. 15, 17). exts, exotesta; extg, exotegmen; cr, crystal.*

FIGURES 18–21.—*18, 19. Scanning electron micrograph (SEM) of mature nonappendaged seed of* Gynotroches axillaris *and longitudinal section (LS) of its seed coat.—20, 21. SEM of mature nonappendaged seed of* Pellacalyx *cf.* saccardianus *and LS of its seed coat. Scales = 200 µm (Figs. 18, 20) and 50 µm (Figs. 19, 21). exts, exotesta; ents, endotesta; extg, exotegmen; mtg, mesotegmen; entg, endotegmen.*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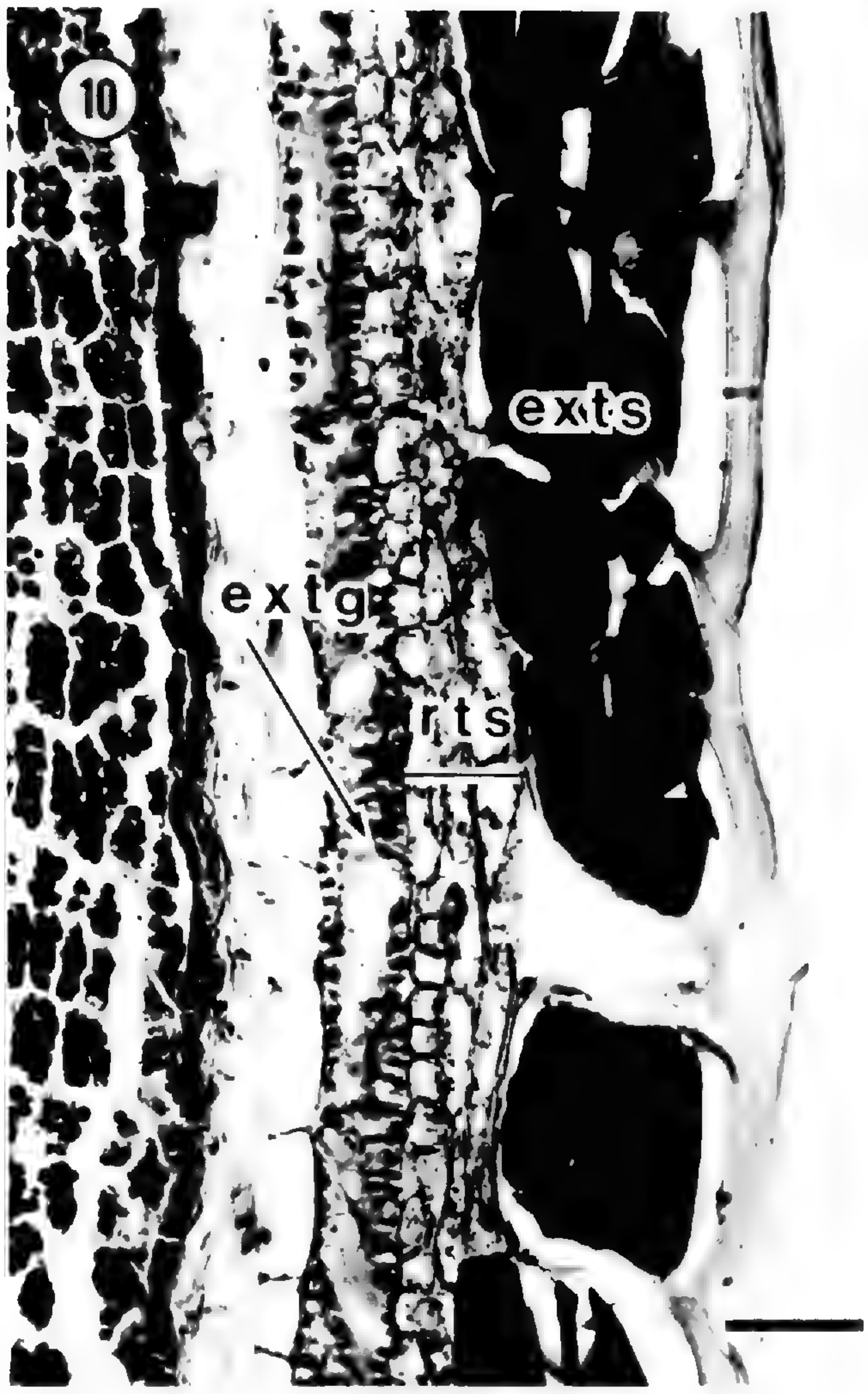
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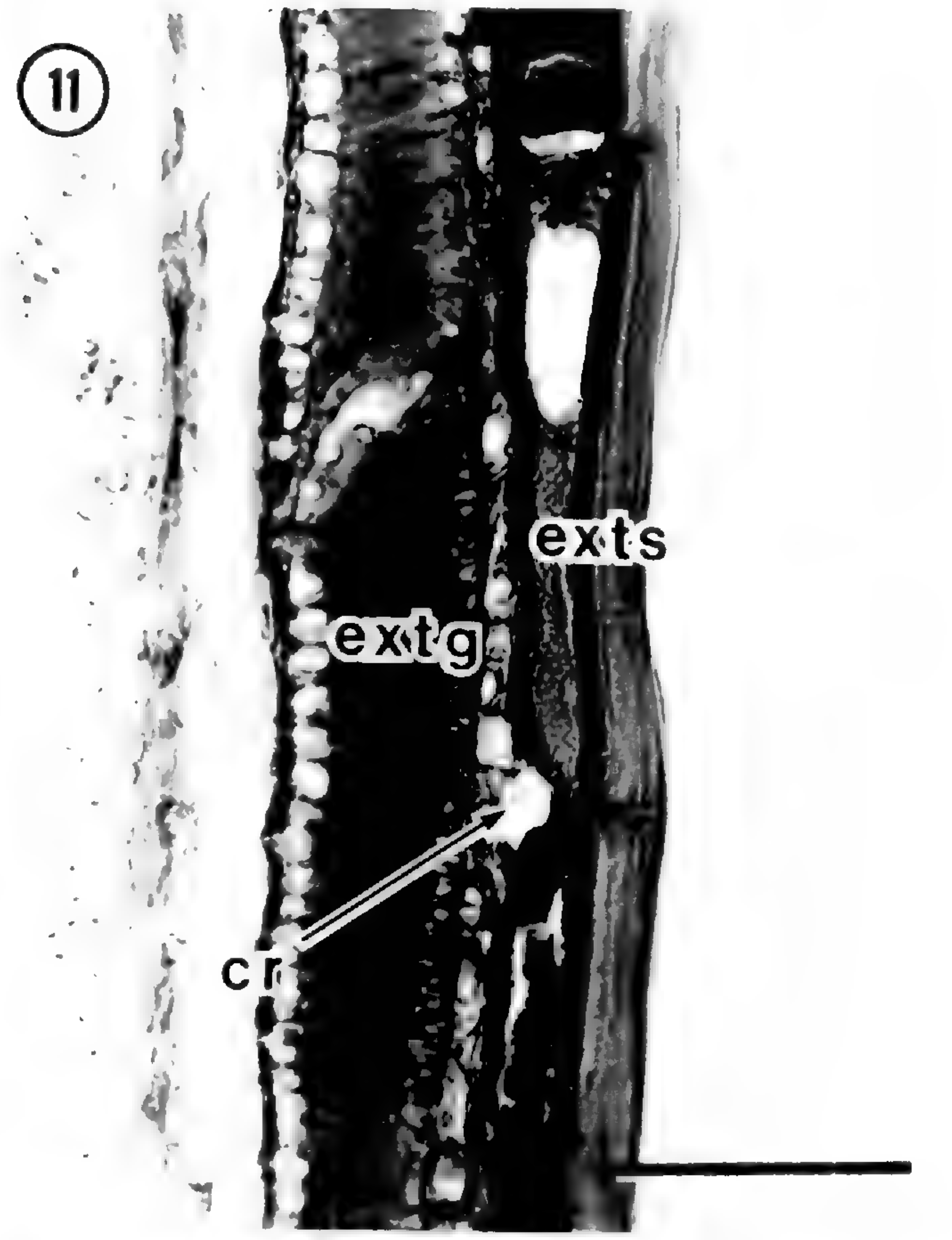
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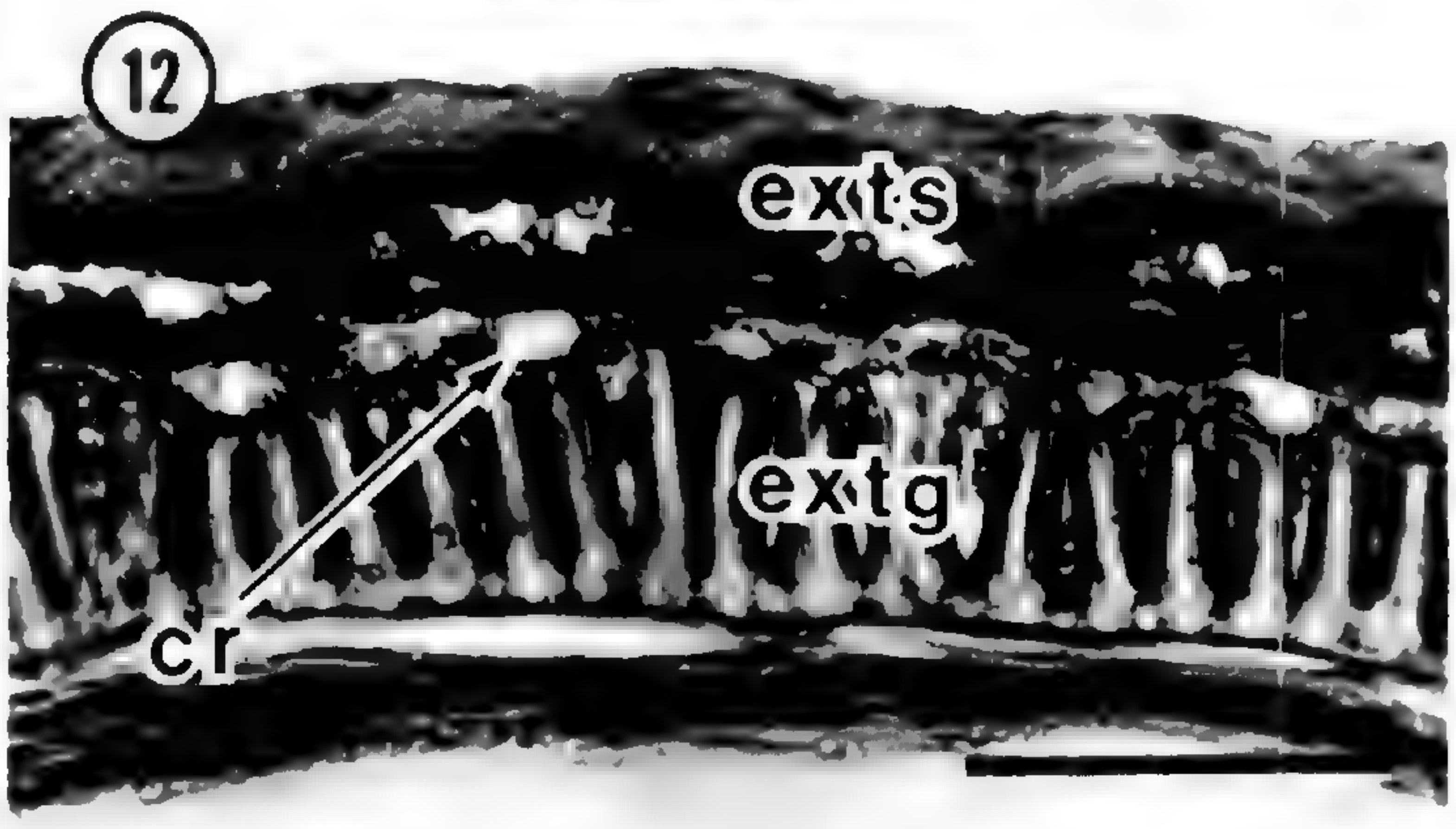
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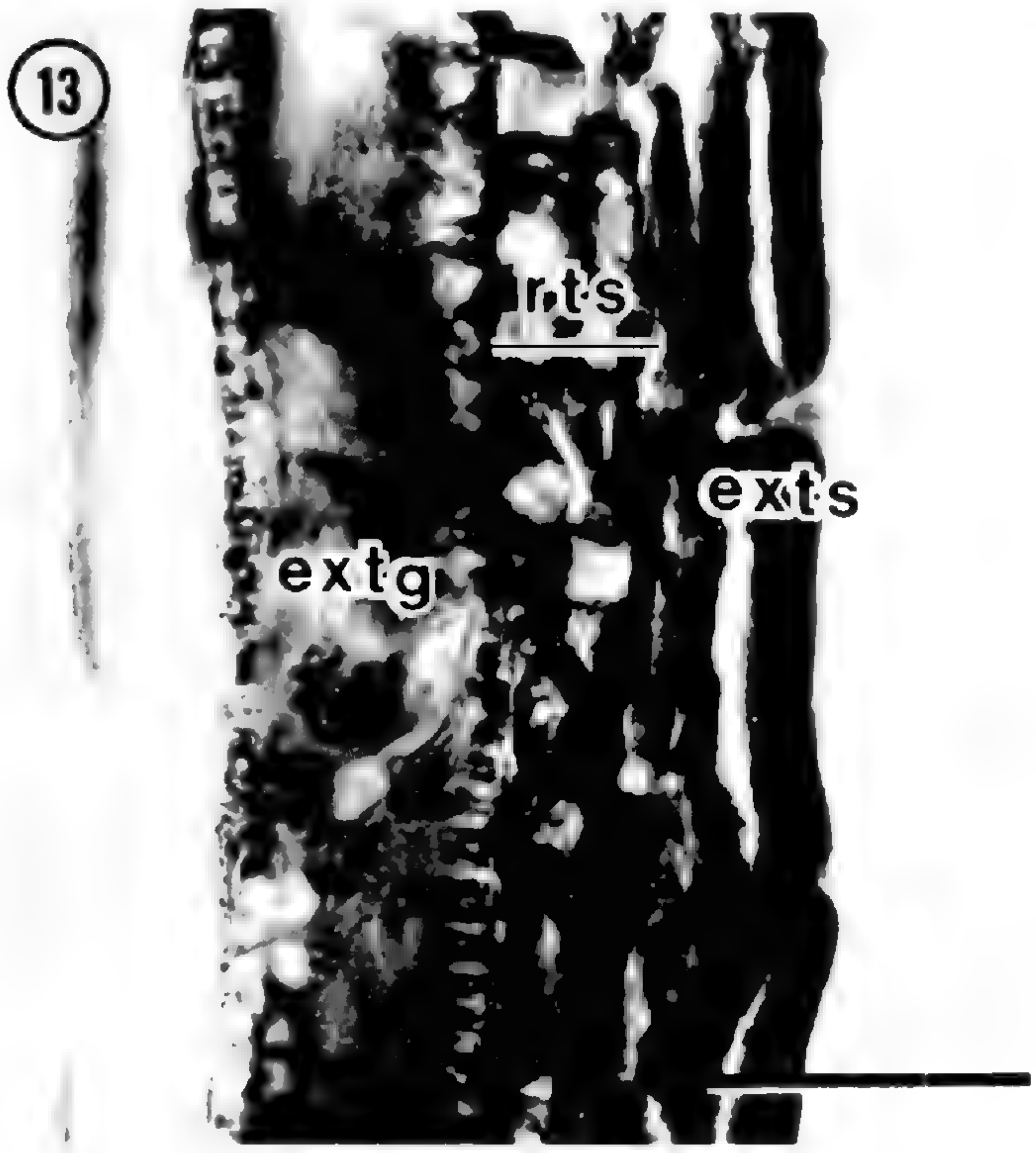
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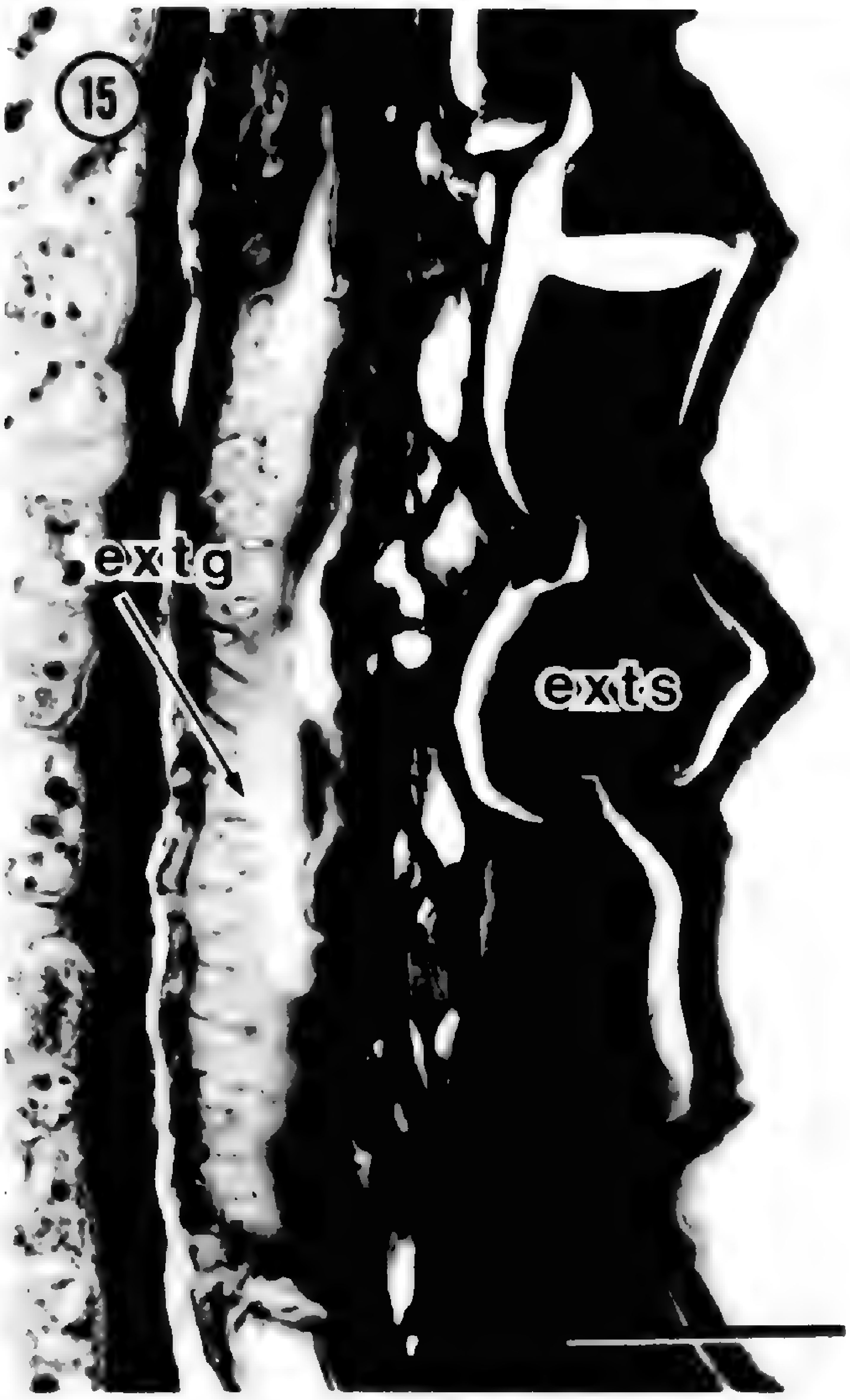
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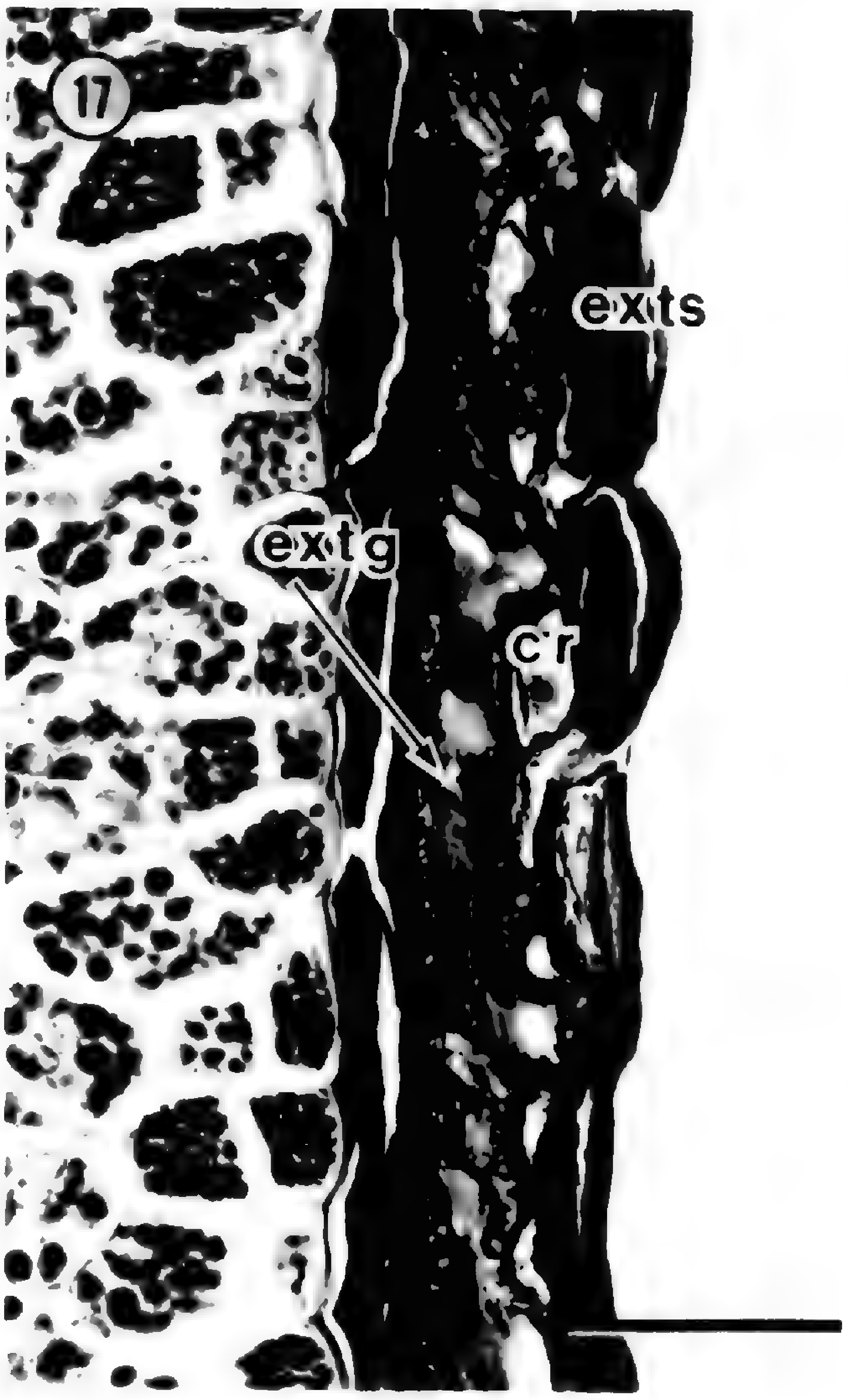
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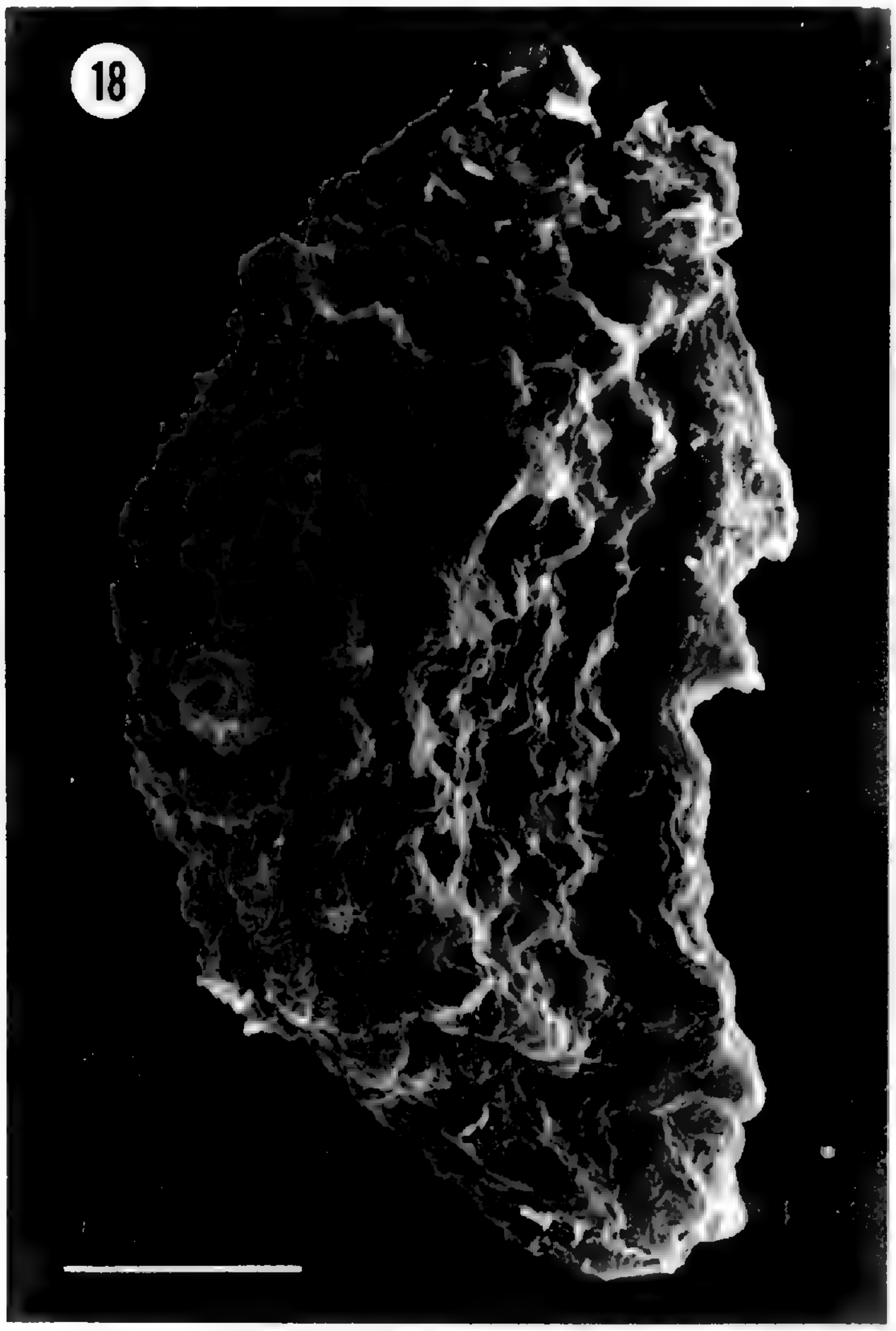
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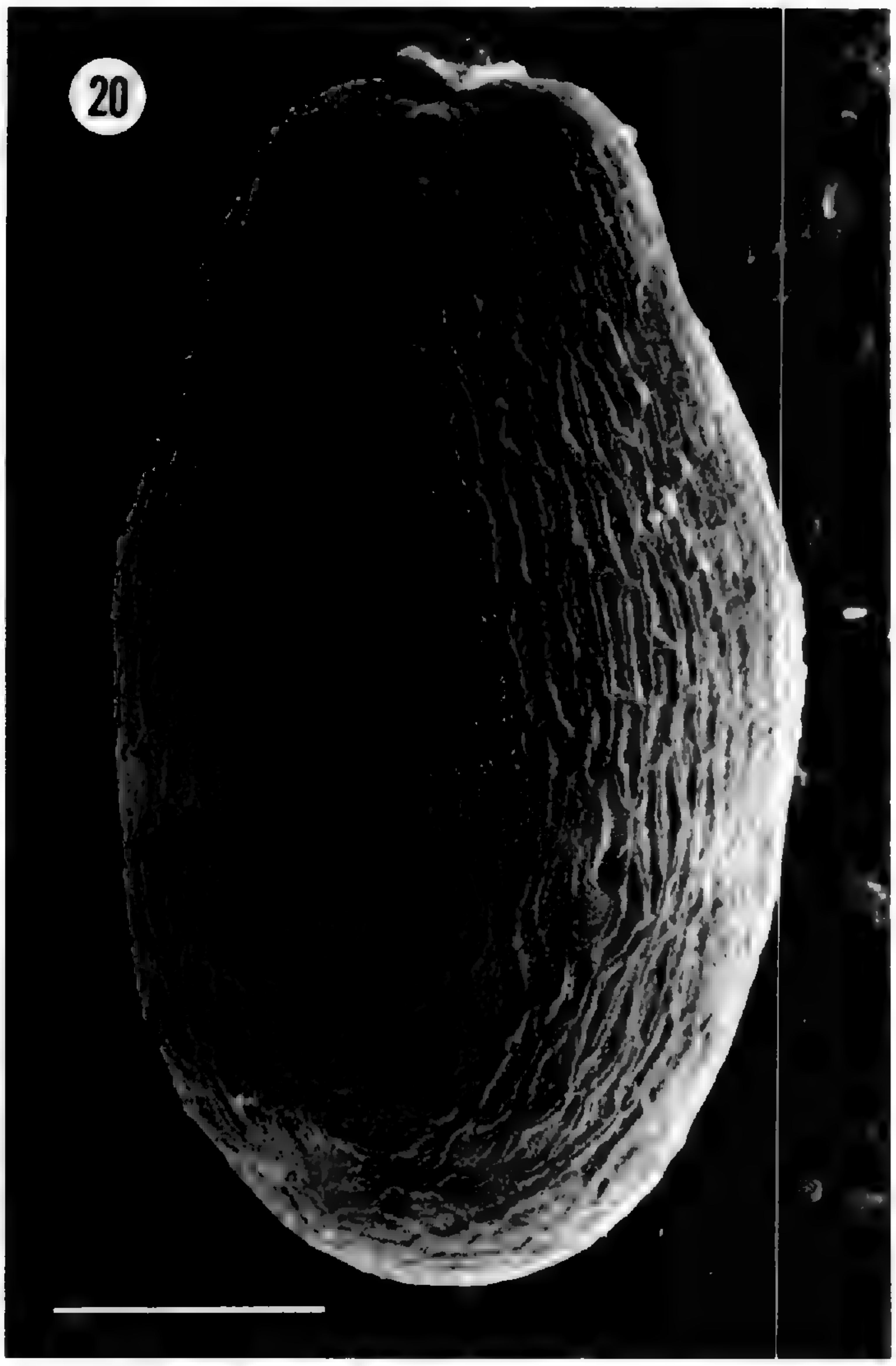
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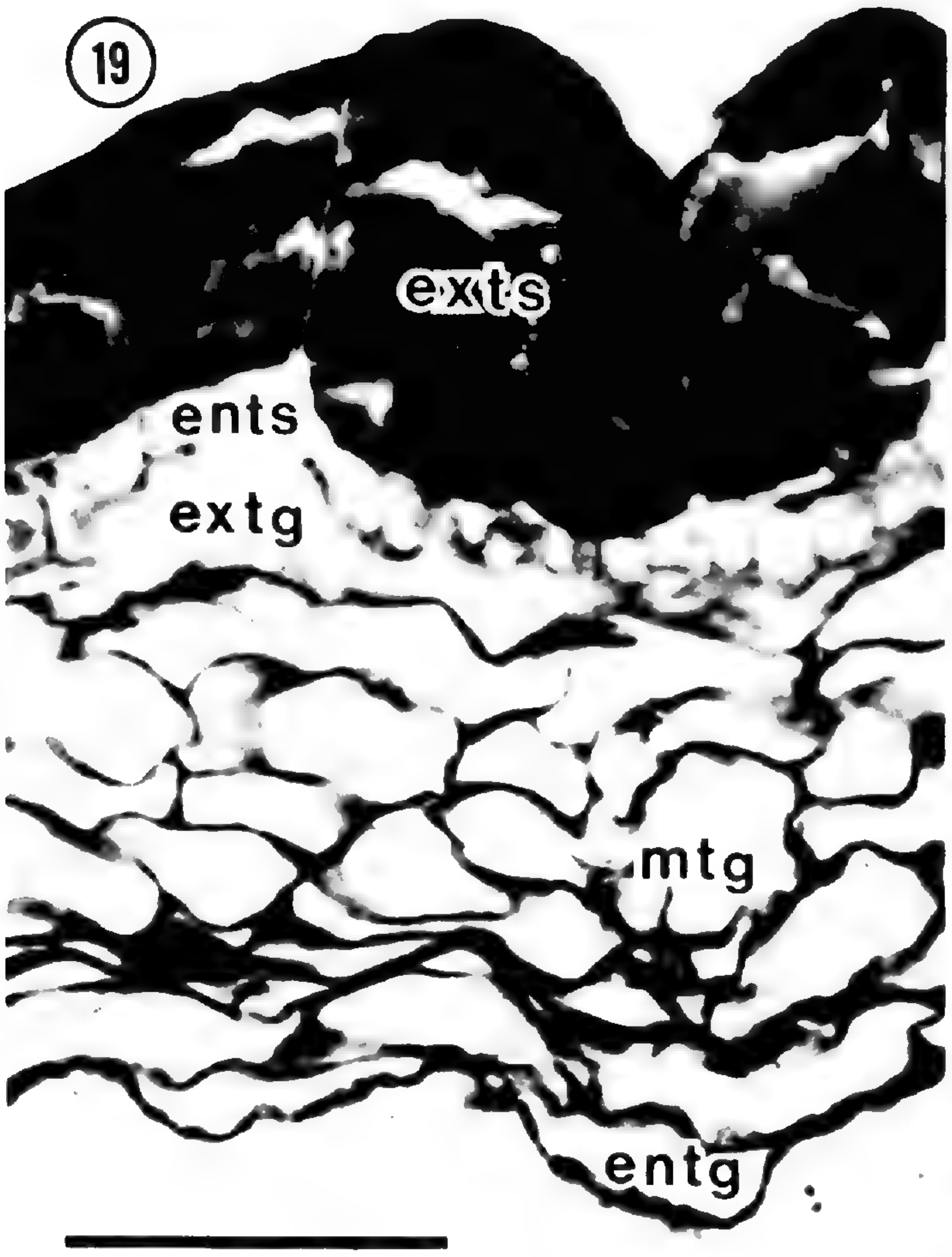
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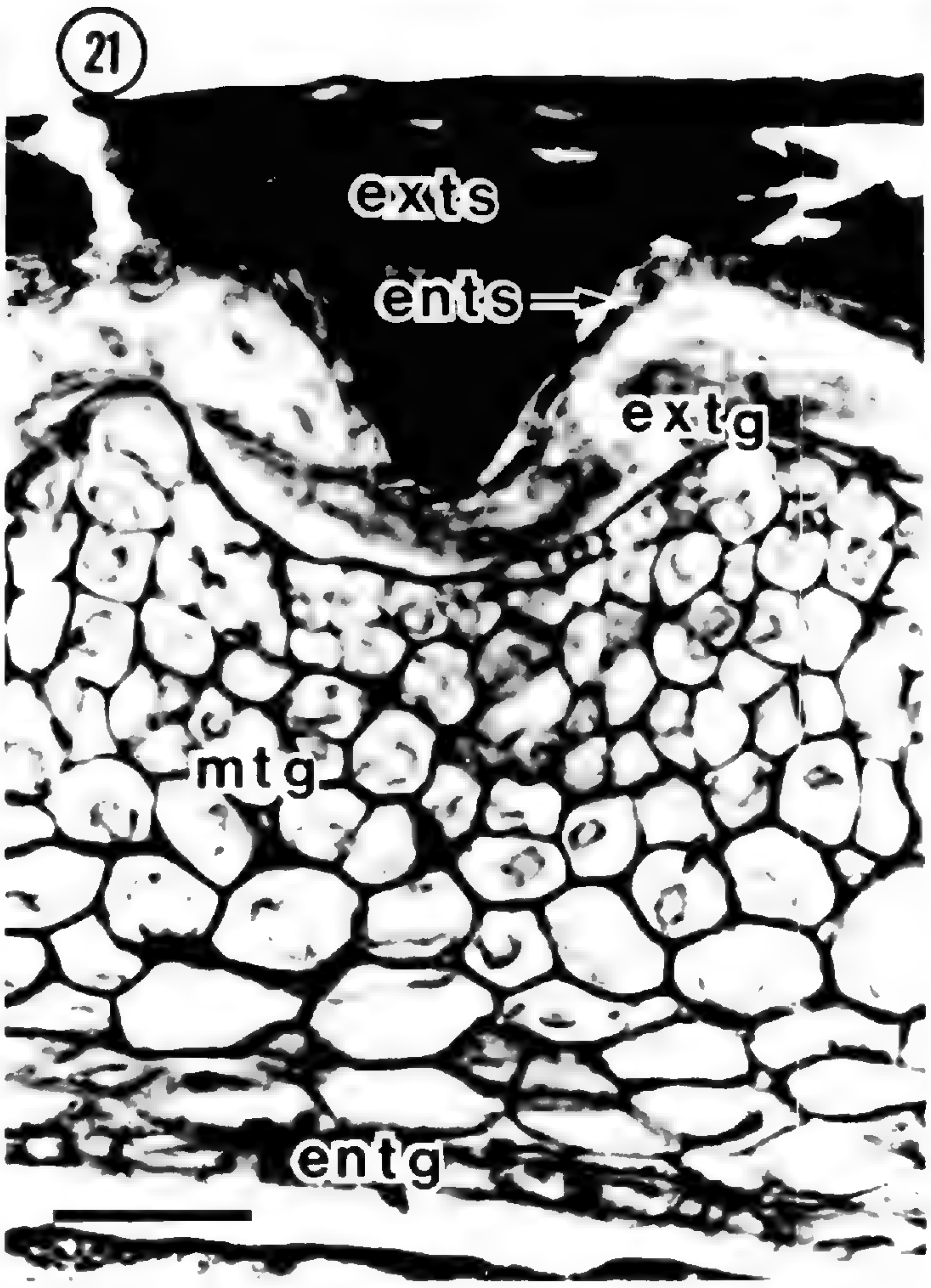
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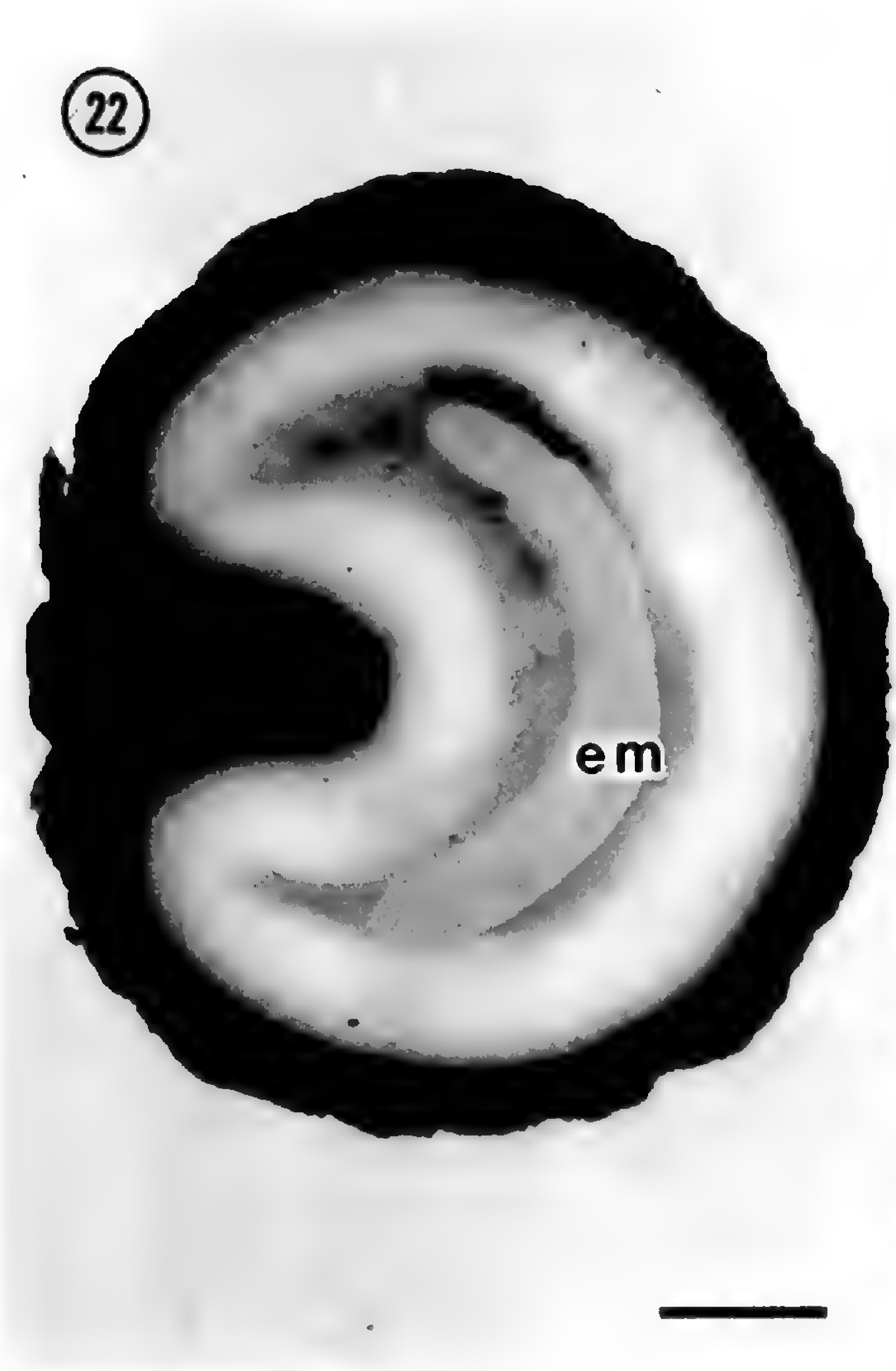

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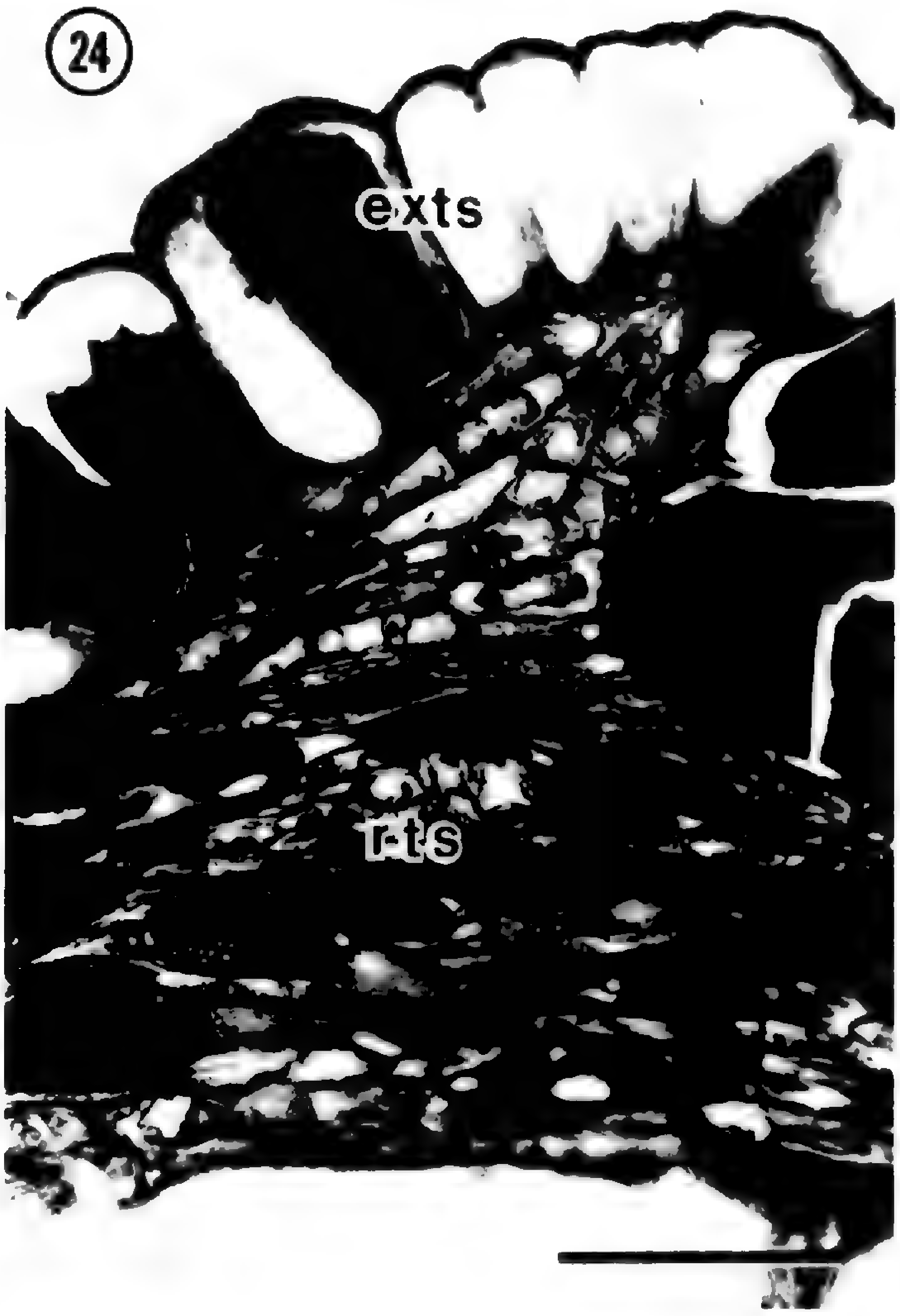

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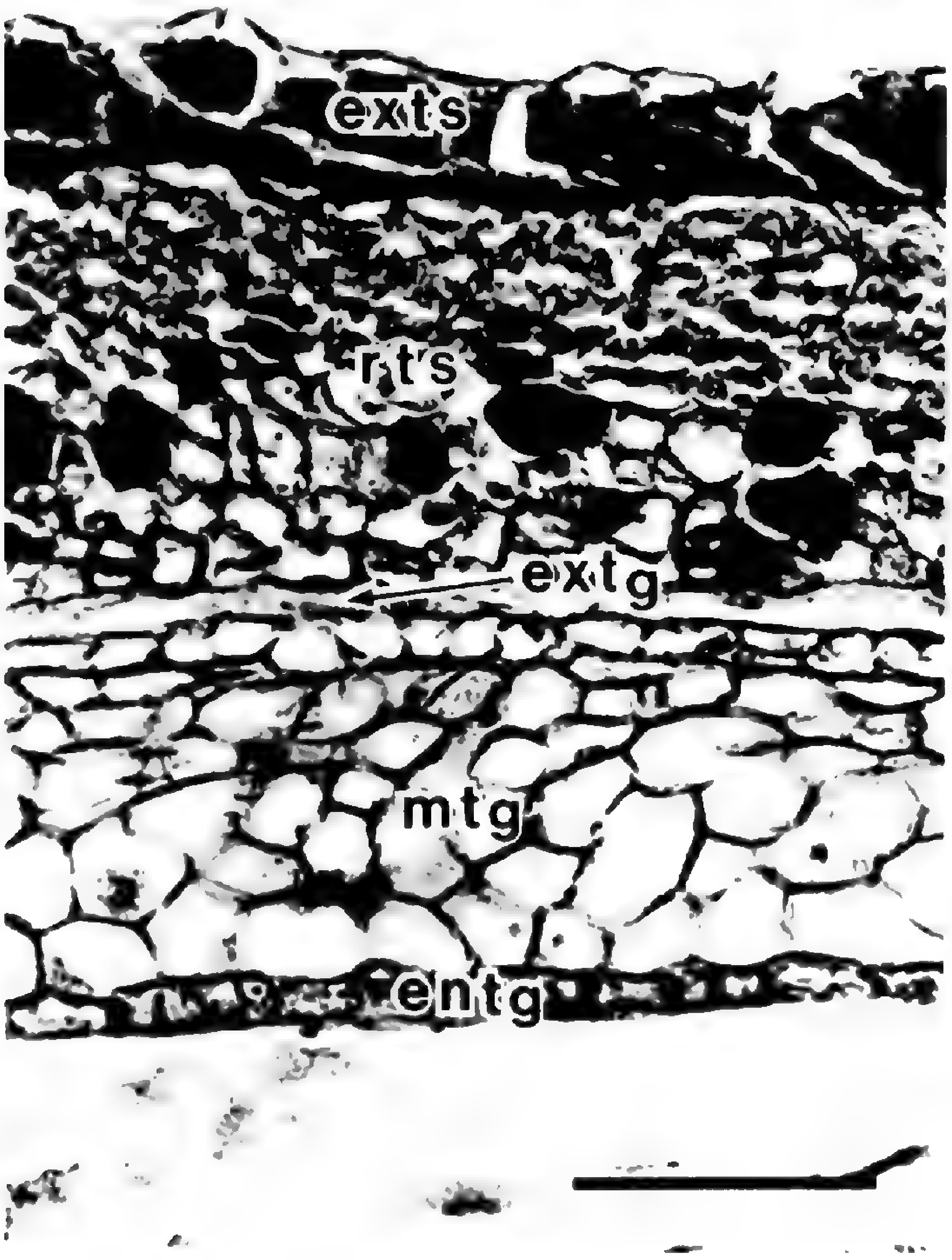

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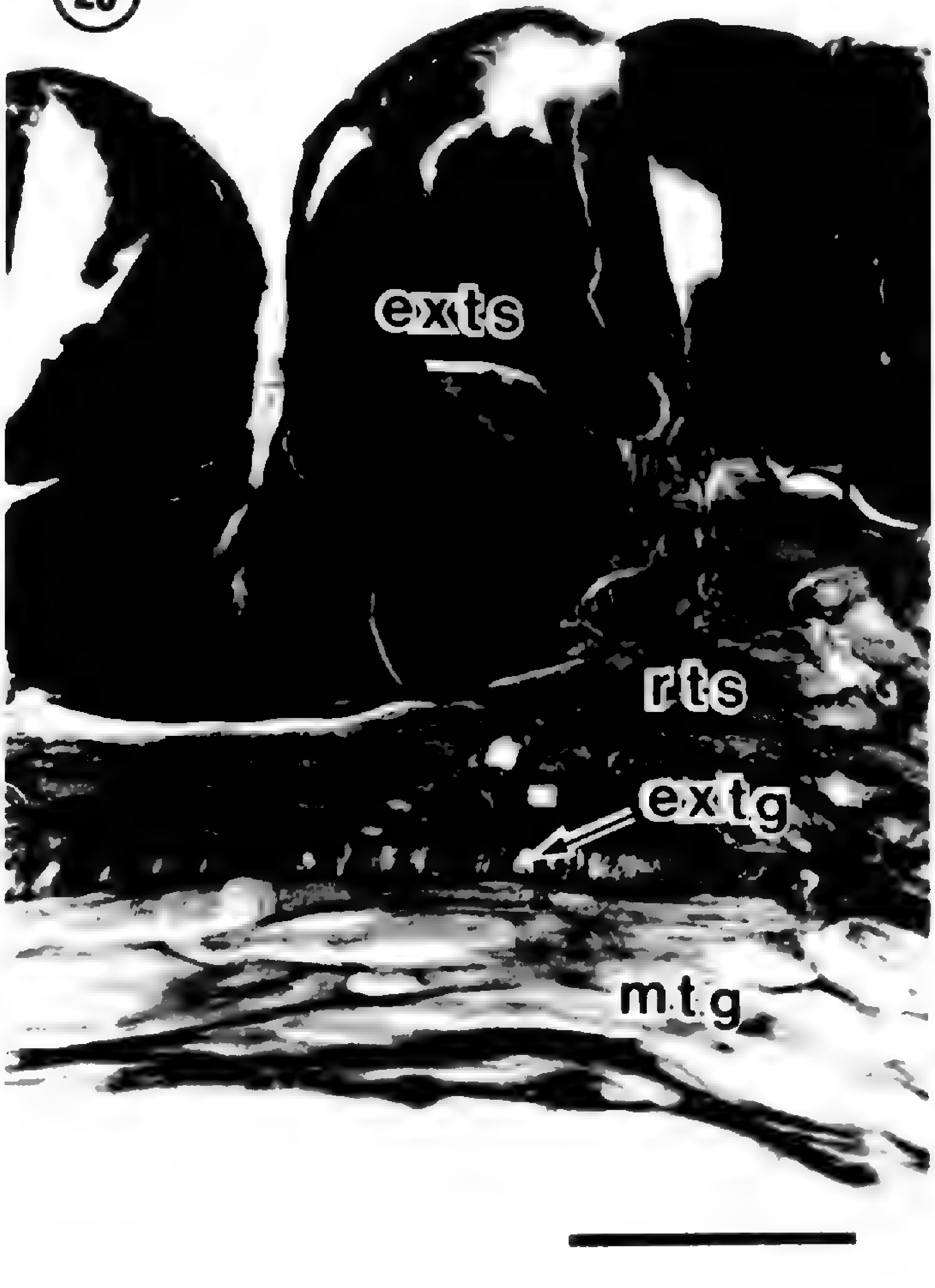

about 1.5 mm long and 0.5 mm thick (R–A) to 0.3 mm thick (L–L). A raphe is relatively conspicuous.

The mature seed coat is 0.12–0.14 mm thick and comprises a thick testa and a thick tegmen (Fig. 19). At the mature embryo sac stage, the outer and the inner integuments are 2 cells thick and 6–8 cells thick, respectively; a nonmultiplicative outer integument is characteristic of the genus. Even in the mature seed coat, all integumentary cell layers persist and form a 1-cell-layered exotesta, a 1-cell-layered endotesta, a 1-cell-layered exotegmen, a 4–6-cell-layered mesotegmen, and a 1-cell-layered endotegmen (Fig. 19). The exotesta is composed of remarkably enlarged, thick-walled, and tanniferous cells; the endotesta of much smaller and unspecialized cells; the exotegmen of radially elongate, thick-walled, fibrous cells; the underlying meso- and endotegmen of nonspecialized but somewhat thick-walled cells. Because of the very conspicuous development of the exotesta, the seed coat of *Gynotroches* is exotestal.

Corner (1976, 1: 161; 2: 260, fig. 315) reported that the mesotegmen (= "mesophyll") is eventually crushed, and interpreted the cell layers below the exotegmen as the "nucellus." However, since the nucellus disintegrates earlier, even in ovular stages (Juncosa, unpubl.), Corner seems to have misunderstood the persistent meso- and endotegmen as the "nucellus."

Pellacalyx. The mature seeds of the genus are elliptic-oblong and small, often with an areolate surface. The shape and size of the mature seeds differ somewhat from species to species (Hou, 1958). The mature seed of *P. lobbii* and *P.* cf. *saccardianus* (Fig. 20) that were investigated in this study are both ellipsoid. Their size is 1.7–1.8 mm long and 0.7–1.1 mm in diameter in *P. lobbii* and 1.2–1.4 mm long and 0.7–0.8 mm in diameter in *P.* cf. *saccardianus.*

The mature seed coat of *Pellacalyx lobbii* and *P.* cf. *saccardianus* is nearly the same, 0.26–0.28 mm thick in total. The seed coat, like that of *Gynotroches,* is composed of a thick testa and a thick tegmen (Fig. 21). The outer and the inner integument are 2 cells thick and 6–8 cells thick, respectively; all cell layers persist up to the mature seed coat stage, although the tegmen may further increase its thickness. Thus the mature seed coat comprises a 1-cell-layered exotesta, a 1-cell-layered endotesta, a 1-cell-layered exotegmen, a 6–9-cell-layered mesotegmen, and a 1-cell-layered endotegmen (Fig. 21). Exotestal cells are enlarged, thick-walled, and tanniferous; endotestal cells are much smaller and not specialized; cells of the exotegmen are longitudinally elongate, thick-walled, and fibrous; and those of the underlying meso- and endotegmen somewhat thick-walled. An undulation or "ribbon-like" structure (Corner, 1976) of the endotesta and the exotegmen is characteristic of the genus. As in the case of *Gynotroches,* Corner (1976, 1: 161, 2: 261, fig. 316) erroneously described the "nucellus" as persistent. But the nucellus that he considered is evidently the persistent meso- and endotegmen, because the nucellus completely disappears at a much earlier stage (Juncosa, unpubl.).

Carallia. The shape of the mature seed differs from species to species: oblong, oblong-ellipsoid, oblong-ovoid, ovoid, or reniform; the seed surface is areolate or corrugate; the size varies between 3 × 1.5 mm and 11 × 4 mm (Hou, 1958). The mature seeds examined of *C. brachiata* and *C. calophylloidea* are reniform, with the micropylar end close to the chalazal end and curved linear embryos (Fig. 22). The size is 5.5–6.0 mm long and 5.0–5.2 mm in diameter (when measured along the longest direction and the thickest middle part of the seed body). The mature seed of *C. eugenioidea,* another species investigated, is oblong-ovoid, and, probably like those of most other species, has a straight linear embryo; it is 3.0 mm long and 1.5 mm in diameter.

The mature seed coat of *Carallia brachiata* is 0.33–0.40 mm thick and is apparently composed only of a thick testa with exotestal cells extremely enlarged, thick-walled, and tanniferous (Fig. 24). Unlike the seed coat of *C. eugenioidea,* there is no tegmen, as Corner (1976) indicated. At the mature embryo sac stage, however, the outer and the inner integuments are 3–4 cells thick and 6–7 cells thick, respectively. Later, the young seed coat is evidently composed of a thicker testa and a thicker tegmen, where the differentiation of a

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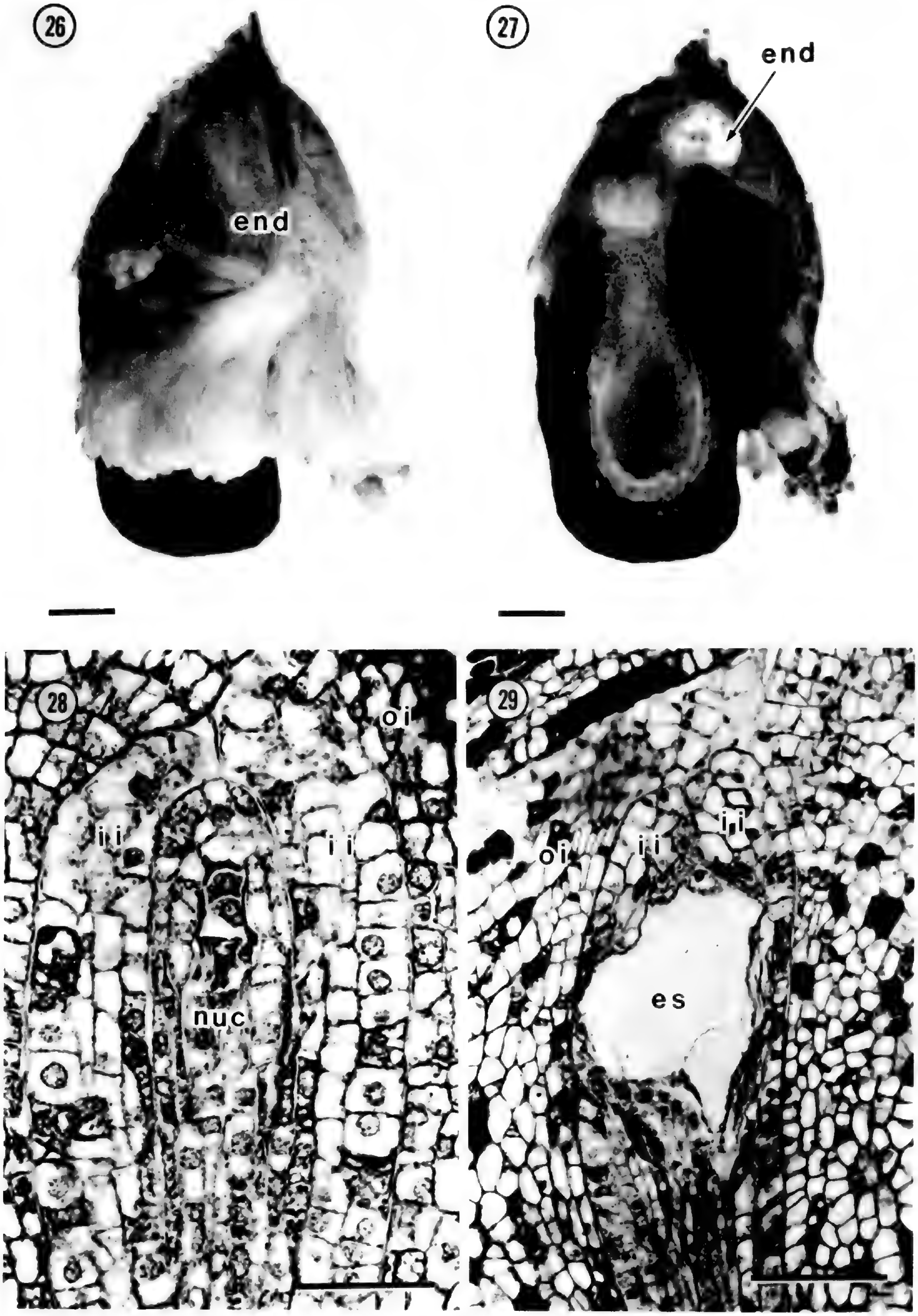
FIGURES 22–25.—*22. Longitudinal hand section of mature nonappendaged seed of* Carallia brachiata.—*23. Longitudinal section of young seed coat of* C. brachiata.—*24. Transverse section (TS) of mature seed coat of* C. brachiata.—*25. TS of mature seed coat of* C. eugenioidea, *with persistent tegmen. Scales = 1 mm (Fig. 22) and 100 µm (Figs. 23–25). em, embryo; exts, exotesta; rts, meso- and endotesta; extg, exotegmen; mtg, mesotegmen; entg, endotegmen.*



FIGURES 26–29. Ceriops tagal.—*26. Mature seed covered with overflowing endosperm.—27. Longitudinal hand section of mature seed showing thick seed coat and endosperm.—28. Longitudinal section (LS) of a young ovule showing that both inner and outer integuments are multiplicative.—29. LS of a mature ovule with an*

TABLE 2. *Comparison in ovule, seed and fruit morphology, and putative methods of seed dispersal.*

Tribe/Genus[1]	Ovules per Carpel[2]	Seeds per Fruit[2]	Seed Size	Seed Form	Fruit	Putative Methods of Seed Dispersal
Tribe Macarisieae						
Blepharistemma	2	6	medium	arillate	capsular	ants (birds?)
Cassipourea	2	(4–)6(–8)	medium	arillate	capsular	ants (birds?)
Comiphyton	2	1	medium	arillate	capsular	ants (birds?)
Anopyxis	2	10	medium	winged	capsular	wind
Macarisia	2	10	medium	winged	capsular	wind
Sterigmapetalum	2	10–12	medium	winged	capsular	wind
Tribe Gynotrocheae						
Crossostylis	2	several–many	small–medium	arillate	capsular	ants and/or birds
Gynotroches	many	many	small	nonappendaged	baccate	birds or mammals
Pellacalyx	many	many	small	nonappendaged	baccate	birds or mammals
Carallia	2	1(–5)	small–medium	nonappendaged	baccate	birds or mammals
Tribe Rhizophoreae						
Bruguiera	2	1	large	nonappendaged	indehiscent, hard-walled	sea water
Ceriops	2	1	large	nonappendaged	indehiscent, hard-walled	sea water
Kandelia	2	1	large	nonappendaged	indehiscent, hard-walled	sea water
Rhizophora	2	1	large	nonappendaged	indehiscent, hard-walled	sea water

[1] Tribal positions of genera follow Melchior (1964) and Floret (1976).

[2] Data from Alston (1925), Arènes (1954), Floret (1974, 1976), Geh & Keng (1974), Hou (1958, 1968), Sprague & Boodle (1909), Steyermark & Liesner (1983), Tomlinson et al. (1979), and our observations.

1-cell-layered exotegmen apparently occurs (Fig. 23). The structure of the exotegmen in the young seed coat in *C. brachiata* looks the same as those of other genera that have the persistent exotegmen. In *C. brachiata* the whole tegmen seems to degenerate as the seed develops. The meso- and endotesta, 10–20 cells thick in total, comprise much smaller cells than those of the exotesta.

The mature seed coat of *Carallia eugenioidea*, like that of *C. brachiata*, has a thick exotesta that comprises extremely enlarged, thick-walled, tanniferous cells (Fig. 25); the total thickness of the seed coat is 0.21–0.39 mm. The meso- and endotesta are histologically very similar and about 4–8 cell layers thick in total. Their cells may contain crystals. *Carallia eugenioidea*, unlike *C. brachiata* but like *Gynotroches* and *Pellacalyx*, has a persistent tegmen, which comprises a 1-cell-layered fibrous exotegmen and a 4–5-cell-layered underlying mesotesta. The endotegmen appears to have nearly collapsed at maturity. At the mature embryo sac stage, the outer and the inner integument are only 3 cells thick and 5–6 cells thick, respectively. Therefore, even in postfertilization stages, nearly all cell layers of the inner integument appear to remain uncrushed.

Both *Carallia brachiata* and *C. eugenioidea* have no vascular bundles in the integuments or seed coats (except where a raphal vascular bundle is continued from a funicle). Because of the very

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organized embryo sac. The inner integument is being broken by an enlarging embryo sac. Scales = 1 mm (Figs. 26, 27), 50 µm (Fig. 28), and 100 µm (Fig. 29). end, endosperm; ii, inner integument; oi, outer integument; es, embryo sac; nuc, nucellus.

TABLE 3. *Comparison in seed anatomy. Abbreviations: oi, outer integument; ii, inner integument; exts, exotesta; mts, mesotesta; ents, endotesta; extg, exotegmen; mtg, mesotegmen; entg, endotegmen; ts, testa. Seed coat categories follow Schmid (1986).*

Tribe/Genus[1]	(Seed Form)	Thickness of Integuments[2] (Cell Layers)		Mature Seed Coat	
		oi	ii	Total Thickness (mm)	Composition
Tribe Macarisieae					
Blepharistemma	(arillate)	3–4	4–5	0.20–0.22	exts + mts + ents + extg (+ mtg?)
Cassipourea	(arillate)	3–6	5–8	0.16–0.22	exts + mts + ents + extg
Comiphyton	(arillate)	?	?	0.14–0.18	exts + mts + ents + extg
Anopyxis	(winged)	4–5	6–7	0.09–0.11	exts (+ mts + ents) + extg
Macarisia	(winged)	?	?	0.05–0.07	exts (+ ents) + extg
Sterigmapetalum	(winged)	2–4	8–10	0.08–0.10	exts + extg
Tribe Gynotrocheae					
Crossostylis	(arillate)	4–5	9–11	0.19–0.20[3] 0.06–0.09[4]	exts + mts + ents + extg[3] exts (+ mts + ents) + extg[4]
Gynotroches	(nonappendaged)	2	8	0.12–0.14	exts + ents + extg + mtg + entg
Pellacalyx	(nonappendaged)	2	6–8	0.26–0.28	exts + ents + extg + mtg + entg
Carallia	(nonappendaged)	3–4	5–7	0.21–0.40	exts + mts + ents (+ extg + mtg + entg)[5]
Tribe Rhizophoreae					
Bruguiera	(nonappendaged)	14–19	5–9	0.79–0.85	ts
Ceriops	(nonappendaged)	8–16	4–5	0.65–1.30	ts
Kandelia	(nonappendaged)	11–16	3–5	0.70–0.90	ts
Rhizophora	(nonappendaged)	13–18[6]	4–6[6]	0.60–1.00	ts

[1] Tribal positions of genera follow Melchior (1964) and Floret (1976).

[2] In *Cassipourea* and *Sterigmapetalum*, inner and outer integuments are both initially two cells thick and later increase their thickness (Tobe & Raven, 1987a); this multiplicative nature of the integuments was further confirmed in *Blepharistemma*, *Ceriops*, and *Kandelia* in the present study and therefore is probably true of all other genera of Rhizophoraceae when they have thick integuments. Measurements of the thickness of the integuments were made on mature ovules with organized embryo sacs.

[3] Data from *Crossostylis grandiflora*.

[4] Data from *Crossostylis biflora* and *C. multiflora*.

[5] In *Carallia* there appears to be a variation with respect to the seed coat structure and vasculature. See text for details.

[6] Data from Carey (1934: 393, fig. 3).

conspicuous development of the exotesta as a mechanical structure, the seed coat of *Carallia* is exotestal.

NONAPPENDAGED VIVIPAROUS SEEDS

Bruguiera, *Ceriops*, *Kandelia*, and *Rhizophora*. The mature seed taken from the indehiscent hard-walled fruit is cylindrical, 6.0–8.0 mm long, and 3.0–3.5 mm in diameter (*C. tagal*; Figs. 26, 27). The mature seed contains ample endosperm, as do those of the inland genera, but the endosperm of all the mangrove genera except *Bruguiera* characteristically extrudes from the micropyle and overflows the seed to fill up the space between the fruit wall and the seed (Haberlandt, 1895; Cook, 1907; Carey, 1934; Juncosa, 1982, 1984b). Such an endosperm structure is most conspicuous in *Ceriops* (Figs. 26, 27), least so in *Kandelia*.

The mature seed coat anatomy does not show any diversity and is nearly the same in all four mangrove genera (Cook, 1907; Carey, 1934; Tobe, unpubl.). The mature seed coat is 0.6–1.3 mm thick in total and comprises only a thick testa; it completely lacks the tegmen. Although the massive inner integument is present at ovular stages (Fig. 28), it completely disintegrates in pre- and post-fertilization stages (Fig. 29; see also Cook, 1907; Carey, 1934). The testa is 20–60 cells thick but it is apparently undifferentiated and merely com-

TABLE 3. *Continued.*

Mature Seed Coat		
Category	Seed Coat Vasculature Present (+) or Absent (−)	Endosperm Overflow from Embryo Sac (+) or Not (−)
exotestal	−	−
exotestal	−	−
exotestal	−	−
exotestal-exotegmic	−	−
exotestal-exotegmic	−	−
exotestal-exotegmic	−	−
exotestal[3]	−	−
exotestal-exotegmic[4]		
exotestal	−	−
exotestal	−	−
exotestal	−[5]	−
undifferentiated	+	+
undifferentiated	+	+
undifferentiated	+	+
undifferentiated	+	+

prises many tanniferous or nontanniferous cells and vascular tissues. According to Carey (1934), in *Rhizophora mucronata* "the outer integument [= testa] is differentiated into two zones, an outer which contains the extensive vascular supply, and an inner in which the cells are regularly arranged and meristematic," but in *Ceriops candolleana* the inner one "is not sharply defined as it is in *Rhizophora*." On the basis of our observations, the vascular strands, which are profusely branched in the testa, are distributed in the middle part of the testa in all the species examined, but they certainly do not always demarcate the inner zone. Since the seed coat anatomy of mangrove genera is not directly comparable with those of inland genera, it can be designated for our discussion as an "undifferentiated" seed coat.

DISCUSSION

As described above, the seeds of Rhizophoraceae show certain fundamental differences in their morphology and anatomy. These features are summarized in Tables 2 and 3. In Table 2, the methods of seed dispersal are also indicated as a basis for subsequent discussions. Despite the diversity of these characters, there are several major character coincidences in certain groups of genera. All Macarisieae with a superior ovary (i.e., unspecialized ovary position), and *Crossostylis* (Gynotrocheae), with an inferior ovary (i.e., derived ovary position), always have either an aril or a wing on the seed; in contrast, the remaining genera, which have an inferior or semi-inferior ovary, lack any sort of seed appendage. Anatomically, all Macarisieae and Gynotrocheae (all inland groups) basically have a similar mature seed coat structure and consistently have a well-developed exotesta and (fibrous) exotegmen; their seed coat is either exotestal or exotestal-exotegmic. In contrast, all Rhizophoreae (the mangrove group) do not have a histologically differentiated seed coat, and they entirely lack a tegmen.

AFFINITIES OF RHIZOPHORAEAE

The accumulating data strongly confirm that Rhizophoraceae are monophyletic. In particular, the combination of subdermally initiated laticifers[4] in the gynoecial wall (and sometimes even in other floral parts) with colletors[5] is unique to Rhizophoraceae (see also Juncosa & Tomlinson, this volume b). Dahlgren (this volume), on the basis of a cladistic approach incorporating various vegetative, reproductive (including embryological), and chemical characters, suggests that Rhizophoraceae are closely related to Elaeocarpaceae of Malvales and Celastraceae of Celastrales and possibly with Erythroxylaceae of Geraniales. We agree with this suggestion. In searching for closely related families, Dahlgren selected as plesiomorphies of Rhizopho-

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[4] Juncosa & Tomlinson (1987) reported the presence of the subdermally initiated laticifers in mangrove genera; Floret (1974: 502, pl. 2, figs. a–c) figured this particular cell layer in the ovary wall of *Comiphyton gabonense*, although he did not specify it in the text. We confirmed the presence of laticifers in the ovary wall or calyx wall of *Gynotroches* (Gynotrocheae), *Anopyxis*, *Blepharistemma*, *Cassipourea*, and *Sterigmapetalum* (Macarisieae) but not in *Pellacalyx*. Material of *Macarisia* was not available to check this character.

[5] The occurrence of colleters has been recorded in *Cassipourea* (Alston, 1925), *Rhizophora* (Gill & Tomlinson, 1969; Lersten & Curtis, 1974), *Bruguiera* and *Kandelia* (Tomlinson et al., 1979; Metcalfe & Chalk, 1950, 1: 602; Hou, 1958). We confirmed the presence of colleters in all other genera available: *Carallia* (Gynotrocheae), *Blepharistemma*, *Macarisia*, and *Sterigmapetalum* (Macarisieae).

raceae the presence of an endothelium, the presence of an aril, the exotegmic seed coat, a chlorophyllous embryo, a Pvc-type sieve-element plastid, the presence of certain types of alkaloids, and the occurrence of a combination of some embryological features. We add the possession of deeply incised petals, because such petals are also undoubtedly plesiomorphic in Rhizophoraceae and Elaeocarpaceae. In addition, the occurrence of multiplicative inner and outer integuments may be more strongly emphasized as another symplesiomorphy shared by all of the families mentioned above.

From the viewpoint of seed morphology and anatomy, *Blepharistemma*, *Cassipourea*, and *Comiphyton* of Macarisieae best agree with Elaeocarpaceae and Celastraceae in having arillate seeds and a fibrous exotegmen (and albuminous seeds and linear embryos; Weibel, 1968; Corner, 1976). The only conspicuous difference between these three genera of Macarisieae and Elaeocarpaceae–Celastraceae is the absence of a persistent meso- and/or endotegmen in the latter. In Rhizophoraceae, a persistent meso- and endotegmen occurs only in *Gynotroches*, *Pellacalyx*, and certain species of *Carallia*, all of which are undoubtedly specialized genera in the family as discussed later. Seed morphology and anatomy have not been investigated fully in Elaeocarpaceae and Celastraceae, and therefore it cannot be determined with certainty that this difference will hold up when more information is available. Critical, however, is the fact that the arillate seeds occur in the genera of Macarisieae that have a superior ovary (a plesiomorphy), and that a fibrous exotegmen is common to all inland genera, which are less advanced in general than the mangrove genera. These features support Dahlgren's suggestion that the presence of an aril and a fibrous exotegmen is plesiomorphic in Rhizophoraceae and justify the use of those seed features in searching for related families.

Comparisons with Anisophylleaceae may also be needed. Even though embryological evidence as well as various other lines of evidence suggest that this family is distinct (Tobe & Raven, 1987b), wood anatomy (Keating & Randrianasolo, this volume; Baas, pers. comm.), and floral morphology (Tobe Baas, pers. comm.), and flora morphology (Tobe & Raven, in press) link it with Rhizophoraceae. Wood and leaf anatomy particularly suggest that Anisophylleaceae and Gynotrocheae may be closely related. Our observations, however, indicate that Anisophylleaceae lack subdermally initiated laticifers and colleters, both of which are characteristic of Rhizophoraceae and support their interpretation as a closely linked monophyletic evolutionary unit not directly related to Anisophylleaceae. The present study further shows that, even apart from the presence or absence of an aril, the seed morphology and anatomy of Anisophylleaceae differ greatly from those of Rhizophoraceae in completely lacking a tegmen (see Tobe & Raven, 1987b, for data on Anisophylleaceae). Therefore, Anisophylleaceae seem clearly to be much more distantly related to Rhizophoraceae than to Elaeocarpaceae and Celastraceae; Rhizophoraceae and Anisophylleaceae are evidently more distantly related than we have suggested elsewhere (Tobe & Raven, in press).

Dahlgren (this volume) has suggested that Elaeocarpaceae have probably been misplaced in Malvales and ought to be transferred near Celastraceae of Celastrales sensu Dahlgren, along with Rhizophoraceae. In terms of seed coat anatomy, most Malvales other than Elaeocarpaceae (e.g., Bombacaceae, Malvaceae, Sterculiaceae, and Tiliaceae) are characterized by a palisadal structure of exotegmen, which is unknown in Elaeocarpaceae (see Corner, 1976). Thus the seed coat anatomy also supports the exclusion of Elaeocarpaceae from Malvales and, as already discussed above, their close relationships with Rhizophoraceae and Celastraceae.

EVOLUTION OF SEEDS IN RHIZOPHORACEAE

As discussed above, the arillate seeds of *Blepharistemma*, *Cassipourea*, and *Comiphyton* (Macarisieae) and *Crossostylis* (Gynotrocheae) apparently represent an archaic, ancestral state in Rhizophoraceae. Judged from the distribution of seed characters in Rhizophoraceae (Tables 2, 3), some of the specialized seed types seem clearly to have evolved more than once.

In Macarisieae, arillate seeds (in *Blepharistemma*, *Cassipourea*, and *Comiphyton*) and winged seeds (in *Anopyxis*, *Macarisia*, and *Sterigmapetalum*), both types borne in capsular fruits, are probably dispersed by ants and wind, respectively; arillate seeds might also be dispersed by birds (see Ridley, 1930; van der Pijl, 1969, for general discussions of seed dispersal). What may have induced an evolutionary change from ant dispersal to wind dispersal is uncertain. Anatomically, in contrast with a relatively thick seed coat of arillate seeds (ca. 0.2 mm thick), the seed coat of winged seeds is thinner (less than 0.1 mm thick). The thinner seed coat might be adaptive in lightening the seeds for wind dispersal. Despite this innovation in seed dispersal, however, the area of distribution of the genera with winged seeds is at present restricted. *Anopyxis* is restricted to West Africa, *Macarisia* to Madagascar, and *Sterigmapetalum* to the Amazon (see Juncosa & Tomlinson, this volume b, for a distribution map). In contrast, *Cassipourea*, which has arillate seeds, is widely distributed in Africa, India, and South America. *Blepharistemma* and *Comiphyton*, also with arillate seeds, are confined to the Kerela district of southwestern India and West Africa, respectively.

The seeds of *Crossostylis*, which traditionally has been assigned to Gynotrocheae, resemble those of *Blepharistemma*, *Cassipourea*, and *Comiphyton* in having an aril and in being produced in capsular fruits. The distribution of *Crossostylis* (comprising 13 species) at present is restricted to and scattered in Polynesian islands, considerably separated from that of Macarisieae; it partly overlaps with the distribution area of the rest of Gynotrocheae and of Rhizophoreae. These facts may suggest that the arillate, small–medium-sized seeds of *Crossostylis* are now or formerly were dispersed by birds from one island to another. Ridley (1930: 423–424) discussed bird-dispersed arillate seeds. Van der Pijl (1969: 30) gives an example: in Indonesia, the fruit-pigeons (*Carpophaga*) eat nutmeg with its aril ("arillode") and disseminate it outside the region. Variation in seed size and seed coat anatomy within the genus may reflect complex methods of seed dispersal.

The nonappendaged seeds of *Carallia*, *Gynotroches*, and *Pellacalyx* (Gynotrocheae), which are borne in baccate fruits, are much smaller than the arillate seeds of Macarisieae in general. The number of seeds per fruit is either 1(–5) (*Carallia*) or ca. 20–40 (*Gynotroches* and *Pellacalyx*). Those seeds are very hard and were difficult to section with a microtome. Fruit and seed structure of these genera seem to indicate that the seeds are endozoochorous and dispersed by birds or mammals. Bird or bat dispersal seems to provide a likely explanation of the wide distribution of these genera throughout the islands of southeastern Asia, west to India and Madagascar (*Carallia*).

Seeds of the four mangrove genera—*Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora* of Rhizophoreae—produce viviparous seedlings in indehiscent hard-walled fruits. They do not exhibit histological differentiation in their seed coats, probably because the seeds are protected by the fruit wall and therefore are not specialized against external environments. When they fall from the parent plant, the dropped fruits or seedlings are undoubtedly dispersed by sea water, as discussed by many workers (e.g., Ridley, 1930; Hou, 1958). The mangrove genera are at present best represented from the western Pacific to the Indian Ocean; *Rhizophora* is pantropical (Graham, 1964). *Rhizophora*, the most widely distributed genus of the family, is also the only one that is wind pollinated (Tomlinson et al., 1979), a system that might be well suited to newly colonized habitats.

To sum up, the seeds of Rhizophoraceae seem to have evolved as the result of adaptation to changes in seed dispersal methods, that is, from ant dispersal to dispersal by wind, bird, mammal or water. The diversity in the seed morphology and anatomy, in conjunction with the diversity of fruit structure, is well explained by such changes in the methods of seed dispersal, and vice versa. However, the actual methods of dispersal of the seeds of the nonmangrove genera are very poorly known and should be studied in the field.

PHYLOGENETIC RELATIONSHIPS WITHIN RHIZOPHORACEAE

The accepted infrafamilial classification of Rhizophoraceae is based primarily on androecial position (i.e., perigynous or epigynous), the number of carpels or ovarian locules, and the number of ovules per carpel (e.g., Melchior, 1964). Data from seed morphology and anatomy and fruit structure generally support the traditional classification in separating Macarisieae, Gynotrocheae, and Rhizophoraceae as distinct units.

For the cladistic analysis, we chose 16 characters whose character-state evaluations were possible; these include characters of embryology, seed morphology and anatomy, and floral morphology (Table 4). The character-state evaluation in Rhizophoraceae was made on the basis of outgroup comparison with Elaeocarpaceae and/or Celastraceae. Data on Rhizophoraceae, Elaeocarpaceae, and Celastraceae were obtained from the following references: Rhizophoraceae—Schimper (1893), Haberlandt (1895), Cook (1907), Carey (1934), Melchior (1964), Floret (1974, 1976), Corner (1976), Tomlinson et al. (1979), Juncosa (1982, 1984a, b), Tobe & Raven (1987a), and present study; Elaeocarpaceae—Mauritzon (1934), Venkata Rao (1953), Corner (1976), Cronquist (1981), and Hyland & Coode (1982); Celastraceae—Mauritzon (1936), Berkeley (1953), Adatia & Gavde (1962), Copeland (1966), Corner (1976), and Cronquist (1981). Results of character-state evaluation within the Rhizophoraceae are provided in Table 4, their distribution in the family in Table 5, and a cladogram based on these features in Fig. 30.

The cladogram (Fig. 30) indicates that, except for six genera of Macarisieae, the eight remaining

TABLE 4. *Character-state evaluation of some selected reproductive characters in Rhizophoraceae.*

Character	Plesiomorphy[1]	Apomorphy
1. Ovary position	superior	inferior or semi-inferior
2. Numbers of ovules per carpel	2	many
3. Structure of nucellus	crassinucellate	tenuinucellate
4. Number of archesporial cells in ovule	many	1
5. Formation of endothelium	occurs	absent
6. Nature of outer integument	multiplicative	not multiplicative
7. Integumentary (or seed coat) vasculature	absent	present
8. Development of endosperm	not overflow from embryo sac	overflow
9. Seedling	not viviparous	viviparous
10. Fruit morphology	capsular	baccate or indehiscent
11. Type of seed appendage	aril	wing
12. Presence or absence of seed appendage	present	absent
13. Total thickness of mature seed coat	> 0.1 mm	< 0.1 mm
14. Histological differentiation of seed coat	occurs	does not occur
15. Development of exotegmen	persistent, fibrous	early disintegration
16. Development of meso- and endotegmen	early disintegration	persistent

[1] All plesiomorphies occur not only in some or all inland genera of Rhizophoraceae but also are common to the outgroups, e.g., Elaeocarpaceae and Celastraceae. References for data on each family are presented in the text.

genera of the family share an inferior or semi-inferior ovary (a synapomorphy). The genera of Macarisieae retain many plesiomorphic features, including a superior ovary. Within Macarisieae, Floret (1976) recognized three subgroups on the basis of floral and seed characters: 1) *Anopyxis*, *Macarisia*, and *Sterigmapetalum*; 2) *Blepharistemma*, *Comiphyton*, and *Cassipourea* subg. *Dactylopetalum*; and 3) the three remaining subgenera of *Cassipourea* (see Tobe & Raven, 1987a, for revision). Later, emphasizing probable coincidences in the seed morphology and anatomy, but on the basis of meager data, we suggested closer affinities among *Anopyxis*, *Macarisia*, and *Sterigmapetalum* on the one hand, and among *Blepharistemma*, *Cassipourea*, and *Comiphyton*

TABLE 5. *Distribution of character states of some selected reproductive characters in Rhizophoraceae. Plesiomorphy (−); Apomorphy (+). Character numbers correspond to those given in Table 4.*

	Character															
Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Blepharistemma (BLE)[1]	−	−	−	?	−	−	−	−	−	−	−	−	−	−	−	−
Cassipourea (CAS)	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Comiphyton (COM)	−	−	−	?	−	−	−	−	−	−	−	−	−	−	−	−
Anopyxis (ANO)	−	−	−	?	−	−	−	−	−	−	+	−	+	−	−	−
Macarisia (MAC)	−	−	−	?	−	−	−	−	−	−	+	−	+	−	−	−
Sterigmapetalum (STR)	−	−	−	−	−	−	−	−	−	−	+	−	+	−	−	−
Crossostylis (CRS)	+	−	−	−[2]	−	−	−	−	−	−	−	−	−	−	−	−
Gynotroches (GYN)	+	+	+	+	−	+	−	−	−	+		+	−	−	−	+
Pellacalyx (PEL)	+	+	+	+	−	+	−	−	−	+		+	−	−	−	+
Carallia (CAR)	+	−	−	+	−	−	−	−	−	+		+	−	−	−	+
Bruguiera (BRU)	+	−	−	?	+	−	+	+	+	+		+	−	+	+	−
Ceriops (CER)	+	−	−	−[3]	+	−	+	+	+	+		+	−	+	+	−
Kandelia (KAN)	+	−	−	?	+	−	+	+	+	+		+	−	+	+	−
Rhizophora (RHZ)	+	−	−	?	+	−	+	+	+	+		+	−	+	+	−

[1] Three-letter abbreviations given in parentheses are used in a cladogram (Fig. 30).

[2] Data from personal observations on *Crossostylis grandiflora*.

[3] The number of archesporial cells in an ovule in the mangrove genera is not well documented; Karsten (1891) described two megaspore mother cells in *Ceriops candolleana*. This character must be confirmed in this and other mangrove genera.

on the other (Tobe & Raven, 1987a). The present study confirms the relationships that we suggested then. Character-state comparisons indicate that *Anopyxis, Macarisia,* and *Sterigmapetalum* share the synapormorphies winged seeds and a thinner seed coat, and thus constitute a single clade. On the basis of seed morphology and anatomy, therefore, we propose the division of Macarisieae into two subtribes: 1) Cassipourinae, comprising *Blepharistemma, Cassipourea,* and *Comiphyton*; and 2) Macarisinae, comprising *Anopyxis, Macarisia,* and *Sterigmapetalum.* Wood anatomy (van Vliet, 1976) and leaf architecture (Keating & Randrianasolo, this volume) do not provide a clear distinction between the two subtribes; wood anatomical comparison rather suggests that *Comiphyton* is intermediate between *Macarisia* (Macarisinae) and *Cassipourea* (Cassipourinae) (van Vliet, 1976). An overall comparison of their vegetative morphology (Sprague & Boodle, 1909), however, suggests close affinities between *Anopyxis* and *Macarisia.* Leaf anatomy strongly supports our suggested subtribal classification (Baas, pers. comm.): *Anopyxis–Macarisia(–Sterigmapetalum)* have a nonpluriseriate epidermis and a differential hypodermis, whereas *Blepharistemma–Cassipourea(–Comiphyton)* have a pluriseriate epidermis but lack a discernible hypodermis. For further elucidation of the relationships in this group, a comprehensive study of the largest and most widely distributed genus, *Cassipourea,* seems essential.

Crossostylis, which has been placed in Gynotrocheae, shares only one apomorphy (an inferior ovary) with any group other than the six genera of Macarisieae. Apart from the ovary position, in contrast, *Crossostylis* agrees nearly completely with Macarisieae in many plesiomorphic features. Juncosa & Tomlinson (this volume b) summarize that *Crossostylis* shares stilt roots, roots having no hairs, bijugate phyllotaxy, imbricate stipules, flat floral apices, and several-layered laticifers with other Gynotrocheae (sometimes excepting *Pellacalyx*), and shares most of these features also with Rhizophoreae. It is uncertain whether those shared structures represent apomorphic character states or not, but at least some of them are probably synapomorphies, suggesting phylogenetic affinities of *Crossostylis* with the rest of Gynotrocheae and all Rhizophoreae.

Crossostylis, however, is clearly distinguished from other Gynotrocheae and all Rhizophoreae in not sharing the apomorphies noncapsular fruit and the nonappendaged seed. The cladistic analysis thus indicates mutual closer affinities between the rest of Gynotrocheae and all Rhizophoreae, and leaves *Crossostylis* in a distinct evolutionary line. Juncosa (unpubl.) suggests an intermediate position for *Crossostylis* between Macarisieae and Gynotrocheae, and we agree with this interpretation. *Crossostylis* seems to be more appropriately assigned to its own tribe, Crossostylideae, as also suggested by Juncosa (pers. comm.).

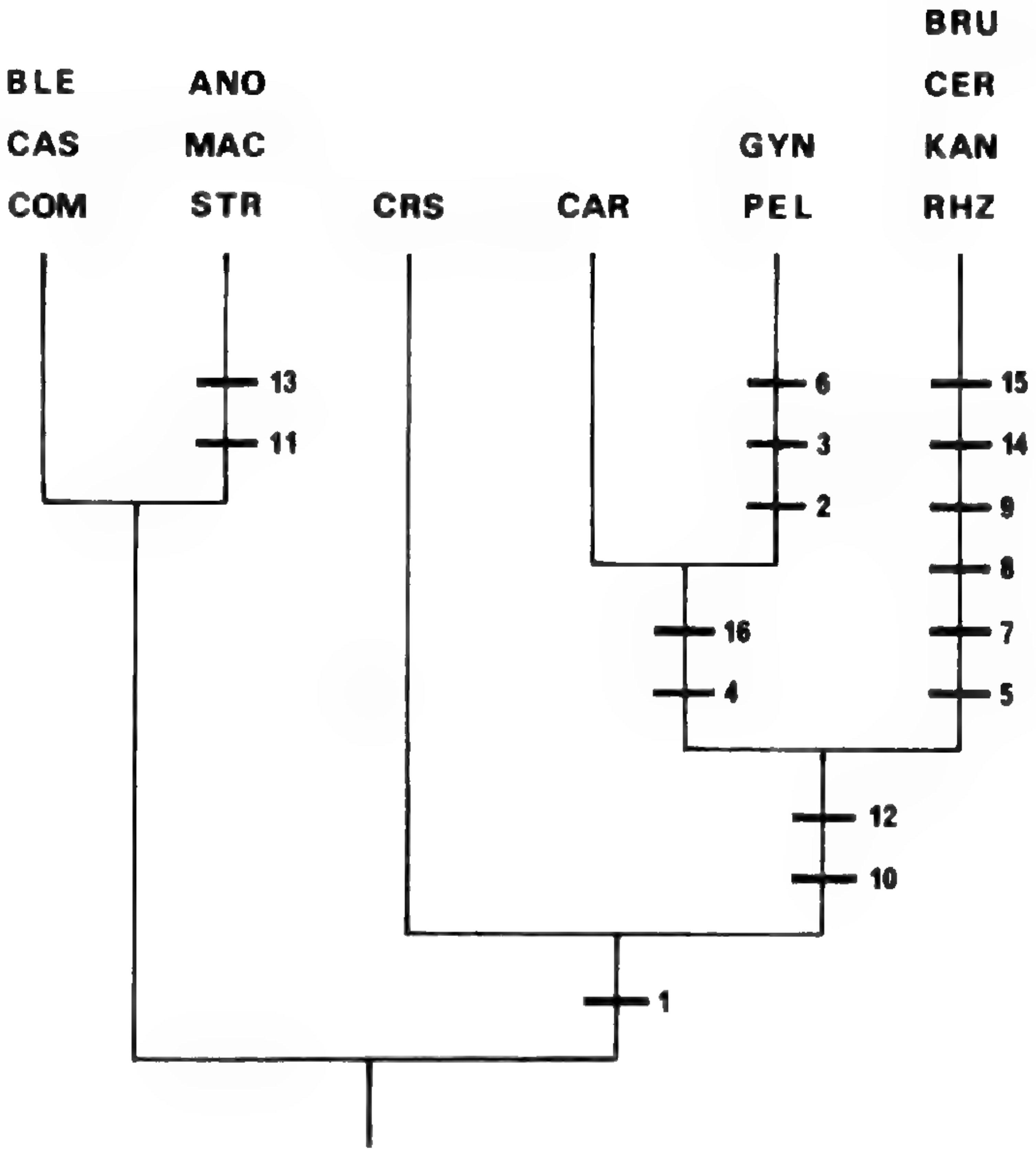

FIGURE 30. *A cladogram illustrating evolutionary interrelationships of the genera of Rhizophoraceae. Character numbers 1–16 and three-letter abbreviations of genera are shown in Tables 4 and 5, respectively.*

Carallia, Gynotroches, and *Pellacalyx* have been grouped in Gynotrocheae; this treatment seems reasonable because as a group they have no synapomorphies with Rhizophoreae. The three genera share two synapomorphies: a one-celled ovuled archesporium and a persistent meso- and endotegmen (although the latter feature may be inconsistent in *Carallia*). *Gynotroches* and *Pellacalyx* closely resemble each other in sharing the following additional apomorphies: a multiovulate carpel, a tenuinucellate ovule, and a nonmultiplicative outer integument; in contrast, *Carallia* is characterized by retaining the plesiomorphic states of those characters. Thus, we suggest that *Gynotroches* and *Pellacalyx* should be segregated as a subtribe Gynotrochinae, and *Carallia* should be treated as the monogeneric subtribe Carallinae.

In considering the phylogenetic relationships of *Carallia,* the diversity within the genus must be taken into account. For example, with respect to the mature seed coat structure, Corner (1976) described "tegmen without trace" in *Carallia* *brachiata*; likewise, Juncosa (unpubl.) did not see a tegmen in *C. borneensis*. We did not observe a tegmen in the mature seed coat of *C. brachiata*, either (Fig. 24). In contrast, in the mature seed coat of *C. eugenioidea* (Fig. 25) and in the younger seed coat of *C. brachiata* (Fig. 23), we observed thick, distinct tegmic cell layers, the outermost of which even assumed the fibrous, exotegmenlike structure that is characteristic of all other inland genera. In its lack of a tegmen in the mature seed coat, *Carallia* might be compared to Rhizophoreae; however, when they are compared throughout their ontogeny, they appear to be quite distinct. Thus, in Rhizophoreae, the inner integument or young tegmen soon disintegrates because of the enlargement of the embryo sac in postfertilization stages, but in *Carallia* it does not disintegrate until much later, and it may even persist, as in *C. eugenioidea*. Furthermore, in *Carallia* the outermost cell layer of the inner integument differentiates into the fibrous exotegmen, but in Rhizophoreae such a histological differentiation has not been observed.

The thickness and vasculature of the outer integument in *Carallia* seems to be diverse. According to Juncosa (unpubl.), *C. borneensis* has a 7–15-cell-layered outer integument at anthesis, which is vascularized as it is in Rhizophoreae. However, in the samples of *C. brachiata* and *C. eugenioidea* we observed, there were only 3–4-cell-layered outer integuments at the mature embryo sac stage; the outer integument of those two species has not space for vascularization at that stage, and no vascular bundles were observed in testae even in later stages, although the raphe always contained some vascular tissues.

To sum up, we suggest that in *Carallia*, as well as in *Gynotroches* and *Pellacalyx*, the tegmen was originally persistent, but that a tegmenless seed coat (as in *C. brachiata* and *C. borneensis*) apparently evolved, almost certainly independently from Rhizophoreae. Likewise, the vasculature of the testa in *Carallia* seems to have been acquired only in certain species of the genus with an extremely thickened outer integument or testa, but probably independently of the evolutionary line leading to Rhizophoreae.

Although *Carallia* is diverse, it apparently should continue to be placed in Gynotrocheae, along with *Gynotroches* and *Pallacalyx*.

The four mangrove genera—*Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora*—share the following synapomorphies: endothelium not formed, outer integument vascularized, endosperm overflowing, viviparous seedlings, testa not differentiated histologically, and tegmen lacking. Thus, the mangrove genera undoubtedly form a coherent group, Rhizophoreae. Wood anatomy (van Vliet, 1976), leaf architecture (Keating & Randrianasolo, this volume), leaf anatomy (particularly stomatal type; Baas, pers. comm.), and consistent distinct chromosome number ($2n = 36$; Yoshioka et al., 1984) also support the coherence of Rhizophoreae. The cladistic analysis indicates that Rhizophoreae have direct relationships with Gynotrocheae (not including *Crossostylis*), rather than with Macarisieae.

On the basis of our cladistic analysis, we suggest the following revised classification:

Family Rhizophoraceae (not including Anisophylleaceae)
- Tribe Macarisieae
  - Subtribe Cassipourinae
    - *Blepharistemma*
    - *Cassipourea*
    - *Comiphyton*
  - Subtribe Macarisinae
    - *Anopyxis*
    - *Macarisia*
    - *Sterigmapetalum*
- Tribe Crossostylideae
    - *Crossostylis*
- Tribe Gynotrocheae
  - Subtribe Carallinae
    - *Carallia*
  - Subtribe Gynotrochinae
    - *Gynotroches*
    - *Pellacalyx*
- Tribe Rhizophoreae
    - *Bruguiera*
    - *Ceriops*
    - *Kandelia*
    - *Rhizophora*

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THE CONTRIBUTION OF LEAF ARCHITECTURE AND WOOD ANATOMY TO CLASSIFICATION OF THE RHIZOPHORACEAE AND ANISOPHYLLEACEAE[1]

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ABSTRACT

Leaf-architectural and wood-anatomical data on the 18 genera traditionally considered to comprise the Rhizophoraceae were analyzed for insight on the intergeneric affinities. The four genera of the tribe Anisophylleae, considered on other lines of evidence to comprise the family Anisophylleaceae, are not readily separated using new data from leaf structure, or from a new look at the wood-anatomical literature. Leaves of both families are elliptic, and few features distinguish the two families or help separate the tribes of Rhizophoraceae s. str. or help separate the tribes. Anisophylleaceae have no marginal teeth or glands; they differ mainly from the Rhizophoraceae in having alternate leaves and no stipules. Leaves of the tribes Macarisieae, Gynotrocheae, and Rhizophoreae show some tribal-level variations in secondary venation, crystal type and distribution, and a few other features. The Rhizophoraceae leaves have an apiculate glandular tooth known as the Macarisioid type. Wood features, analyzed from the literature, do not readily distinguish the two families. Possible affinities of the Anisophylleaceae are not easily established using vegetative data. The Rhizophoraceae share a number of features with Celastraceae, Eleaocarpaceae, Hugoniaceae, Lepidobotryaceae, and Oxalidaceae.

The Rhizophoraceae are a family of tropical-forest and mangrove trees variously considered as comprising either 14 or 18 genera, a disparity coming from inclusion of the genera *Anisophyllea*, *Combretocarpus*, *Poga*, and *Polygonanthus* as a tribe Anisophylleae vs. their exclusion as the family Anisophylleaceae. Tobe & Raven (1987a) discussed the taxonomic history of the Anisophylleaceae, while van Vliet (1976) and Juncosa & Tomlinson (this volume) provided a detailed taxonomic background on the Rhizophoraceae (sensu lato). However, to place this contribution in perspective, a brief review follows.

Among modern systems, the genera of Anisophylleae have been included as a tribe in the Rhizophoraceae by Melchior (1964) and Takhtajan (1980), and by Thorne (1983) as a subfamily. Dahlgren (1983) and Cronquist (1983) recognized the separate family Ansiophylleaceae. In a review of the taxonomy and ecology of the Asian Rhizophoraceae, Hou (1958) included the genera of Anisophylleae. Prance et al. (1975) also followed this approach in a revision of Amazonian Rhizophoraceae. Van Vliet (1976), in a detailed analysis of the wood anatomy, concluded that the Rhizophoraceae comprise 18 genera arranged in four tribes (see Table 1), including the four genera assigned to the tribe Anisophylleae. Van Vliet (1976) concluded that wood-anatomical data provide no convincing case for excluding the Anisophylleae. This is no doubt partly due to the unusual amount of variation in the three tribes of the Rhizophoraceae s. str. In Table 1, we recognized a fifth tribe, Hypogyneae, which was separated from the tribe Macarisieae by Steyermark & Liesner (1983) on the basis of several morphological features (but cf. Juncosa and Tomlinson, this volume). Tobe & Raven (1987a) found that floral, seed, and embryo-

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TABLE 1. *Selected leaf characters of the genera of Rhizophoraceae and Anisophylleaceae.*[1]

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
	Phyllotaxy	Stipules	Margin	Margin glands	Venation type	Rank	Highest vein order	Areoles	Free endings	Tracheoids
Macarisieae										
Anopyxis	O	+	E	+	Eb	3r0	5–6	P	1–7	–
Blepharistemma	O	+	E, T	+	Eb	3r0–3r3	6–7	P	0–5	–
Comiphyton	O	+	E	+	E	3r1	6	P	0–2	–
Macarisia	O	+	E, T	+	E, Eb	2r0	6–7	P	0–3	F
Cassipourea	O	+	E, T	(+)	B, R	1r3-3r0	5–7	I	0–8	+, –
Sterigmapetalum	O	+	E	+	B	3r0-4r0	6	I	0–3	–
Gynotrocheae										
Carallia	O	+	E, T	+	B, E	1r2	5–7	I	0–6	F
Crossostylis	O	+	E, T	+	B, Eb	1r3–3r0	7	P	2–9	–
Gynotroches	O	+	E	?	E	3r0	7	I	0–9	–
Pellacalyx	O	+	E	+	Eb	2r3	6	P	3–10	–
Rhizophoreae										
Bruguiera	O	+	E	+	B	2r0–3r0	5–7	I	0–8	C
Ceriops	O	+	E	?	B	3r2	5–6	I	0–4	?
Kandelia	O	+	E	–	B	3r0	6	I	0–6	C
Rhizophora	O	+	E	–	B	3r0	6–8	I	0–4	?
Anisophylleaceae										
Anisophyllea	A	–	E	+	A, B	2r0–4r1	6–10	I	0–18	–, F
Combretocarpus	O	–	E	–	Eb	4r2	6	I	0–4	F
Poga	A	–	E	–	Eb	2r0	6–10	I	3–20	C
Polygonanthus	A	–	E	–	Eb	4r1	5	I	0–6	–

[1] Symbols used: 1. Phyllotaxy: O = opposite, A = alternate; 2. Stipules: + = present, – = absent; 3. Margin: E = entire, T = toothed; 4. Marginal glands: + = present, (+) = uncommon or doubtful, – = not detected; 5. Venation: A = acrodromous, B = brochidodromous, E = eucamptodromous, Eb = basally eucamptodromous and distally brochidodromous, R = reversed eucamptodromous; 6. Rank: e.g., 1r2 = first rank, second of three subranks (see Hickey, 1977); 7. Highest vein order present; 8. Areoles: P = polygonal, I = irregular; 9. Number of free vein endings per areole; 10. Tracheoids (terminal idioblastic sclereids): + = present, – = absent, F = few, C = common; 11. Marginal venation: F = fimbriate, I = incompletely looped, L = looped, Im = intramarginal vein; 12. Sclereids (diffuse): – = absent, A = astrosclereids; 13. Adaxial epidermis surface cell shape: P = polygonal, S = sinuous, I = interlocking, * = some larger cells present with radiating neighbors; 14. Hypoderm: + = present, – = absent; 15. Abaxial epidermis surface cell shape: P = polygonal, S = sinuous, I = interlocking, * = surface papillate; 16. Stomata: B = brachyparacytic, P = paracytic, C = cyclocytic, Ai = anisocytic, An = anomocytic, D = diacytic; 17. Fibers at veins: + = present; 18. Crystal type: D = druse, P = prismatic, S = crystal sand, – = absent; Crystal distribution: R = random, V = clustered along veins, Mv = along midvein only; Crystal frequency: A = abundant, Vc = very common, C = common, F = few; 19. Trichomes (simple): C = common, F = few, – = absent.

logical characters do not support segregation of this tribe.

The ordinal position of the 18 genera is even less agreed upon than the family composition. Melchior (1964) and Takhtajan (1980) assigned the Rhizophoraceae, including Anisophylleae, to the Myrtales. However, the consensus of the symposium on Myrtales at Sydney in 1981 (see Dahlgren & Thorne, 1984) was that the family should be excluded from that order. Cronquist (1983) retained the two families apart in his Rosidae with Anisophylleaceae in Rosales and Rhizophoraceae in the Rhizophorales. Dahlgren (1983) placed the Anisophylleaceae in the Corniflorae (Cornales) and the Rhizophoraceae in the Myrtiflorae (Rhizophorales). Thorne (1983) placed his Rhizophoraceae s. l. in the Corniflorae (Cornales). While a large literature has developed on various aspects of mangrove biology and management (see Rollet, 1981), the evolutionary relationships of the mangrove genera and their relatives remain much less studied.

Leaf architecture of samples of all genera of Rhizophoraceae and Anisophylleaceae is examined in this study to assess the contribution of foliar

TABLE 1. *Continued.*

11.	12.	13.	14.	15.	16.	17.	18. Crystal			19.
Marginal venation	Sclereids	Adaxial epidermis	Hypoderm	Abaxial epidermis	Stomata	Fibers at veins	Type	Distribution	Frequency	Trichomes
I, L	–	P	–	P	?	+	P	R, V	C	C
L	–	P	–	S	Ai, C	+	P	R, V	C	F
L	–	P	–	P	An, B	+	P	R	A	F
L	–	P	+	?*	?	+	P	R, V	Vc	–, C
L, I	–	P	–	P	B?	+	P	R, V	F, A	–, C
I, L	–	P	–, +	P	B, Ai	+	P	R, V	C, F	–
I, L	–	P*	–	P	B?	+	D	R	F	–
L	–	P	–	P	B, An	+	D	R, V	F, A	–
I, L	–	P	–	P	B, An	+	D	V	A	–
L	–	P	–	P	?	+	D	V	F	–
I, L	A, –	P	–	P	C	+	D	R, V	A	–
L	A?	P	–	P	C	+	D	R	A	–
L, F	–	P	–	P	C	+	S	R	C	–
L	A	P	+	P	C	+	D	R, V	C	–
I, L, Im	–	P, S, I	–	P, S, I	An, D, P	+	D	R, V	C, A	–
I, L	–	P	–	P	?	+	–	?	?	–
I	–	P	–	P	An, D, B	+	D	R, V	C, F	–
L	–	P*	–	P	P, An	+	–	?	?	–

characters to several taxonomic problems. Histological features detectable from cleared whole leaves are included in the observations. The leaf-architecture scheme developed by Hickey (1973, 1979), and later applied by Doyle & Hickey (1976), Hickey & Wolfe (1975), and Hickey & Doyle (1977) has supplied a practical basis for gathering and interpreting these data in an evolutionary context. In addition, we have reviewed the wood-anatomical data from the comprehensive studies of Marco (1935) and van Vliet (1976). Using these data we will assess the intergeneric variability, the degree to which tribal groupings can be supported, and whether the exclusion of Anisophylleaceae from Rhizophoraceae can be sustained. These are the easier tasks. More complex is an assessment of the position of the Ansiophylleaceae among the angiosperms.

MATERIALS AND METHODS

The leaf sample, including 53 specimens representing all 18 genera, was obtained from the herbaria of the Missouri Botanical Garden (MO), Paris (P), and some individual collectors. In addition, descriptions were amplified after inspecting all Rhizophoraceae slides deposited in the National Cleared Leaf Collection currently deposited at the Peabody Museum of Yale University. All specimens are cited following generic descriptions.

All of the leaves were studied as safranin-stained clearings. The permanent specimens prepared for this study were cleared in 5% NaOH followed when necessary by 5.25% $NaHCO_3$ (commercial laundry bleach). Chloral hydrate was avoided, as it tends to destroy the differential stainability of venation. The clearings were dehydrated to 95% ethanol, stained in 0.5% safranin-O in 95% ethanol, dehydrated to toluene, and mounted between glass plates in cover glass resin. Hickey's (1979) descriptive protocol was followed. Leaf rank on a scale of 1–4 with three subdivisions within each rank, as presented by Hickey (1977 and pers. comm.), was scored for each specimen. The term "domain" is used to denote the area bounded by veins of a given rank, except that intercostal area is used instead of "secondary domain." The shape of intercostal areas and higher-order domains is a useful measure of the regularity of architectural organization (Hickey, pers. comm.).

Except where descriptions from other literature are specifically noted, all of the descriptions given here and used for discussions and conclusions are restricted to the specimens cited. No claim is made that the sample observed encompasses all of the variation, particularly in the larger genera.

OBSERVATIONS

Anisophyllea R. Br. ex Sabine (Figs. 32–39)

Leaves are chartaceous to membranaceous, entire, markedly asymmetrical in most species, ovate on one side, elliptic to obovate on the other. Those of *A. pomifera* are symmetrical and suborbiculate. Vincent & Tomlinson (1983) described the marked dimorphy in *A. disticha*. Venation is acrodromous, basal or suprabasal; the primary vein is slightly curved and is the same size as or larger than the acrodromous secondaries. Secondaries are perfect, extending more than ⅔ the distance toward the apex. Simple intersecondaries are present or absent. The uniformly curved secondaries originate from the primary at a narrow or wide acute angle, the upper more obtuse or acute than the lower. Tertiaries are percurrent and forked or unforked and may be acute or perpendicular to the primary vein; angle of origin is acute or right, exmedially or admedially to the secondaries. Quaternary veins may be percurrent or not and are random orthogonal to the tertiaries. Stomata appear to have 2 large paracytic guard cells surrounded by 8–10 smaller epidermal cells with radiating anticlinal walls. The margin in *A. meniandii* has shallow convex glands that are not approached by any larger veins. Minor veins in the area often have tracheoidal endings but do not closely approach the gland. Other species have no detectable glands.

Specimens examined. *Anisophyllea apetala* King: SARAWAK. *Clemans & Clemans 21596* (MO). *A. boehmii* Engl.: Burundi, *Reekmans 2686* (MO). *A. cinnamomoides* (Gardner & Champ.) Alston: Sri Lanka, *Meijer 1709* (MO), *Macnae s. n.* (1968) (US; LJH 1855). *A. disticha* (Jack) Baillon: Sumatra, *Toroes 2610* (US; LJH 1856); Borneo, *Elmer 20409* (MO). *A. griffithii* (Jack) Baillon: North Borneo, *Anderson 4290* (MO). *A. meniandii* Aubrév. & Pellagrin: Liberia, *Jacques-Georges 25941* (MO). *A. poggei* Engl. ex De Wild & T. Durand: Congo, *Makany 1054* (MO). *A. pomifera* Engl., Malawi, *Pawek 7414* (MO).

Anopyxis (Pierre) Engl. (Figs. 1, 2)

Leaves are symmetrical, oblanceolate, with an attenuate apex and cuneate base. The texture is membranaceous and the margin entire. The eucamptodromous pattern tends toward brochidodromy distally. The primary vein is moderately thick and straight. Secondary veins have a widely acute divergence, are uniform base to apex, and curve uniformly toward the margin. Long sinuous intersecondaries are common. Tertiary veins are acute exmedially and right or obtuse admedially. They are often percurrent with intersecondaries and, distally, with secondaries. Tertiary veins are generally oblique to the primary vein. Quaternary and quinternary veins produce orthogonal domains of irregular shape. The polygonal islets are often formed in interquinternary domains. Occasional marginal glands are vascularized by short straight veins that originate on a secondary arch. The gland is a shallow mound on the edge of the entire margin.

Specimen examined. *Anopyxis calaensis* Sprague: Nigeria, *Kennedy 1561* (MO).

Blepharistemma Wall. ex Benth. (Figs. 3–6)

The leaf is symmetrical and elliptic, obovate, or lanceolate with an acute apex and an acute or obtuse base. Texture is chartaceous or membranaceous. The margin is shallowly toothed in *B. corymbosum* or entire in *B. membranifolia*. Eucamptodromous secondaries originate from the straight primary vein at a uniform wide acute or acute angle. In the distal half of *B. membranifolia* the secondaries are brochidodromous. Occasional simple intersecondaries are present and may be exmedially forked. Tertiary veins are sinuously percurrent, often forked, forming polygonal domains with intersecondaries. Tertiary angles of origin are variable, but the tertiaries tend to be oblique to the primary vein. They originate mostly orthogonal to the secondaries but may be exmedially acute. Quaternaries and quinternaries form irregular orthogonal domains. Teeth are shallow, strongly asymmetric, and curved inward to a small concave sinus. An asymmetrical turbinate gland having a superficial columnar epidermis protrudes from the apex parallel to the margin or incurved toward the sinus. A single vein the diameter of a secondary originates from a secondary arch and curves apically to the sinus, ending in the tooth apex, just below the gland. Just inside the margin, tertiary and quaternary veins branch off from the tooth vein and become part of the looped marginal venation.

Specimens examined. *Blepharistemma corymbosum* Wall. & Benth.: India, *Metz 713* (P). *B. membranifolia* (Miq.) Ding Hou: India (CAZ).

Bruguiera Lam. (Fig. 27)

Leaves are coriaceous or chartaceous, entire, symmetrical, elliptic or oblong, with an acute apex and base. Venation, not easily seen, is brochidodromous with tertiary and quaternary arches or with a tendency toward a strong (sub)marginal secondary collector vein. Secondaries diverge from the stout, straight primary vein at a wide-acute to acute-decurrent angle and meet the superadjacent secondaries at an obtuse or right angle. The upper secondaries may be more obtuse than the lower. Intersecondaries are simple or composite and are often admedially ramified or "perfect admedially." Tertiary arches may enclose the secondaries and form an intramarginal vein. Tertiaries originate from either side of the secondaries at acute, right, or obtuse angles. Tertiaries may be randomly forked and may form large polygonal domains elongated parallel to the secondaries. Quaternary veins have a random polygonal relationship to the tertiaries. The margin has occasional shallow glands, obscurely vascularized in the existing preparations.

Specimens examined. Bruguiera gymnorrhiza (L.) Lam.: cultivated (FTG) [RCK 1443]; Ryukyu Islands, *Kokuhara & Sunagawa 83* (US; LJH 1851). *B. parviflora* (Roxb.) Wright & Arn.: Australia, *Blake 16995* (US; LJH 1852).

Carallia Roxb. (Fig. 21)

Leaves are chartaceous to membranaceous, symmetrical, entire or toothed, elliptic, obovate or ovate, mucronate or acute at the apex and acute to decurrent at the base. Venation is brochidodromous or eucamptodromous basally and brochidodromous distally. Secondary veins diverge at a narrow or wide acute angle from the straight primary, at a uniform angle, or more widely acute angle approaching the apex. Secondaries in brochidodromous segments join the superadjacent secondaries acutely and may be enclosed by tertiary and higher-order arches. Tertiaries may diverge at right angles or be acute exmedially and obtuse admedially. Tertiaries ramify randomly and may be retroflexed; the branches are sometimes aligned with the secondaries and intersecondaries. Intersecondaries are basally simple, distally composite, or forked. In *C. brachiata,* intersecondaries evenly divide the intercostal areas and join the superadjacent secondary high in the intercostal area. Teeth in *C. fascicularis* are acuminate, closely spaced, and are basally and distally concave. Veins originate from eucamptodromous arches (tertiary and higher sized) and enter the teeth symmetrically. They pass off higher-order loops and veinlets obtusely, forming garland connections below the teeth. *Carallia brachiata* had no expressed teeth but regular, papillate, nonstaining glands. Vascularization is often by an approaching marginal loop or several small anastomosing veins that often flare just below the gland. Hou (1958) reported the teeth to be dense in juvenile leaves and quite variable for the genus in general.

Specimens examined. Carallia brachiata (Lour.) Merr.: Hainan, China, *Lau 488* (MO); Indochina, *Pierre 683* (A, MO). *C. fascicularis* Guillaumin: Cochinchina, *Poilane 116* (US; LJH 1848). *C. integerrima* DC.: India, *Saldana 15267* (US; LJH 1850). *C. lucida* Roxb.: Burma, *Gallatly 783* (US; LJH 1849).

Cassipourea Aubl.
(Figs. 13–16, 19, 20)

The leaf is symmetrical and elliptic to wide ovate (to orbiculate in *C. rotundifolia*). Texture is chartaceous to coriaceous, and the margins are entire or shallowly toothed. The straight primary vein is attached to brochidodromous secondaries, which in turn pass off tertiary and quaternary loops. Secondary arches attach to superadjacent secondaries at acute, right, or obtuse angles. In *C. rotundifolia,* the venation pattern is reverse eucamptodromous with retroflexed secondaries. Secondary veins have a wide-acute, uniform angle of origin from the primary vein. They form regular intercostal areas. Intersecondaries are simple, short, and forked, or long, then extending to the secondary arches. There may be several per intercostal area. Tertiary veins are obtuse or random admedial to the secondaries, and acute or random exmedially. Tertiaries are forked and not often percurrent. Tertiary domains are irregularly polygonal, with several extending across an intercostal area. Quaternary veins originate randomly, forming irregular, well- or poorly defined domains. Teeth are very shallow with a slightly convex glandular surface that may have a tuft of simple trichomes. No sinus is distinguished distal to the apex. Teeth are vascularized by a single arching vein originating from a secondary arch. As the vein curves apically toward the tooth, it passes off tertiary and quaternary loops. No marginal glands were detected in *C. ceylanica.*

Specimens examined. Cassipourea brittoniana Fawcett & Rendle: Jamaica, *Award & Proctor 14422* (GH, US: LJH 1198). *C. barteri* (Hook. f.) N. E. Br.: Cote d'Ivoire, *Chevalier 19981* (P); *C. ceylanica* (Gardn.) Alston: Sri Lanka, *Mueller et al. 69042737* (MO); Sri Lanka, *Cooray 70040204R* (US: LJH 1854). *C. elliptica* Poir.: British Honduras, *Schipp 254* (GH; LJH 1302). *C. guianensis* Aublet: Puerto Rico, *Liogier 10575* (GH; LJH 1199); Brazil, *Dahlgren & Sella 86* (US: LJH 1853). *C. gummiflora* Tul. var. *gummiflora*: Madagascar, *Boivin s.n.* (1851) (P). *C. peruviana* Alston: Peru, *Croat 20518* (MO); Peru, *Klug 2235* (GH: LJH 1301). *C. rotundifolia* (Engl.) Alston, Tanganyika, *Schlieben 3552* (GH; LJH 1303).

Ceriops Arn. (Figs. 28, 29)

Leaves are coriaceous, entire, symmetrical, oblong, with a rounded apex and an acute, decurrent base. Venation is obscure, brochidodromous. Secondaries diverge from the straight primary moderately acutely, the upper ones somewhat more obtuse than the lower. Secondary arches join the superadjacent secondaries obtusely. Intersecondaries are simple, equally dividing the intercostal areas. Tertiary veins originate at obtuse or right angles admedially and exmedially and may be admedially ramified. Quaternary veins branch from transverse tertiaries and run parallel to the secondaries. Occasional convexities in the margins do not look glandular and are not obviously vascularized.

Specimens examined. Ceriops boiviniana Tul.: Madagascar, *Gentry 11901* (MO: LJH 4512); Comoro Isl., *Lorence 2872* (MO).

Combretocarpus Hook. f. (Fig. 40)

Leaves are membranaceous, entire, symmetrical, elliptic, with an obtuse apex and acute base. Secondaries arising from the straight primary vein are brochidodromous distally and eucamptodromous basally. Secondaries arise at a uniform, narrowly acute angle and are uniformly concave. The brochidodromous secondaries join superadjacent secondaries at right angles. Simple intersecondaries are present. Tertiary veins are percurrent and arise from both sides of secondaries at right angles. Tertiaries are oblique to the midvein at a uniform angle. Quaternary veins are orthogonal to tertiaries. Looped venation is typical at the margin but a straight collector vein may be present. No teeth or marginal glands were detected.

Specimen examined. Combretocarpus rotundatus (Miq.) Danser: North Borneo, *van Niel 4271* (MO).

Comiphyton Floret (Figs. 7, 8)

Leaves are symmetrical, narrowly oblong, with an acuminate apex and obtuse base. Texture is membranaceous, and margins are entire. Eucamptodromous secondaries arise from a straight primary vein at a moderately acute divergence angle with the upper veins more obtuse than the lower ones. The secondaries are uniformly curved with lower secondaries being longer and more strongly ascending. The few short intersecondaries are exmedially forked. Tertiary veins are sinuously percurrent and oriented at approximately right angles to the primary vein, especially the outer ones. They are acute exmedially and obtuse admedially. Quaternary and quinternary veins arise orthogonally and form irregular polygonal domains. No teeth are expressed, but shallow, marginal, domelike glands are present. Short, single veins arise from secondary or tertiary loops and end directly below a gland. The leaf venation drawings of Floret (1974) agree with my observations.

Specimen examined. Comiphyton gabonensis J. J. Floret: Gabon, *Le Testu 5918* (P).

Crossostylis Forster & G. Forster (Fig. 23)

Leaves are chartaceous, entire or toothed, symmetrical, wide oblong to narrow obovate, with an acute or obtuse apex and an acute to subdecurrent base. Venation is brochidodromous or sometimes basally eucamptodromous. Secondaries arise with a narrow- or wide-acute divergence from the straight primary vein. Secondaries are uniformly curved, join the superadjacent secondaries at right angles, and are enclosed by tertiary and quaternary arches. Tertiary veins are usually forked, originating at random angles. Quaternary and quinternary veins form irregularly polygonal domains and are often retroflexed. Teeth are shallowly crenate with a fine glandular apiculum. A single, conspicuous tooth vein originates at a secondary or higher-order arch, which becomes smaller in diameter distally. Smaller veins of the marginal reticulum attach decurrently to the tooth vein.

Specimens examined. Crossostylis biflora Forster: Samoa, *Veupel 493* (US: LJH 2256); Tahiti, *Balgooy 1715* (MO); *C. multiflora* Brongn. & Gris.: New Caledonia, *McPherson 2344* (MO).

Gynotroches Blume (Fig. 24)

Leaves are chartaceous, entire, elliptic with an acuminate apex and an acute base. Venation is eucamptodromous with secondaries uniformly curved after diverging at a wide acute angle from the straight primary. Intersecondaries are admedially simple and exmedially composite. Tertiary veins are acute exmedially, obtuse admedially, and admedially and transversely ramified. Quaternaries and quinternaries are polygonal to irregular. Uncommon marginal, glandlike, shallow protuberances are not consistently vascularized. An enlarged vein may end in the vicinity, but it may not originate as deeply as a secondary or tertiary arch.

Specimens examined. Gynotroches axillaris Blume: Philippines, *Wenzel 1323* (MO); MO 2227076 (MO).

Kandelia Wight & Arn. (Figs. 30, 31)

Leaves are chartaceous, entire, symmetrical, obovate, with an obtuse apex and an acute base.

Venation is obscure, brochidodromous, with secondaries arising at a moderately acute angle from the straight primary vein. Upper secondaries are more obtuse than lower secondaries. Secondary arches join the superadjacent secondaries at right or obtuse angles. Simple or composite intersecondaries are present. Tertiary veins diverge from secondaries at right angles from both sides and may be transversely ramified. No marginal glands were detected.

Specimens examined. *Kandelia candel* (L.) Druce: Taiwan, *Murata & Nishimura 31214* (MO); Taiwan, *Peng 6042* (MO).

Macarisia Thouars

Leaves are symmetrical or asymmetrical, elliptic to suborbiculate. The apex is emarginate, or rounded, or acute or acuminate, and the base is acute to decurrent. The texture is chartaceous or coriaceous and the margin entire or shallowly toothed. Eucamptodromous secondary veins diverge moderately acutely and uniformly from the straight primary vein. They are gradually apically curved and unbranched. Secondaries in the distal half of the leaf may be brochidodromous. The few intersecondaries are short and ramify into tertiaries. Tertiary veins may be sinuously percurrent, and connections to secondaries are at right angles or variable. In *M. lanceolata* the tertiaries are admedially obtuse and exmedially acute. Tertiaries are oriented relatively uniformly at right angles to the primary vein. Quaternary veins are orthogonal to tertiaries, forming irregular polygonal domains. Higher-order veins are indistinguishable in a reticulum. Areole veinlets often anastomose to form smaller suspended islets within an areole. Teeth are shallow, and strongly asymmetric; they have rounded convex bases leading to shallow, rounded, concave sinuses above the glandular apex. The turbinate gland points apically and is surrounded by a tuft of simple trichomes. A single vein originates from a secondary arch and curves toward the tooth apex where it flares slightly. It does not supply the sinus. Tertiary and smaller veins that form marginal loops or the submarginal reticulum merge decurrently or randomly with the tooth vein.

Specimens examined. *Macarisia lanceolata* Baillon: Madagascar, *Capuron 11.339SF* (MO). *M. pyramidata* Thouars: Madagascar, *Serv. Forestier 11R460* (MO); Madagascar, *Dorr 4495* (MO).

Pellacalyx Korth. (Fig. 22)

Leaves are chartaceous, entire, symmetrical, oblong, with an acuminate apex and an obtuse base. Venation is eucamptodromous basally and looped brochidodromous distally. Uniformly curved secondary veins diverge from the straight primary at a uniform, widely acute angle. Secondaries are enclosed by tertiary and higher-order arches. Intersecondaries are short, admedially simple, and exmedially composite. Tertiary veins are transversely ramified and originate from secondaries acutely, both admedially and exmedially. Quaternary and quinternary veins are random. Depressions in the leaf margin contain round, flat-topped glands. A single strong vein arises from a tertiary eucamptodromous loop and ends just at the margin below each gland.

Specimen examined. *Pellacalyx frustulata* Merr.: Philippines, *Wenzel s.n.* (1915) (MO).

Poga Pierre (Figs. 42, 43)

Leaves are chartaceous or membranaceous, entire, symmetrical, elliptic, oblong or lorate, with an acuminate or emarginate apex and an acute base. Venation is brochidodromous with tertiary and higher-order arches, or eucamptodromous at the base becoming brochidodromous distally. The straight or curving primary vein, often distally forked, produces secondaries at a wide acute angle, with upper secondaries often more obtuse than the lower. Secondary arches join the superadjacent secondaries at acute angles. Intersecondaries are simple at the primary vein, becoming composite exmedially. Tertiary veins are sinuous and obliquely percurrent, joining secondaries or intersecondaries. Tertiaries arise at acute angles admedially from secondaries and at right angles exmedially, or their course may be irregular. Quaternary veins are random, often retroflexed, forming incomplete domains. Quinternary veins may be retroflexed in any orientation. No marginal glands were detected.

Specimens examined. *Pogo oleosa* Pierre: Cameroon, *Zenker s.n.*, (1909) (US: LJH 1858); Nigeria, *Ariwaodo s.n.* (1983) (FHI).

Polygonanthus Ducke (Fig. 41)

Leaves are membranaceous, entire, elliptic, with an acuminate apex and an asymmetric, acute base. Eucamptodromous secondaries arise at a wide acute angle from the straight primary vein. A few of the ascending secondaries connect brochidodromously. Some dominant secondaries show an incipient suprabasal acrodromy. Simple intersecondaries are long, robust and common. Tertiary veins are straight, percurrent, and oblique to the midvein at a constant angle. Tertiaries diverge at right angles from both sides of secondaries. Quaternary veins form regular polygonal domains, often elongated parallel to the secondaries. Quinternary veins arise randomly from lower-order veins. No marginal glands were detected. At the leaf tip, the midvein ends at the margin similarly to tooth vasculature in the Macarisieae.

Specimen examined. Polygonanthus amazonicus Ducke: Brazil, *daSilva 4486* (MO).

Rhizophora L. (Figs. 25, 26)

Leaves are coriaceous, entire, symmetrical, oblong or elliptic with an obtuse apex and an acute base. Venation is brochidodromous, and the secondary arches may form a strong composite collector vein. Secondaries diverge from the straight primary at a right or acute (decurrent) angle. The divergence angle is uniform, or the upper and lower secondaries may be more acute than the middle sets. Secondary arches join superadjacent secondaries at acute, right, or obtuse angles. Intersecondaries are absent or simple and arising from primary veins or from secondary loops; they are obmedially ramified parallel to the secondaries. Tertiaries arise at a right angle from both sides of secondaries, are not percurrent, are often orthogonal with intersecondaries, and often are admedially ramified forming a random reticulum with no directional orientation to the primary vein. No marginal glands were detected.

Specimens examined. Rhizophora mangle L.: Florida, *Curtiss 5438* (US: LJH 1846); Hawaii, *Degener & Wielbese 3363* (MO). *R. mucronata* Lam.: Caroline Isl., *Anderson 1049* (US: LJH 1847). *R. stylosa* Griffith: Australia, *Gill 220-4* (MO).

Sterigmapetalum Kuhlm. (Figs. 17, 18)

The leaves are symmetrical, oblanceolate or elliptic, with an acute or emarginate apex and a rounded to acute decurrent base. The leaves are entire-margined and chartaceous. Venation is looped brochidodromous, and secondaries have an acute to wide acute divergence from the straight primary vein. Secondaries are uniformly spaced with the arches fusing with the superadjacent secondaries at obtuse or right angles. Composite intersecondaries may be present. Tertiary veins originate mostly at right angles exmedially and admedially, and are oblique to the primary vein at a constant angle. Tertiaries are forked percurrent, producing irregular but evenly sized domains. Quaternary veins are orthogonal to tertiaries. Quaternary and higher-order loops festoon the secondary arches. Veinlets in the areoles often anastomose to form small suspended islets. Rarely a flattened marginal gland is found that may be directly vascularized by a single vein arising from a tertiary loop. The illustration of leaf architecture by Steyermark & Liesner (1983) agrees with these observations.

Specimens examined. Sterigmapetalum guianense Steyerm. subsp. *ichunense* Steyerm. & Liesner: Venezuela, *Liesner 7314* (MO); Venezuela, *Clark 7275* (MO).

DISCUSSION

VENATION PATTERNS

Brochidodromy and eucamptodromy appear to be quite closely related since intermediate forms are often found. In intermediate leaves, the distal secondary veins are always brochidodromous and the proximal secondary veins always eucamptodromous. The ontogeny of lamina tissue in many dicot leaves begins with the blocking out of the distal portion of the lamina, while the proximal portion is produced later following intercalary growth of the midrib. In early developmental stages of *Fuchsia* and *Hauya* (Onagraceae; Keating, unpubl.), brochidodromous leaves appear to have more or less simultaneous lamina inception with unified marginal growth. The cross attachment of secondary arches to the superadjacent secondaries occurs as the marginal expansion is slowing down. In eucamptodromous leaves, the later basipetal inception of secondaries on the midrib is followed by an acropetal marginal expansion of the lower lamina. This produces apically arching secondaries that eventually dissipate in submarginal loops parallel to the margin.

Transitions between distal brochidodromy and basal eucamptodromy are commonly found in *Anopyxis*, *Carallia*, *Crossostylis*, and *Pellacalyx* of the Rhizophoraceae, as well as *Combretocarpus*, *Poga*, and *Polygonanthus* of the Anisophylleaceae.

The developmental transition from brochidodromy to eucamptodromy suggests a phylogenetic recapitulation, but further, it is certainly clear that the two venation patterns are closely related with eucamptodromy always appearing later in development. The data of Hickey & Wolfe (1975) show that brochidodromy is stratigraphically earliest, and it tends to have the lowest rank order (organizational complexity and regularity) of any type of angiosperm venation pattern.

Rhizophoreae, having the most coriaceous leaves, are exclusively brochidodromous with well-developed secondary arches meeting the superadjacent secondaries at an obtuse angle. These arches have tended to become straightened, forming a submarginal collector vein, a tendency shown by no other tribe. This implies a leaf ontogeny with little if any basal acropetal expansion. Instead, it can be hypothesized that the leaves have a uniform marginal expansion, followed by a more abrupt cessation of expansion and a more synchronized final marginal differentiation.

Tertiary veins in the Rhizophoraceae generally do not show predictable patterns in most genera. They are generally forked, not percurrent, and have irregular domains. Branching from secondaries is acute to obtuse and seldom sufficiently well developed to be called orthogonal, or regularly polygonal.

Areolation is most commonly imperfect, although it may be well developed in *Blepharistemma*, *Comiphyton*, and *Macarisia* of the Macarisieae, and in *Combretocarpus* of the Anisophylleaceae. Free vein endings are variable within each tribe but generally fewer than seven. The highest number, to greater than 20 in *Anisophyllea*, is large for both families.

The most distinctive pattern of secondary architecture is found in *Anisophyllea*, most species of which show basal and suprabasal acrodromy (Fig. 32). Some species (*A. griffithii*, Fig. 33, and a specimen of *A. pomifera*) are not acrodromous but rather eucamptodromous with irregular spacing of the pinnate secondaries on the midvein. All specimens of the other three genera of Anisophylleaceae are eucamptodromous, often with distal brochidodromy. *Polygonanthus* has some secondaries that show the tendency toward strong ascending curvature parallel to the margin as seen in *Anisophyllea*.

MARGINAL TEETH AND GLANDS

As leaf teeth in the Rhizophoraceae are best developed in the Macarisieae, we will refer to them as the Macarisioid type. The teeth are best developed and largest in *Blepharistemma* (Figs. 3–5), although conspicuous expression can also be found in the genera *Macarisia* (Figs. 10–12), *Cassipourea* (Figs. 13, 14), and in *Carallia* of the Gynotrocheae. In Macarisieae, the teeth are markedly asymmetric, having a gently convex margin proximal (basal) to the tooth apex. The apex is incurved facing directly onto an abruptly or gradually concave sinus.

Tooth vascularization is always by a single vein usually originating from an ascending secondary vein or tertiary loop. It may begin below the tooth and curve gradually toward the apex, entering the tooth symmetrically (Figs. 11, 12). In other cases, the vein originates directly opposite the tooth apex and follows a straight course toward the distal margin of the tooth, supplying the sinus as well as the apex (*Blepharistemma*, Fig. 5). The tooth vein is usually more strongly developed than the neighboring veins, which often join it oriented randomly or decurrently. The tooth vein ends slightly flared at the margin, which is surmounted by a turbinate, rounded or flattened gland. On expressed teeth, glands are often incurved toward the sinus. They often show no stainability and often have a surface of columnar cells. No visible epithem appears within the lamina distal to the vein. On leaf margins with glands but no expressed teeth, the relationship between veins and glands is not basically different from those leaves with expressed teeth.

Carallia fascicularis shows an unusual tooth for the family. It is concave on both sides, very frequent and conspicuous, and is vascularized by one vein with tertiary garland connections to the neighboring tooth veins.

Lersten & Curtis (1974) reported on the structure of colleters as found at the base of stipules in *Rhizophora mangle*. They are not regularly associated with vascularization, and they appear from the evidence presented to have no obvious relationship to glandular teeth in other genera of the family.

Within the available data, there are no strong correlations between the degree of expression of glands and teeth with the habit or habitat. It can be noted in general that the four specialized mangrove genera have more coriaceous leaves than the inland genera. Givnish (1979) reviewed the statistical data showing a correlation between toothed (nonentire) leaves and a thin, noncoriaceous lamina. He also noted that deciduous leaves are toothed more frequently than evergreen leaves. If the ancestors of Rhizophoraceae were thin-leaved and possibly from seasonal habitats, the nontoothed leaves are clearly derived. On the other hand, the best-developed teeth are found only on plants with eucamptodromous venation, while brochidodromous leaves have very reduced teeth/glands or no marginal features at all. Hickey & Wolfe (1975) presented stratigraphic evidence that the brochidodromous pattern is primitive in angiosperms. While it is tempting to regard teeth in Rhizophoraceae as a reduction series, this cannot be taken as proven.

EPIDERMIS AND STOMATA

The paradermal outline of the anticlinal walls of epidermal cells is not particularly useful systematically in these genera. In nearly all specimens, cells are polygonal (isodiametric or elongated up to 2:1 length/width ratios) and are the same on both surfaces. *Blepharistemma* has sinuous abaxial epidermal cells, *Macarisia* and *Poga* have papillate abaxial epidermal surfaces. *Anisophyllea* species vary in cell outline from polygonal to undulate to interlocking shapes with the two surfaces matching or not. In some genera, occasional larger rounded cells occur that have more radiating neighbors than most of the smaller cells. Such large cells were found in *Carallia* and *Pellacalyx* of the Gynotrocheae, and in *Anisophyllea* and *Polygonanthus* of the Anisophylleaceae.

Observations on stomatal types are difficult in some cases, as they may be quite obscure in clearings. Nevertheless, a few conclusions seem valid. The Rhizophoreae are quite distinct with their apparently cyclocytic patterns (Figs. 27, 29, 31). The subsidiary cells appear narrow and differentiated from other epidermal cells. They vary in number from 5 to 8–10 cells surrounding the guard cells. Stomata are exclusively abaxial in all genera observed. While the brachyparacytic pattern is most common in all other genera of both families, anomocytic and anisocytic types were noted as well.

IDIOBLASTIC CELLS

The Macarisieae and Hypogyneae are distinguished by having prismatic crystals with small druses rarely present (*Blepharistemma*). All other genera studied have only druses, no prismatics. Occasional specimens have no crystals. Druses in the Rhizophoreae are normally birefringent but have centers that appear dark or extinct under polarized light. This phenomenon was also noted in *Pellacalyx*, a genus otherwise clearly belonging to Gynotrocheae.

In the Gynotrocheae, druses tend strongly to cluster along veins with only a few scattered randomly in the mesophyll. In other tribes, the distribution of crystals varies among the genera. Crystals may cluster nonexclusively at the veins, and many are scattered randomly. In this respect, the Anisophylleaceae are unexceptional.

Foliar sclereids of several types were noted in this study in both families. A series of studies by Rao & Bhattacharya (1978), Rao et al. (1978), and Rao & Das (1979) have also called attention to these cell types, particularly in the tribe Rhizophoreae. "Diffuse polymorphic sclereids" (Rao et al., 1978), here called astrosclereids, are found in *Bruguiera*, *Ceriops*, and *Rhizophora* (Figs. 25, 26) of the Rhizophoreae and in *Pellacalyx* of the Gynotrocheae. A second type, the terminal tracheoid, is characteristic of *Macarisia*, *Cassipourea*, *Crossostylis*, *Bruguiera*, and *Kandelia* (Fig. 30) of the Rhizophoraceae, as well as in *Anisophyllea*, *Combretocarpus*, and *Poga* (Fig. 43) of the Anisophylleaceae. Only in Rhizophoreae are astrosclereids and terminal tracheoids commonly found together.

FAMILY AND TRIBAL DELIMITATION: RHIZOPHORACEAE

A review of the available leaf-architectural and histological data (Table 2) demonstrates much overlap in most features and an apparent relatedness among all of the genera. Yet a few characters readily distinguish the tribes. The Macarisieae and Hypogyneae have prismatic crystals in the leaves, and the Hypogyneae are further differentiated by having mostly looped brochidodromous leaf venation instead of mostly eucamptodromous as found in the Macarisieae.

In several genera of the Macarisieae (*Anopyxis*, *Blepharistemma*, *Comiphyton*, *Macarisia*), the leaf-rank organization is unusual: the tertiary veins and areolation show a high level of organization while the secondaries are less well organized. Normally, rank order increases proceed in ascending order from secondaries through tertiaries to the organization of areoles (Hickey, 1977). Following current practice (Levin, 1986; Hickey, pers. comm.) we have ranked the leaves according to the highest level obtained so that the maximum evolutionary advancement is reflected in the classification. In his study of the leaf architecture of Euphorbiaceae: Phyllanthoideae, Levin (1986) hypothesized that venation where secondaries are less well organized than tertiaries represents a regression of rank order. He found this type among leaves from arid, arctic, and alpine habitats. What its significance is in the Macarisieae remains obscure, as these genera do not face such environmental stresses.

The Gynotrocheae and Rhizophoreae are distinguished from the Macarisieae by having druses in the leaves. The Rhizophoreae have coriaceous leaves with brochidodromous venation and a cyclocytic stomatal pattern unique in the family. Also, three of the four genera in this tribe have astrosclereids in the leaves. The Gynotrocheae have chartaceous leaves and brachyparacytic or other noncyclocytic stomata. In many respects the Rhizophoreae are the most unified and specialized group of genera due to their mangrove habit, vivipary, chromosome morphology (Yoshioka et al., 1984), bijugate phyllotaxy (Tomlinson & Wheat, 1979), and the leaf

TABLE 2. *Summary of leaf characters of the Anisophylleaceae and tribes of Rhizophoraceae.*

	Macarisieae	Hypogyneae	Gynotrocheae	Rhizophoreae	Anisophylleaceae
Shape	elliptic, obovate, oblanceolate, suborbiculate, symmetrical, or asymmetrical	elliptic, oblanceolate, ovate (wide or narrow) orbiculate	elliptic, obovate, ovate (often narrow)	elliptic, occasionally obovate	elliptic, suborbiculate, symmetrical or asymmetrical
Apex	acuminate to emarginate or rounded	acuminate to emarginate or rounded	acuminate to obtuse	acute to obtuse	acuminate to rounded or emarginate
Base	decurrent, acute to obtuse	decurrent, acute to rounded	decurrent, acute to occasionally obtuse	decurrent to acute	decurrent to acute or rounded
Margin	toothed or entire	toothed or entire	toothed or entire	entire	entire
Texture	membranous or coriaceous	chartaceous or coriaceous	chartaceous	chartaceous or coriaceous	chartaceous
Primary vein	straight; normal to enlarged	straight; normal	straight; normal to enlarged	straight; normal to enlarged	straight; normal; one to several
Secondary type	eucamptodromous to distally brochidodromous	looped brochidodromous to brochidodromous; one reverse eucamptodromous	brochidodromous, eucamptodromous to distally brochidodromous	brochidodromous	brochidodromous, eucamptodromous, acrodromous
Secondary vein origin	wide to narrow acute	wide to medium acute	wide to narrow acute	wide to narrow acute	basal to suprabasal and strongly ascending to wide acute
Intercostal areas	regular or irregular	regular, occasionally irregular	regular or irregular	mostly regular	regular or irregular
Rank order	2r0–3r1	1r3–4r0	1r0–3r0	2r0–3r2	2r0, 4r1
Intersecondaries	short, forked to long, sinuous	simple or composite long or forked	simple or composite often forked	simple or composite often obmedially ramified	none, few, or common; short, long; simple to distally composite
Tertiary veins	random angle; sinuous percurrent or forked	acute to obtuse angle; forked or percurrent; occasionally parallel to secondaries	right to obtuse admedially; right to acute exmedially transverse or parallel to secondaries; ramified or forked	usually right admedially & exmedially; occasionally obtuse or acute	right or acute; sinuous or forked percurrent; mostly alternate

TABLE 2. *Continued.*

	Macarisieae	Hypogyneae	Gynotrocheae	Rhizophoreae	Anisophylleaceae
Tertiary domains	irregularly polygonal	irregular or regular polygonal	irregular	irregularly polygonal; occasionally parallel to secondaries	irregular polygonal
Highest order	5–7	5–7	5–7	5–8	5–10
Areole development	mostly imperfect, few well developed	imperfect to well developed	incomplete to imperfect	incomplete, imperfect to well developed	incomplete, imperfect to well developed
Areole shape	irregular, polygonal	irregular to polygonal to rectangular	irregular; occasionally polygonal	irregular to polygonal	irregular to polygonal
Free endings	0–2, 1–7, 1–5	0–2, 0–8, mostly < 0–4	1–3, 0–6, 2–9, 3–10	0–4, 0–8	0–2, 3–9, 10–18, 15–> 20
Tracheoidal endings	none	to 70% only in *Cassipourea ceylanica*	none	none or common	none to few to > 50%
Marginal venation	looped; occasionally incompletely looped	looped or incompletely looped	looped or incompletely looped	looped or incompletely looped	looped to incompletely looped; often intramarginal vein
Crystal type	prismatics, rare druses	prismatics	druses, small to medium	druses, sand and small prismatics	druses
Distribution	along veins or random in mesophyll	along veins or random in mesophyll; occasional in epidermis	along veins; random mesophyll or epidermis	along veins, random mesophyll	along veins, random mesophyll
Adaxial epidermis shape	polygonal	polygonal	polygonal; occasionally larger rounded cells	polygonal	polygonal to undulate to interlocking; occasionally large centered cells
Length/width ratio	1–1.5:1	1–2:1	1–2:1	1–2:1	1:1, 1–2:1
Abaxial epidermis shape	polygonal	polygonal	polygonal	polygonal	polygonal to interlocking (same as adaxial epidermis)

TABLE 2. *Continued.*

	Macarisieae	Hypogyneae	Gynotrocheae	Rhizophoreae	Anisophylleaceae
Relative size	same or smaller than adaxial	same or usually smaller than adaxial	same or smaller than adaxial	same as adaxial	same or smaller than adaxial
Stomate type	brachyparacytic, anisocytic, few diacytic, anomocytic	brachyparacytic, anomocytic, paracytic (few diacytic, anisocytic)	brachyparacytic, few anomocytic, anisocytic	obscure but probably all cyclocytic with 5–10 subsidiary cells	brachyparacytic, anisocytic, diacytic, paracytic, anomocytic
Position	abaxial	abaxial	abaxial	abaxial	abaxial
Sclereids	absent	absent	absent	astrosclereids in 3 of 4 genera	absent
Trichomes	absent to very common simple; near veins or random	absent to occasional, simple, long; near veins and lamina	absent	absent	absent to occasional, simple, short to long
Hypoderm	occasional, 2 layered	occasional, 2 layered	absent	usually present, 2 layered	absent

features mentioned above. Juncosa (1984b) found that *Rhizophora* has the most specialized shoot apical morphology and hypocotylar anatomy, with *Bruguiera* more transitional to inland genera of Rhizophoraceae. Leaf samples of *Bruguiera* showed the lowest rank order and the highest number of free vein endings for the tribe, but they are not otherwise distinctive architecturally.

The principal morphological diagnostic features of the Anisophylleaceae are the alternate leaves and the absence of stipules. No microscopic features absolutely distinguish its four genera from the Rhizophoraceae. Features not shared by Rhizophoraceae are asymmetrical leaves, teeth and marginal glands almost entirely absent, acrodromous venation, highest vein order to ten, and free vein endings per areole to greater than 20. But within the Anisophylleaceae these features characterize fewer than all of the species of one genus. All remaining recorded features are also found within the range of the variable tribes of Rhizophoraceae and supply no basis for separating the Anisophylleaceae from the Rhizophoraceae. A good case can be made that the Rhizophoreae are the most distinctive group based on their various specializations, including cyclocytic stomata, unusual druse crystals, high-ranking brochidodromous venation, vivipary, and mangrove habit. Yet much other available evidence argues for the obvious relatedness of the 14 genera of Rhizophoraceae s. str. and for their general similarity to the Anisophylleaceae. The only "teeth" in the Anisophylleaceae, the shallow marginal glands in *Anisophyllea meniandii*, are too simple structurally to allow an opinion on their origin or homologies.

COMPARISONS WITH LEAVES OF OTHER FAMILIES

The leaf architecture of the Rhizophoraceae is sufficiently generalized that comparisons with this aspect of other families is usually not particularly useful in affirming relationships. However, several of the families mentioned below are distinctly unlike the Rhizophoraceae. Each of the families was chosen by Dahlgren (this volume) for closer scrutiny after extensive comparisons using a broad data base. We compared all of the available cleared specimens in the National Cleared Leaf Collection, singling out those genera and species in particular that had the most elaborate, character-rich architecture.

The most useful characters appear to be of complex genetic origin, including secondary architecture, leaf shape, marginal configuration (tooth shape, gland type, and orientation of the related venation). The marginal configuration of the Cunonioid/rosoid leaf, with the internal epithem and the strongly converging marginal veins producing a hydathodal tooth, appears complex and monophyletic. It appears nowhere else than in the rosoid alliance as understood in all of the major current phylogenetic systems. However, there is insufficient information on the Macarisioid tooth type. The apiculate, deciduous gland serviced by a usually small single vein seems widespread and is probably not monophyletic, at least as the structure is detected in clearings.

Celastraceae

The ovate or elliptic leaves of this family are brochidodromous or eucamptodromous and of generally low rank order; the margins are faintly toothed and structurally Macarisioid. *Elaeodendron aethiopicum* and *Celastrus pringlei* have a single dominant vein that arises from a secondary or tertiary loop. It ends just below an apicular gland that is oriented adjacent to or points toward a sinus. All associated minor veins are decurrent on the dominant veinlet and do not participate in vascularizing the gland. In *Celastrus racemosus*, the tooth shape is Macarisioid but no dominant vein approaches the substantial gland. Two or three smaller marginal veins approach the gland but not closely.

A number of leaf characters of this family, particularly the secondary and higher order vasculature and the tooth type, are quite compatible with the Rhizophoraceae.

Cunoniaceae

The leaves have prominent teeth with three converging veins leading to an internal epithem. The converging veins have perpendicular cross braces, giving the Cunonioid tooth a unique appearance but not hiding an obvious similarity to the slightly simpler rosoid tooth. This type of tooth was held by Hickey & Wolfe (1975) to be ancestral to the rosoid tooth, an idea compatible with modern ideas concerning relationships between Cunoniales and Rosales. There is no similarity to the Rhizophoraceae at all.

Cyrillaceae

The two specimens available here, representing *Purdiaea nipensis* and *Cyrilla nipensis*, have elliptic to obovate leaves with entire margins. The brochidodromous secondaries are straightened into a collector vein or are looped, respectively. While *Purdiaea* is unexceptional in its higher-order venation and other features, the *Cyrilla* specimen does have incomplete venation with 15–20 vein endings per undefined aerole. It has stellate hairs of a type not seen in the Rhizophoraceae. The absence of teeth makes it impossible to compare marginal features productively, but the trend toward development of a strong submarginal collector vein in *Purdiaea* is not noted in the Rhizophoraceae.

Elaeocarpaceae

Leaves of this family show broad variation in the level of specialization (rank order), ranging from the 1r1 brochidodromous arrangement of *Elaeocarpus arnhemicus* to the 4r leaves of the genus *Sloanea*. Margins are toothed in all specimens seen, and the secondary architecture ranges from brochidodromous to forked craspedodromous. None of the observed patterns of higher-order venation or areolation can negate relationships with the Rhizophoraceae, nor does the tooth type. The teeth are typically Macarisioid with the strong medial vein servicing a prominent apiculate gland that often points to the sinus. The decurrent branching veins attached to the median vein diverge, often in a falcate curve, and they show no tendency to be involved in tooth venation. This family shows the closest resemblance to Rhizophoraceae on the basis of the leaf architecture.

Erythroxylaceae

The leaves examined have a secondary architecture of looped brochidodromous veins with irregular higher-order domains with a few unique or specialized features. Their level of organization is low first rank. Since the margins are entire, no tooth data are available. In most *Erythroxylon* species examined there is a rounded projecting apical gland vascularized by the midrib. They look the most macarisioid-like in a species from Java. Most of the glandular tips do not resemble the marginal features in the Rhizophoraceae. The family has trends of secondary and tertiary architecture unlike the Rhizophoraceae, including helicoid and admedially dendritic fourth- and fifth-order veins (*E. obtusifolium* from Sri Lanka) and secondaries closely spaced with higher-order veins parallel within the intercostal areas (*E. urbanii* from Puerto Rico).

Flacourtiaceae

Leaves of this large family vary greatly in size, shape, and secondary-venation patterns. Among the toothed leaves, two patterns are found, neither resembling the Rhizophoraceae. One of these has a Cunonioid vascular pattern with a strong median bundle that merges with two strongly converging lateral veins just below an apiculate tooth. The three converging veins are perpendicularly cross-braced with three or four minor veins. The other tooth type has one strong medial vein ending at the tooth apex, which may or may not have once had an apicular gland. Only one branch on the distal side passes through the sinus margin, providing it with conspicuous vascularization. No flacourtiaceous leaves seemed to approach the Rhizophoraceae architecturally.

Geraniaceae

Leaves of this family are often toothed and broadly elliptic. A principal characteristic of the family is parallelodromous secondary venation. Higher-order venation is not distinctive, and the low rank order (2r1) reflects the paucity of distinctive comparative architectural characters. The teeth are typically rosoid throughout all samples examined and therefore quite different from the Rhizophoraceae. *Viviana crenata* (Vivianaceae or Geraniaceae) is typically geranioid, including the presence of the rosoid tooth.

Hugoniaceae

The four *Hugonia* leaf specimens examined are generally compatible with Rhizophoraceae. The secondary architecture is eucamptodromous or looped brochidodromous, and the rank order ranges from 2r to 4r. The crenate margins have teeth very similar to the Macarisioid type. The tooth is generally incurved with the deciduous glandular apiculum pointing toward or located in the sinus. A single large vein, apically curved, arises from the secondary arch or loop and ends below the apiculum. It is associated with branching loops and minor veins that recurve or otherwise show no tendency to converge on the tooth. No features negate relationship with the Rhizophoraceae.

Ixonanthaceae

The three genera (five species) sampled here generally resemble the Rhizophoraceae, although the secondary architecture includes semicraspedodromous as well as brochidodromous types. Teeth are not universal but are found in *Octhocosmus*, and in a reduced form in *Ixonanthes*. Best-developed toothed margins are crenate with the glandular apiculae so "distal" on the tooth as to be on the proximal side of the sinus. A prominent vein arises from a secondary loop, sometimes in an organized semicraspedodromous pattern, and ends just below the gland. Some of the minor veins branching from this trace tend to converge toward the pad below the gland. This represents a significant difference from the Macarisioid tooth. Convergence of several veins toward the gland is a major characteristic of the Cunonioid/Rosoid/Fuchsioid type, although it appears to be an independent trend in the Ixonanthaceae. Other distinctive trends in this family include development of an entire leaf with a fibrous marginal vein in *Klainedoxa* and in *Irvingia*, and semicraspedodromous venation in *Octhocosmus*.

Lepidobotryaceae

The materials examined here are ovate leaves with entire margins and eucamptodromous secondary architecture. Intercostal areas are irregular, as are most of the tertiary domains and areoles. Some percurrent tertiaries are present. These unspecialized examples, *Papania scandens* and *Sarcotheca ferruginea*, are generally compatible with the Rhizophoraceae.

Oxalidaceae

Oxalis acuminata and the other species examined are trifoliate with entire ovate leaflets, which may be ciliate, looped brochidodromous, and with percurrent or irregular tertiaries. The reduced number of vein orders, five or six, and generally reduced appearance are compatible with the Rhizophoraceae.

Linaceae

The samples representing seven species are all more specialized than any Rhizophoraceae described. The secondary architecture is brochidodromous or eucamptodromous, but this ends the similarities. Tertiary and quaternary venation is virtually parallel, being perpendicular to the axis of the intercostal areas (*Roucheria griffithiana*) or parallel to them (*Roucheria calophylla*). *Linum* shows tendencies toward acrodromy and has fine, papillate/serrate, unicellular teeth. No multicellular teeth are present. Tooth glands in *Roucheria* are somewhat Macarisioid in appearance, as a median vein arises from a submarginal loop, ending just below the gland. However, there is also a definite tendency for lateral veins to converge toward the gland, a condition not seen in Rhizophoraceae. In *Linum* and *Reinwartia*, the small marginal projections are multicellular but not glandular or vascularized. It seems doubtful that the Rhizophoraceae leaf type has any close relationship with leaves of this family.

Rosaceae

This family is quite variable, and several types of secondary venation and teeth are found that bear much closer examination. *Fragaria* species generally have rosoid teeth, as does *Holodiscus discolor*, although the latter's medial vein is dominant, with the lateral ones being nearly absent. The marginal teeth of *Cotoneaster pyricantha* and *Kageneckia lanceolata* have deciduous apiculae and prominent medial tooth veins. Convergent lateral veins are present at most teeth or may not be obvious. The incurved appearance of the *Cotoneaster* tooth form is remarkably similar to the Macarisioid tooth.

Saxifragaceae

All leaves examined show a typical Rosoid hydathodal tooth with converging marginal veins that end in a flaring submarginal vascular plexus. They show no relationship to structures of the Rhizophoraceae.

Zygophyllaceae

The ovate leaves of this family are generally not toothed, and they have brochidodromous venation with a different appearance of areolation than Rhizophoraceae. One specimen, representing *Guaiacum sanctum* L., is craspedodromous with two or three small pointed teeth. A tooth is vascularized by a craspedodromous secondary vein that ends below its tip. There is apparently no apiculum or epithem at the tooth. Some minor veins form a converging buttress on the tooth vein. Overall, the tooth does not resemble Macarisioid architecture nor do the leaves resemble those of Rhizophoraceae in other respects.

WOOD ANATOMY

In the comparative wood anatomical literature, only two studies were found that were based on a comprehensive generic sample, those by Marco (1935) and by van Vliet (1976).

It should be noted that neither author developed a major operating hypothesis that the genera of Anisophylleae should be segregated as a separate family nor did their data and analyses support that view. Among the wood features they listed, only those mentioned below may have value in distinguishing the families. Table 3 provides a list of features we believe to have promise in differentiating the tribes and families.

Vessel tangential diameters of Anisophylleaceae overlap the high end of the range of Rhizophoraceae values, but they have the highest average and absolute values for this feature. Average vessel element length of the two families overlaps entirely, but Anisophylleaceae are at the short end of the range. Pores per square millimeter are the lowest for Anisophylleaceae with almost no overlap in the ranges for Rhizophoraceae. This correlates well with the high vessel tangential diameters. A computation of relative parabolic flow rates per mm^2 (Zimmermann, 1983) shows equivalent ranges with the Anisophylleaceae producing their flow rates with fewer pores and larger diameters on the average. The calculations were made using pooled data from the literature and are only indicative.

Macarisieae and Gynotrocheae have simple and scalariform perforations, while these in the Rhizophoreae are exclusively scalariform. Rhizophoreae also have the shortest vessel element lengths for the family, a character normally correlated with simple perforations (Dickison, 1975). It may be that efficiency of conduction (high flow rates) is not selected for in the mangroves. The generally small statures, coriaceous leaves, and restriction to saltwater habitats suggest the need to conserve water rather than to maximize its flow.

No other features—including fiber-tracheids, parenchyma or rays—seem to provide distinctive or mutually exclusive characters for the two families. Many of the characters are quite diagnostic for the genera, but differentiation of the tribes and of the two families is less readily accomplished. This is mostly due to very wide variation among the genera of Rhizophoraceae. The obvious distinctiveness of the Rhizophoreae is paralleled by the leaf data and can no doubt be explained by habitat specialization.

In other characters studied, the Anisophylleaceae show no similarity to the Rhizophoraceae. Chenery (1948) and Kukachka & Miller (1980) noted a positive aluminum test for the family, which is not shared by the Rhizophoraceae. Behnke (1981, 1984) noted S-type sieve element plastids in Anisophylleaceae and Myrtales but P-type in the Rhizophoraceae. In their embryological paper, Tobe & Raven (1987a) pointed out strong similarities of the Anisophylleaceae to the Myrtales and distinct differences with the Rhizophoraceae. However, they (1987b) later concluded that Anisophylleaceae and Rhizophoraceae do share enough developmental homologies to hypothesize common ancestry. The

TABLE 3. *Summary of selected wood features of the Anisophylleaceae and tribes of Rhizophoraceae.*

Character	Macarisieae; Hypogyneae	Gynotrocheae	Rhizophoreae	Anisophylleaceae
Vessel frequency (mm^2)	4-41 (138)	3-29	6-68	1-12
Vessel tangential diameter (μm)	21-340	71-300	34-130	84-430
Vessel element length (μm)	520-2,340	420-1,790	220-1,660	220-1,320
Perforations	simple/scalariform	simple/scalariform	scalariform	simple
IV pitting	alternate, opposite, transitional	alternate, opposite, transitional, scalariform	scalariform, transitional	alternate, with frequent coalescent apertures
Vessel-ray pitting	opposite, transitional, scalariform circular to elongate	alternate, opposite, reticulate circular to elongate	opposite to reticulate half-bordered to simple	rare, alternate to reticulate round to elongate
Fiber-tracheid length (μm)	960-3,390	1,210 3,480	libriform only 710-2,400	840-3,220
Ray type, seriation	heterocellular I, II; 1-5 seriate	heterocellular II, 2 distinct sizes; 1-32 seriate	heterocellular II, III, occasionally homocellular; 1-7 seriate	heterocellular II, 2 distinct sizes; 1-20 seriate
Ray tails, sheaths	1-36 square or erect cells	no tails, occasionally sheath cells	infrequent sheath cells	broad multiseriate, occasional sheath cells
Crystals	ray/axial parenchyma solitary, frequent or infrequent	ray/axial parenchyma solitary or clustered, frequent	ray parenchyma solitary	ray/axial parenchyma solitary, usually chambered to absent

perspective of vegetative anatomy alone is insufficient at present to resolve substantially this problem.

On the basis of their lack of vestured pits and intraxylary phloem and because of their possession of the Macarisioid tooth, the Rhizophoraceae s. str. appear to have no relationship to the Myrtales. Leaf teeth as known in all of the Rosales and Myrtales thus far examined are "rosoid," symmetrically vascularized by two to several converging veins surmounted by a secretory epithem, a submarginal foramen, and a connection to the surface through stomatelike pores. The tooth sinus is never reported to be included in the tooth vascularization. As described earlier here, the Macarisioid tooth is different in all respects. Thus far, the closest similarities to the Macarisioid tooth structure, and the general leaf architecture, can be found in the Dilleniid line. The Celastraceae (Celastrales), Elaeocarpaceae (Malvales), and Cyrillaceae (Ericales or Theales) are commonly classified in that lineage. Similarities seem more distant with the Hugoniaceae (Linales of Cronquist), Lepidobotryaceae (Geraniales of Dahlgren), and Oxalidaceae (Geraniales).

Considering that the field of comparative wood anatomy has a long established tradition, the results of comparisons among the families mentioned in this study are uncomfortably ambiguous. The newer field of leaf architecture has an equally well-drawn glossary and some organized preliminary synthesis regarding the character syndromes and their evolution. Here, too, we are left with equally large ambiguities. While the treatments of leaf architecture of families are far fewer than those based on comparative wood anatomy, existing comprehensive collections of cleared leaves should at least partially compensate. Some of these ambiguities may vanish in the future when the developmental bases of architectural forms becomes better understood and when the homologies of features of some of the larger phylads have been studied.

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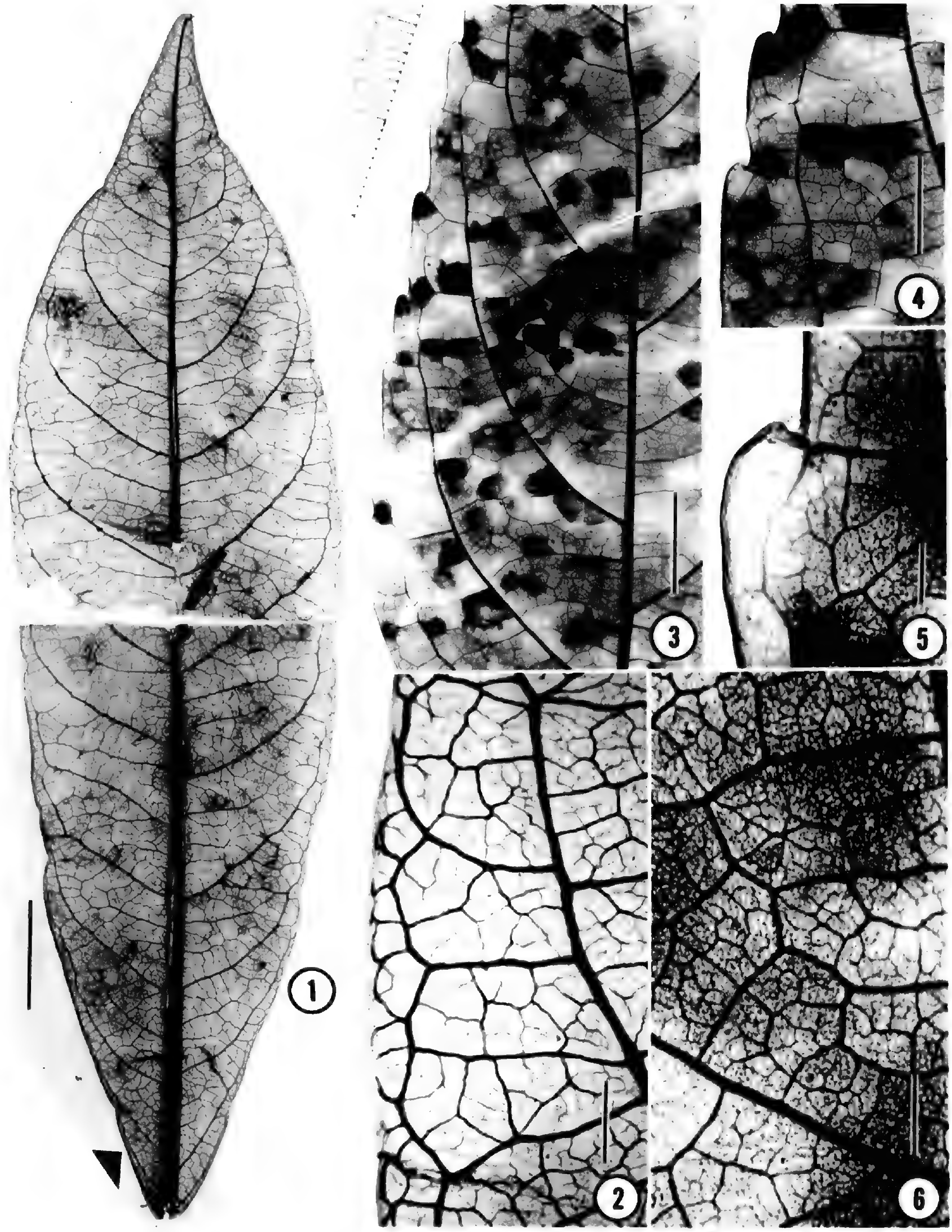
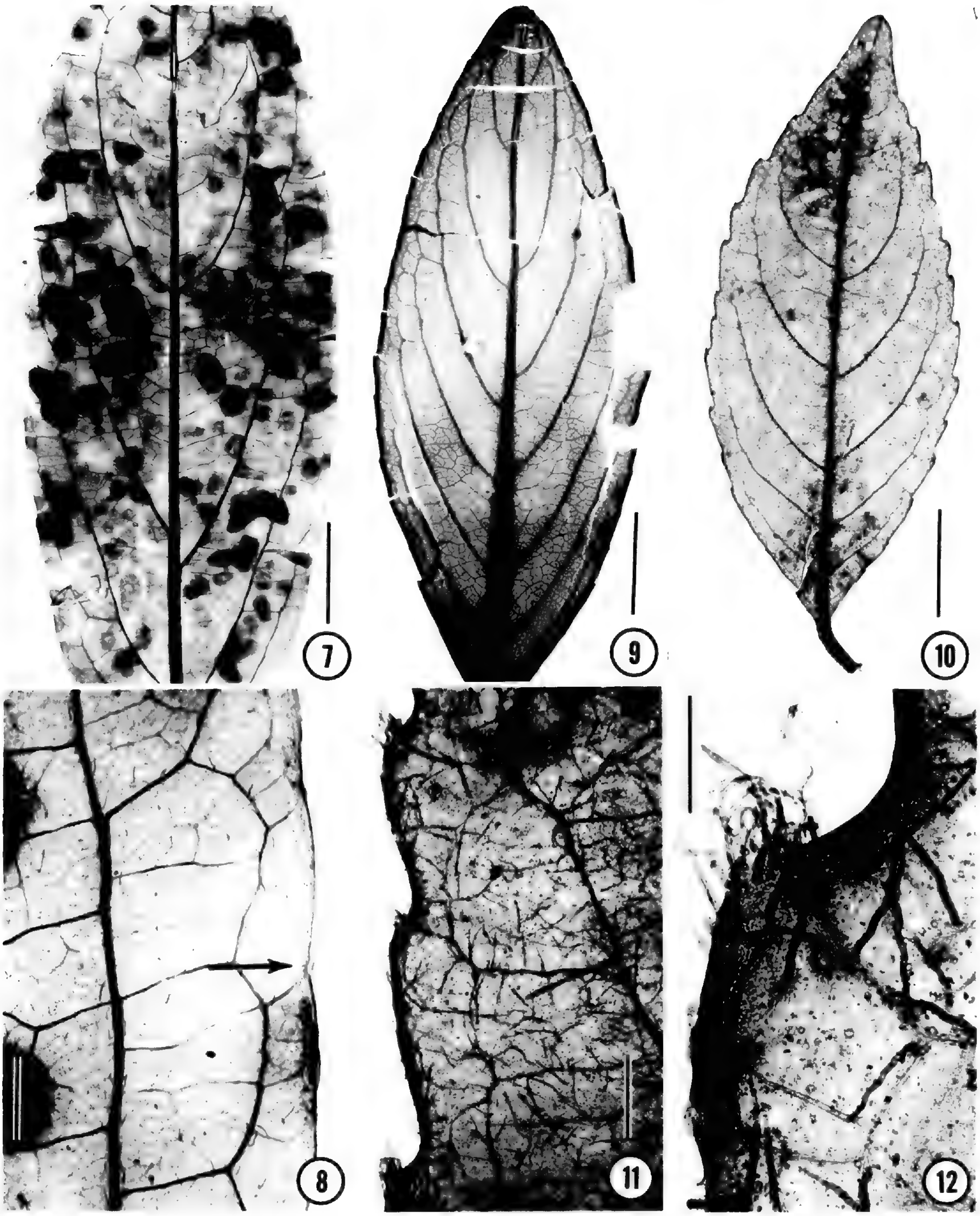
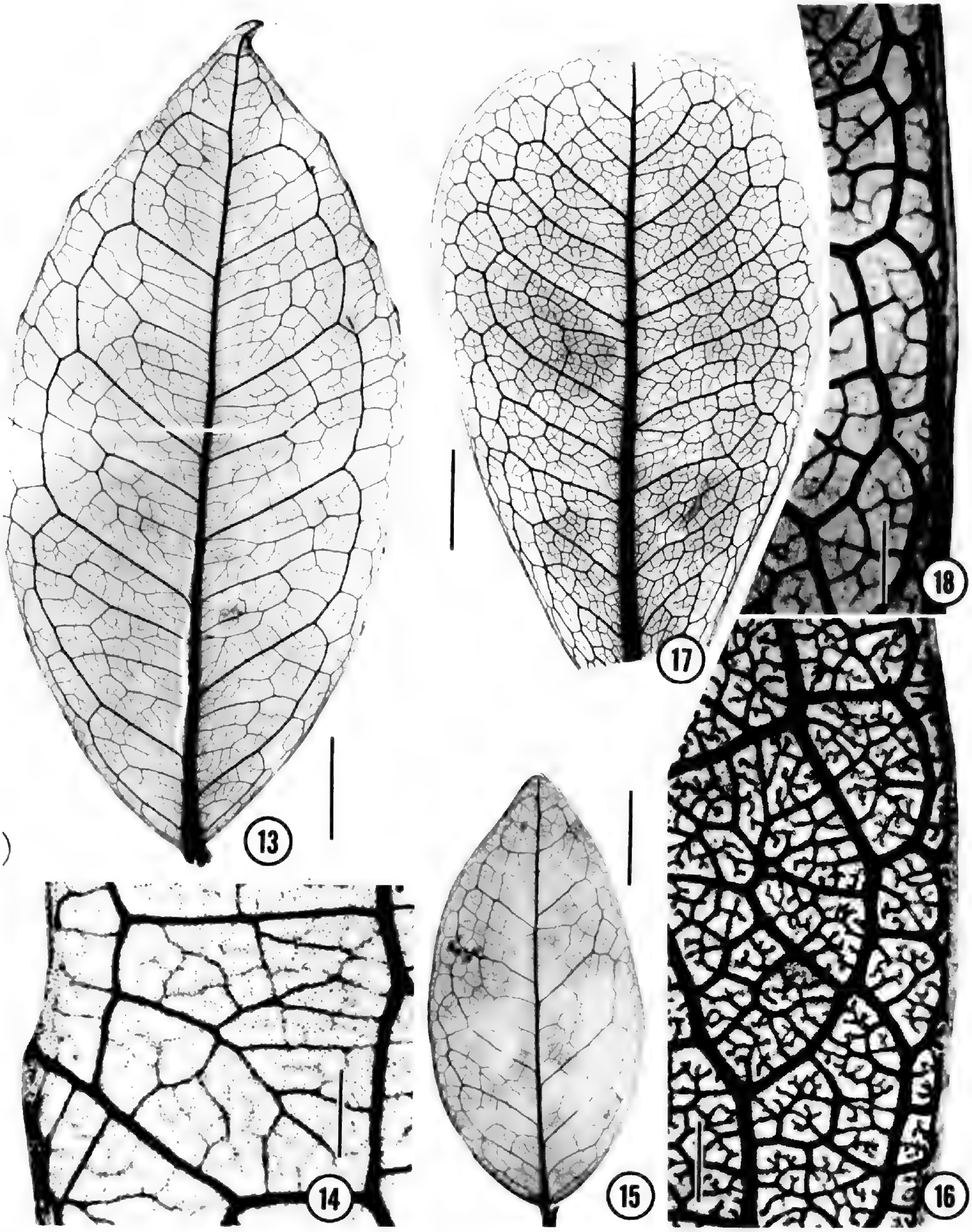


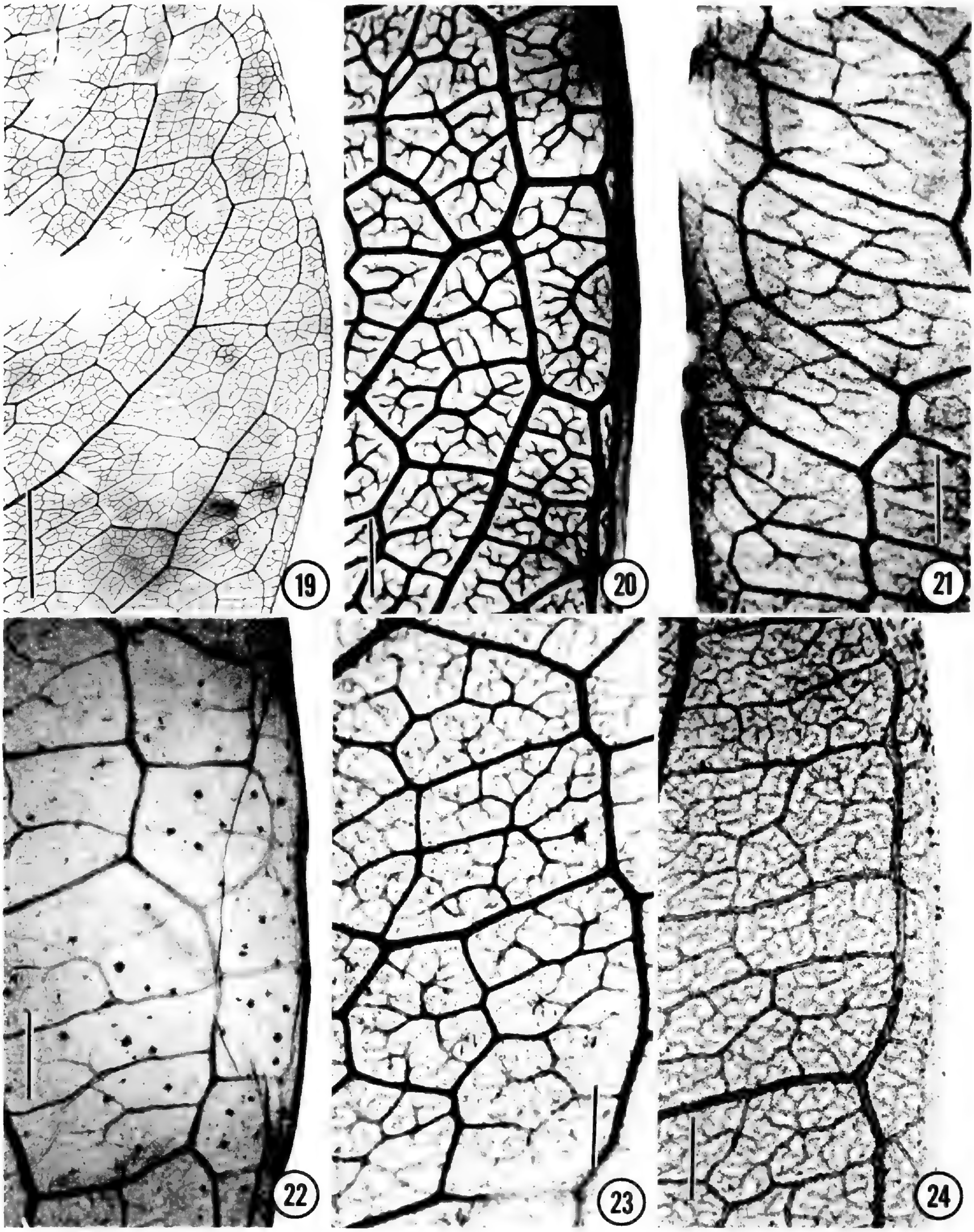
FIGURES 1–6. *Cleared leaves of* Rhizophoraceae.—*1.* Anopyxis calaensis, *showing eucamptodromous venation and entire, irregular margin.*—*2.* A. calaensis, *showing marginal venation and irregular higher-order domains.*—*3.* Blepharistemma corymbosum, *ovate leaf with toothed margin and eucamptodromous venation.*—*4.* B. corymbosum, *leaf margin showing the tooth veins arising from eucamptodromous loops.*—*5. Closeup of tooth in Figure 4 showing the vein bordering the sinus and ending below the apiculate gland.*—*6. Median portion of lamina of* B. corymbosum *demonstrating irregular polygonal tertiary and quarternary domains. Scale lines: Figures 1, 3 = 1 cm; Figures 2, 5, 6 = 1 mm; Figure 4 = 5 mm.*



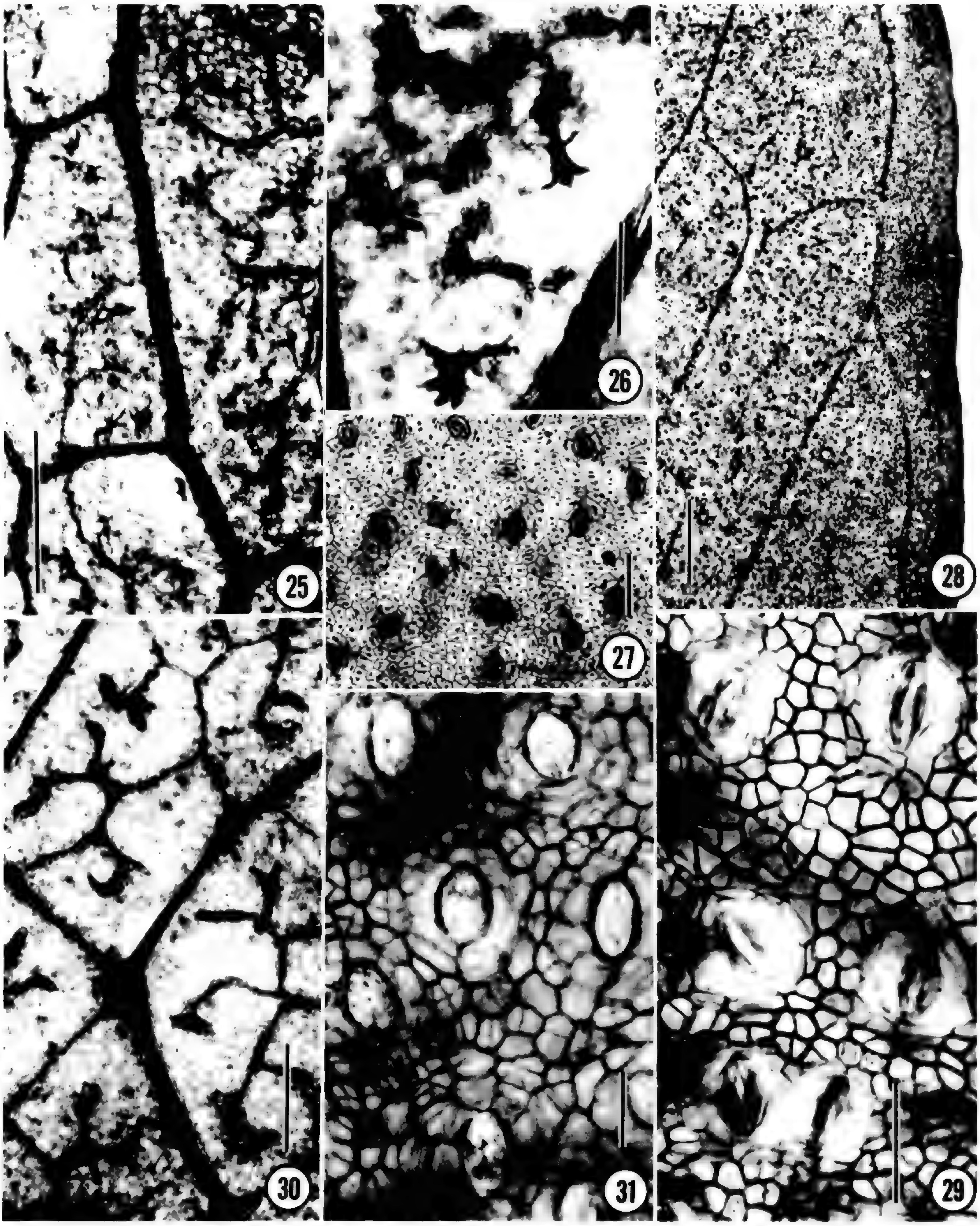
FIGURES 7–12. *Cleared leaves of Rhizophoraceae.*—*7.* Comiphyton gabonensis, *with strongly ascending eucamptodromous secondaries and irregular intercostal areas.*—*8.* C. gabonensis, *margin with reduced "tooth" with apiculate gland (arrow).*—*9.* Macarisia lanceolata, *with reduced teeth.*—*10.* M. pyramidata, *eucamptodromous leaf with well-developed teeth.*—*11.* M. pyramidata, *margin showing single tooth veins arising from the secondary loops.*—*12.* M. pyramidata, *showing vein entering a ciliate tooth from a symmetrical angle. Scale lines: Figures 7, 10 = 1 cm; Figures 8, 11 = 1 mm; Figure 9 = 5 mm; Figure 12 = 500 µm.*



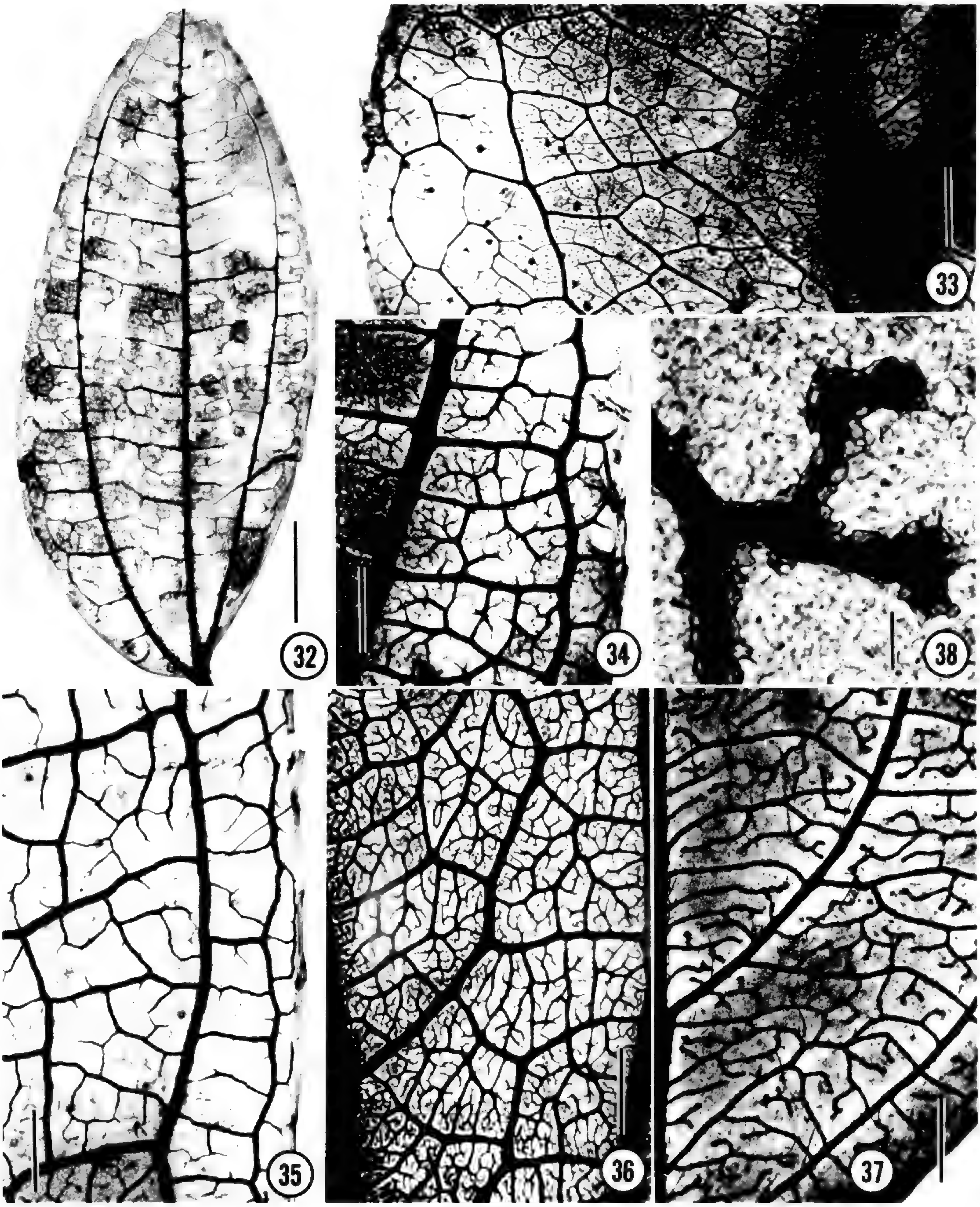
FIGURES 13–18. *Cleared leaves of Rhizophoraceae.—13.* Cassipourea guianensis, *showing looped brochidodromous venation with wide, regular intercostal areas and well-formed intersecondaries.—14.* C. guianensis, *showing single vein leading to small marginal tooth. Note that no other veins converge or participate in vascularizing the tooth.—15.* C. ceylanica, *showing the least organized intercostal areas among any of the cassipoureas examined. The margin is entire.—16.* C. ceylanica, *entire margin, irregular higher-order domains, and imperfect areolation with a highly variable number of free vein endings.—17.* Sterigmapetalum guianense, *showing looped brochidodromous venation and narrow intercostal areas.—18.* S. guianense, *showing the entire margin with looped venation. Scale lines: Figures 13, 15, 17 = 1 cm; Figures 14, 16, 18 = 1 mm.*



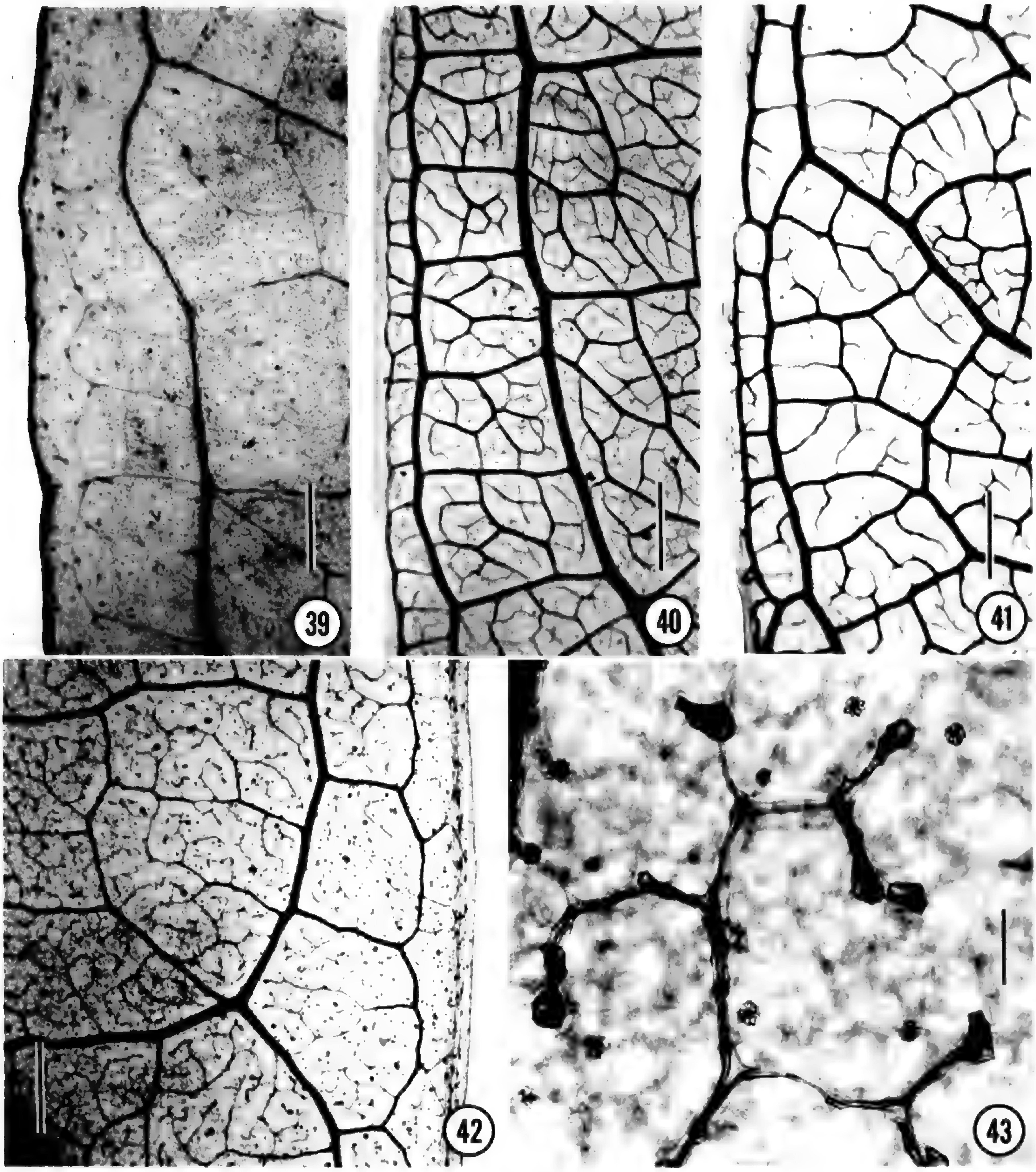
FIGURES 19–24. *Cleared leaves of Rhizophoraceae.—19.* Cassipourea barteri, *showing brochidodromous venation.—20.* C. barteri, *showing entire margin and imperfect areolation.—21.* Carallia brachiata, *with looped and elongated submarginal venation.—22.* Pellacalyx frustulata, *with an entire margin and looped submarginal venation.—23.* Crossostylis multiflora, *showing irregular quaternary domains and imperfect areolation.—24.* Gynotroches axillaris, *with eucamptodromous venation and regular percurrent quaternaries. Scale lines: Figure 19 = 1 cm; Figures 20–24 = 1 mm.*



FIGURES 25–31. *Cleared leaves of* Rhizophoraceae.—*25.* Rhizophora mangle, *showing obscure areolation.*—*26.* R. mangle, *showing astrosclereids in the mesophyll.*—*27.* Bruguiera gymnorrhiza, *showing cyclocytic stomata.*—*28.* Ceriops boiviniana, *leaf margin showing parallel secondaries and tendency toward development of a collector vein.*—*29.* C. boiviniana, *showing cyclocytic stomata.*—*30.* Kandelia candel, *areoles showing veinlets with tracheoidal endings.*—*31.* K. candel, *cyclocytic stomata. Scale lines: Figure 28 = 1 mm; Figures 27, 29, 31 = 100 μm; Figure 26 = 250 μm; Figures 25, 30 = 500 μm.*



FIGURES 32–38. *Cleared leaves of Anisophylleaceae.—32.* Anisophyllea cinnamomea, *leaf with asymmetrical base and basal acrodromous venation.—33.* A. griffithii, *leaf with brochidodromous looped margin and irregular higher-order venation.—34.* A. boehmii, *showing margin of eucamptodromous leaf.—35.* A. meniandii, *leaf with eucamptodromous entire margin.—36.* A. poggei, *mesophyll showing irregular higher-order venation.—37.* A. disticha, *mesophyll showing large, incomplete areolation.—38.* A. disticha, *veinlets showing differentiated sheath cells. Scale lines: Figure 32 = 1 cm; Figures 33–37 = 1 mm; Figure 38 = 100 μm.*



FIGURES 39–43. *Cleared leaves of Anisophylleaceae.—39.* Anisophyllea pomifera, *showing looped margin.—40.* Combretocarpus rotundatus, *margin of eucamptodromous leaf.—41.* Polygonanthus amazonicus, *margin with brochidodromous secondaries and imperfect areolation.—42.* Poga oleosa, *margin with brochidodromous secondaries and imperfect areolation.—43.* P. oleosa, *tracheoidal vein endings and druses. Scale lines: Figures 39–42 = 1 mm; Figure 43 = 100 μm.*

MORPHOLOGY AND PHENETICS OF RHIZOPHORACEAE POLLEN[1]

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ABSTRACT

Pollen morphologic data from light, scanning, and transmission electron microscopy were used in a phenetic analysis to assess variation within and among the four tribes traditionally included in Rhizophoraceae: Anisophylleeae, Gynotrocheae, Macarisieae, and Rhizophoreae. Principal components analysis revealed that pollen of Anisophylleeae is phenetically divergent from that of Gynotrocheae, Macarisieae, and Rhizophoreae, and therefore we recognize this taxon at the family level, Anisophylleaceae. In contrast Rhizophoraceae sensu stricto forms a phenetic continuum, with pollen of Macarisieae intermediate between Gynotrocheae and Rhizophoreae. Endoapertures of Anisophylleaceae pollen, when present, are circular and poorly defined, whereas all species of Rhizophoraceae possess endoapertures with some degree of fusion. Pollen of both families has a generalized angiosperm morphology, thereby providing no palynological basis for assessing relationships to Myrtales or other groups.

Comparative palynology in Rhizophoraceae has focused on the mangrove genus *Rhizophora*, primarily in connection with the recognition and study of paleo-shorelines (Kuprianova, 1959; Langenheim et al., 1967; Assemien, 1969; Rakosi, 1978; Sowunmi, 1981). Consequently, several species of *Rhizophora* have been well documented. Langenheim et al. (1967) used light microscope data (pollen shape and a unique endoaperture system) to characterize *R. mangle*, *R. samoensis*, *R. racemosa*, and *R. harrisonii*. Muller & Caratini (1977) expanded the study of modern Rhizophoraceae by employing transmission electron microscopy (TEM) in addition to light microscopy (LM) and scanning electron microscopy (SEM). Their analysis included three species studied by Langenheim et al. (1967), *R. mangle*, *R. racemosa*, and *R. harrisonii*, as well as *R. mucronata*, *R. stylosa*, *R. apiculata*, *R. lamarckii*, and *R. brevistyla*. Muller & Caratini (1977) essentially confirmed the findings of Langenheim et al. (1967), but underscored that most LM characters exhibit too much overlap to separate species. Although their study lacked the benefit of comparison with other Rhizophoreae (*Bruguiera*, *Ceriops*, and *Kandelia*), as well as other members of the family, they subdivided the *Rhizophora* pollen type into four groups by combining LM data with an SEM analysis of sculpture patterns.

Typically, other pollen studies of the family were accomplished as part of floristic or general morphologic surveys (Erdtman, 1952; Kubitzki, 1965; Huang, 1968; Guers, 1974; Geh & Keng, 1974; Sowunmi, 1974; Straka & Friedrich, 1984; Thanikaimoni, 1986a, 1987). SEM studies have been centered on the tribe Rhizophoreae (Tissot, 1979; Bertrand, 1983; Ludlow-Wiechers & Alvarado, 1983). For complete references to pollen studies in the family, see Thanikaimoni (1972, 1973, 1976, 1980, 1986b).

Little palynologic attention has been directed specifically to the taxonomic integrity within and among the four tribes traditionally included in Rhizophoraceae sensu lato: Anisophylleeae, Gynotrocheae, Macarisieae, and Rhizophoreae. Using LM, SEM, and TEM, we investigated the pollen morphology of all genera in these taxa. Of particular interest is Anisophylleeae, which on the basis of a broad array of characters has been considered to constitute a distinct family, Anisophylleaceae (see other symposium papers). With this in mind, we

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TABLE 1. *Taxa examined, collection data, and plate references.*

OTU	Taxa	Location	Collector/Herbarium	Figures	
				SEM	TEM
	Anisophyllea buttneri Engl.	Gabon	*Thollon 4130* (MO)	2	
A1	*A. disticha* (Jack.) Baill.	Singapore	*Kiah & Leong s.n.* in 1984 (no voucher)	4	36
A2	*A. fallax* Scott Elliot	Madagascar	*Reserves Nat. 2619* (TAN)		40
	A. laurina R. Br.	West Africa	*Fairchild s.n.* in 1927 (US)	1	41
A3	*A. obtusifolia* Engl. & Brehmer	Tanzania (Usambara Mountains)	*Amani River Institute s.n.* (no voucher), Bukit Timah Natural Reserve	3	38, 39
	Combretocarpus rotundatus (Miq.) Dans.	N Borneo	*Tandom 2816* (K)		37
A4	*C. rotundatus*	Brunei	*Juncosa s.n.* in 1983 (no voucher)	7, 8	
A5	*Poga oleosa* Pierre	Cameroon	*Thomas 2273* (MO)	5	
	P. oleosa	Nigeria	*Coombe 186* (K)		43
A6	*Polygonanthus amazonicus* Ducke	Brazil	*Zarucchi 3138* (US)	9	
	P. amazonicus	Brazil	*Pires 1281* (NY)		42
	P. amazonicus	Brazil	*S. R. Hill 12922* (MO)	6	
G1	*Carallia brachiata* (Lour.) Merr.	Australia	*Jackes s.n.* in 1983 (JCT)	35	44
G2	*C. eugenioides* King	Malaysia	*B. C. Stone 15114* (KLU)	33, 34	45
	Crossostylis biflora Forst. (*C. raiateensis* J. W. Moore)	Society Islands	*St. John 17346* (MO)		
G3	*C. grandiflora* (Pancher ex Brogn. & Gris.	New Caledonia	*McPherson 6331* (MO)	31	
	C. grandiflora	New Caledonia	*McPherson 1898* (MO)		46
G4	*Gynotroches axillaris* Blume	Malaysia	*B. C. Stone 15397* (KLU)	30	47
G5	*Pellacalyx* cf. *saccardianus* Scortech.	Malaysia	*B. C. Stone 15396* (KLU)	32	49
	P. pustulata Merr.	Philippines	*Wenzel 1497* (MO)		48
	Anopyxis ealeaensis Sprague	Belgian Congo	*Germain 191* (MO)	23	50
M1	*A. kleineana* (Pierre) Engl.	Cameroon	*Thomas 3464* (MO)	22	51
	Blepharistemma membranifolia (Miq.) Ding Hou	India	*Wallich 1832* (K)		59
M2	*B. membranifolia*	India	*Manilal s.n.* in 1984 (no voucher)	17	
	Cassipourea afzelii (Oliv.) Alston	Liberia	*Baldwin 10609* (MO)	18	
M3	*C. elliptica* (Sw.) Poir.	Panama	*Kirkbride & Duke 1322* (MO)		58
	C. guianensis Aubl.	Brazil	*Nelson 1324* (MO, NY)	19	
	C. gummiflora Tul. var. *verticillata* (N. E. Br.) J. Lewis	Zimbabwe (cultured Harare Bot. Gard.)	*Muller 3558* (SRGH)	21	
	Compiphyton gabonense Floret	Gabon	*Le Tetsu 5918* (P)	10	
M4	*C. gabonense*	Zaire	*Germain 5213* (BR)		62
M5	*Dactylopetalum sessiliflorum* Benth.	Madagascar	*Reserves Nat. 4327* (TAN)	20	60
	D. zenkeri Engl.	Cameroon	*Zenker 4701* (MO)		61
M6	*Macarisia ellipticifolia* Arènes	Madagascar	*Service For. 1972* (TAN)	14	55
	M. humbertiana Arènes	Madagascar	*Humbert 23505* (P)	15	56
	M. lanceolata Baill.	Madagascar	*Service For. 9366* (P)	13	54
	M. lanceolata	Madagascar	Serv. Eaux & Forêt 2955 (TAN)		

TABLE 1. *Continued.*

OTU	Taxa	Location	Collector/Herbarium	Figures SEM	Figures TEM
M7	*M. pyramidata* Thou.	Madagascar	*Service For. 9741* (P)	16	57
	Petalodactylus obovata Arènes	Madagascar	*Alaotra Agric. Sta. 3868* (TAN)		63
M8	*Sterigmapetalum heterodoxum* Steyerm.	Venezuela	*Wingfield 13245* (MO)	11	53
M9	*S. obovatum* Kuhlm.	Brazil	*Maguire et al. 56502* (MO)	12	52
	Bruguiera gymnorrhiza (L.) Lamk.	Madagascar	*Alaotra Agric. Sta. 27552* (TAN)		68
R1	*B. gymnorrhiza*	Madagascar	*Reserves Nat. 9255* (TAN)	28	
	Ceriops tagal (Perr.) C. B. Rob.	Madagascar	*Hervien s.n.* (TAN)		
R2	*C. tagal*	Madagascar	*Dorr & Koenders 3063* (MO)	27	69
R3	*Kandelia candel* (L.) Druce	Japan	*Murata & Nakamura 1142* (MO)	29	67
R4	*Rhizophora mangle* L.	Florida (cultivated)	*Tobe s.n.* in 1981 (no voucher; Fairchild Botanical Garden)	24	66
R5	*R. mucronata* Lamk.	Mozambique	*Torre & Paiva 11483* (MO)		
R6	*R. mucronata*	Madagascar	*Bosser 9947* (TAN)		64
	R. mucronata	Madagascar	*Hervien s.n.* in 1964 (TAN)		
	R. mucronata	Madagascar	*Marot 2602* (TAN)	25	
R7	*R. stylosa* Griff.	Florida (cultivated)	*Tobe s.n.* in 1981 (no voucher; Fairchild Botanical Garden FG69-111)	26	65

conducted a phenetic analysis to assess overall morphologic variation within and among these groups and to test the hypothesis of separate familial status for Anisophylleaceae.

MATERIALS AND METHODS

POLLEN MORPHOLOGY

In our investigation, pollen from 51 collections (representing 39 species of Anisophylleaceae and Rhizophoraceae) was examined by light and electron microscopy (Table 1). Hereinafter, Rhizophoraceae is referred to in the strict sense (i.e., only the tribes Gynotrocheae, Macarisieae, and Rhizophoreae). All pollen were initially treated with the acetic anhydride/sulfuric acid acetolysis mixture of Erdtman (1960). For LM, whole grains were mounted in glycerine jelly and observed with a Leitz Ortholux microscope using transmitted light. Measurements (μm) were based on 10–50 undistorted grains when possible. Pollen for SEM was either air dried from 95% ethanol or critical-point dried, sputter coated with gold, and examined with either an ISI Super II SEM or ETEC Autoscan SEM. Pollen for TEM was processed as reported earlier (Skvarla, 1966) and examined with either a Philips model 200 TEM or Zeiss 10 TEM.

PHENETIC ANALYSIS

Operational Taxonomic Units (OTUs). Data from 27 collections (Table 1) were subjected to a numerical phenetic analysis as Operational Taxonomic Units (OTUs; Sneath & Sokal, 1973). These 27 OTUs represent 26 species (*Rhizophora mucronata* has two OTUs) and were selected if data were obtained for all 33 characters (Table 2).

Characters. The 33 characters (Table 2) used in the phenetic analysis are based on standard palynological data (Erdtman, 1952; Faegri & Iversen, 1975), and include 10 LM (1–10), 13 SEM (11–23), and 10 TEM (24–33) characters. Although most are self-explanatory, several merit elaboration. The variability in polar axis (P) and breadth (E) is often expressed in terms of range or minimum and maximum measurements. We used standard deviation (characters 2 and 4) in-

TABLE 2. *Characters used in numerical analysis.*

Character	Abbreviation	Score
Polar axis (P)		
1. Mean		
2. Standard deviation	(SDP)	
Greatest breadth (E)		
3. Mean		
4. Standard deviation	(SDE)	
5. Polar axis/greatest breadth	(P/E)	
6. Endoaperture fusion	(EF)	
Completely unfused		0
Mostly unfused (< 40%)		1
Mixed (approx. 50%)		2
Mostly fused (> 60%)		3
7. Mean polar length of endoaperture	(PL)	
8. Endoapertural index	(EI)	
9. Mean distance between colpal ends	(DCE)	
10. Polar area index	(PAI)	
Sculpture of mesolcolpia		
11. Psilate	(PS)	
12. Punctate	(PU)	
13. Rugulate	(RU)	
14. Striate	(ST)	
Sculpture of poles		
15. Psilate	(PS)	
16. Punctate	(PU)	
17. Rugulate	(RU)	
18. Striate	(ST)	
Sculpture of mesocolpial margins		
19. Psilate	(PS)	
20. Punctate	(PU)	
21. Rugulate	(RU)	
22. Spinulate	(SP)	
23. Striate	(ST)	
Exine structure		
24. Tectum thickness	(TT)	
25. Height of columellae	(CH)	
26. Maximum width of columellae	(CW)	
27. Foot layer thickness	(FL)	
28. Endexine thickness	(EN)	
29. Tectum thickness ratio	(TT/TET*)	
30. Columellar height ratio	(CH/TET)	
31. Foot layer thickness ratio	(FL/TET)	
32. Endexine thickness ratio	(EN/TET)	
33. Intercolumellar granulation	(IG)	
No granulation		0
Incipient granulation (< 50%)		1
Abundant granulation (> 50%)		2

* TET = total exine thickness.

stead, because it is based on all grains measured and is less affected by sample size or aberrant grains. Character 6, endoaperture fusion, expresses information usually included for Rhizophoraceae pollen (e.g., Muller & Caratini, 1977). It is an ordered multistate character based on increasing percentage of endoaperture fusion and was processed in the same way as quantitative characters (Sneath & Sokal, 1973). Character 8, endoapertural index (EI), is the ratio of polar length of the endoaperture (PL) to polar axis (P). It is a ratio we have constructed to express the relative width of the endoaperture.

The 13 SEM characters describe the sculpture of three parts of the pollen surface: mesocolpia (11–14), poles (15–18), and mesocolpial margins (19–23). Although this information can be condensed into three unordered multistate characters, only ordered multistate characters are acceptable with principal components analysis (Gower, 1966). Therefore, as Gower (1966) recommended, we used binary (0, 1) characters to indicate absence (0) or presence (1) of a particular sculpture pattern.

TEM characters 24–28 were recorded as means of measurements (μm) taken from an average of six negatives. All measurements were mid-mesocolpial on equatorial sections perpendicular to the polar axis. Character 33 is an ordered multistate character based on increasing percentage of intercolumellar granulation. The remaining characters (29–32) are expressions of exine shape, that is, the relative contribution of tectum, columellae, foot layer, and endexine to the total exine thickness. In five cases it was necessary to take TEM data from a different collection of the same species (Table 3). This procedure was followed to insure adequate representation of all taxa.

Numerical Analysis. Phenetic variation was analyzed using NT-SYS (Rohlf et al., 1982), a package of multivariate computer programs designed for use in systematics. The data (Table 3) were standardized (i.e., each character being transformed to have a mean of zero and standard deviation of one), followed by calculation of a Pearson product-moment correlation matrix and principal components analysis (Sneath & Sokal, 1973). A minimum spanning tree (Dunn & Everitt, 1982) was calculated using an average taxonomic distance matrix (Sneath & Sokal, 1973) produced from the standardized data set.

Principal components analysis also produces a matrix of eigenvectors showing character loadings on each component (Table 5). If a character has a loading of 0.9 on component I, then $(0.9)^2$ or 0.81 (81%) of that character is expressed or statistically "explained" on component I and the remaining 19% on other components. Table 5 lists all characters with loadings greater than 0.5. If a character has a positive (+) loading, then OTUs with higher values for that character tend to be found toward the positive end of that component. Higher values include larger quantitative measurements, higher-numbered multistate character states, and binary (0, 1) characters with character state 1.

RESULTS

POLLEN MORPHOLOGY

Detailed LM, SEM, and TEM measurements and observations for 27 collections (Table 1) are given in Table 3, and summarized for Anisophylleaceae and each tribe of Rhizophoraceae in Table 4. The supplemental descriptions below include characters not considered in the numerical analysis, as well as unique morphological features in need of emphasis. Morphological delineation is based on all 51 collections (Table 1).

Anisophylleaceae

LM. Pollen is mainly tricolporoidate (occasionally tricolporate), rarely with two apertures, radially symmetrical, and isopolar. Syncolpate grains are common. Endoapertures, when present, are circular but poorly defined.

SEM (Figs. 1–9). Of special note is *Anisophyllea disticha,* which differs markedly from all other species in this study by having a striate surface.

TEM (Figs. 36–43). In *A. disticha* and *A. obtusifolia,* a narrow and highly undulating columellae layer is present in sectional planes near the equator (Figs. 36, 38). In a different sectional plane of *A. obtusifolia,* and in *A. laurina,* the columellae layer is straight, and the foot layer is thinner than the tectum (Figs. 39, 41).

Gynotrocheae

LM. Pollen is tricolporate, radially symmetrical, and isopolar. Endoapertures in all grains are fused laterally, the only tribe so distinguished.

SEM (Figs. 30–35). A psilate–punctate surface is dominant in this tribe.

TEM (Figs. 44–49). In *Crossostylis grandiflora* a trace of granular matrix similar to that described for Macarisieae (see below) is present at the lower tectum margin (Fig. 46). *Pellacalyx* differs from other Gynotrocheae by having a thin tectum and tall, branched columellae that become shorter at the poles (Figs. 48, 49); granules are suggested beneath the lower tectum margin and the distal parts of the columellae.

Macarisieae

LM. Pollen is tricolporate, rarely dicolporate and tetracolporate, radially symmetrical, and isopolar. Shape has the greatest range of the tribes, from suboblate to prolate (character 5, Table 3).

SEM (Figs. 10–23). This tribe processes variable pollen sculpture (Table 4).

TEM (Figs. 50–63). Intercolumellar spaces are either partially or completely filled with a matrix of granules (Figs. 50, 52, 54, 55, 57, 59). Some columellae also are granular distally. In taxa with prominent fused (zonorate) endoapertures (character 6, Table 2), the endexine is granular in the mesocolpia in the vicinity of the endoaperture.

Rhizophoreae

LM. Pollen is tricolporate, radially symmetrical, and isopolar (except some grains in *Rhizophora mucronata*).

SEM (Figs. 24–29). Pollen of *R. mucronata* has a basically punctate–rugulate surface. However, this pattern varies among the five collections examined (Table 1), as well as within collections. In the collection *A. Torre & J. Pavia 11483* rugulate elements are distinct; some grains in this collection showed a punctate–rugulate surface on one hemisphere and a psilate–punctate surface on the other. Dicolporate grains were common. In the collection *J. Bossier 9947* the surface has a faint rugulate–punctate sculpture, while in the collection *Greve 290* it is psilate–punctate. In the collection *Hervien s.n.,* made in 1964, the pollen grains are psilate–punctate, faintly rugulate–punctate, or distinctly rugulate–punctate. Some dicolporate grains are also present in this collection. In the collection *P. Marot 2602* the grains are rugulate–punctate; some also have spinules. Note that spinules were present on the mesocolpial margins of *Carallia brachiata* (Fig. 35), *C. eugenioides* (Figs. 33, 34), and *Gynotroches axillaris* (Fig. 30).

TEM (Figs. 64–69). Tectum thickness is the most variable of the four groups (character 24, Table 3).

PHENETIC ANALYSIS

Principal components analysis reveals two phenetically distinct groups of OTUs (Fig. 70). One group, consisting of all Anisophylleaceae OTUs, is located toward the positive end of component I and the negative end of component II. The first two components account for 25.5 and 20.7% of the total variation. The other group is an elongated continuum formed by the three tribes of Rhizophoraceae, with Macarisieae OTUs distributed across phenetic space between Rhizophoreae and Gynotrocheae. The minimum spanning tree indicates

TABLE 3. *Data set used in numerical analysis.*[1]

OTU	Characters															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
A1	22	1.2	16	0.8	135	0	2	.08	3	.17	0	0	0	1	0	0
A2	28	3.5	17	3.0	164	0	0	.00	2	.09	0	1	0	0	0	1
A3	26	1.7	20	1.7	131	0	2	.09	3	.14	0	1	0	0	0	1
A4[2]	20	1.2	17	1.7	118	0	0	.00	3	.16	0	1	0	0	0	1
A5[2]	29	2.6	22	1.7	133	0	3	.10	4	.17	0	1	0	0	0	1
A6[2]	28	1.6	25	1.6	114	0	0	.00	5	.17	0	1	0	0	0	1
G1	14	0.6	12	0.6	117	3	2	.27	3	.22	1	1	0	0	1	1
G2	17	1.5	14	1.0	125	3	5	.27	3	.18	1	1	0	0	1	1
G3[2]	15	0.9	14	0.8	105	3	5	.30	2	.14	1	1	0	0	1	1
G4	15	3.0	12	2.3	122	3	4	.29	3	.23	1	1	0	0	1	1
G5	11	1.2	8	0.7	124	3	2	.23	1	.17	1	0	0	0	1	0
M1	24	1.3	22	1.8	106	3	4	.16	4	.15	1	0	0	0	1	0
M2[2]	19	1.6	18	1.1	107	3	4	.19	5	.27	0	1	1	0	0	1
M3	20	1.7	15	1.3	133	2	3	.13	4	.26	0	1	0	0	0	1
M4	17	0.6	13	1.4	129	1	2	.10	2	.11	0	1	0	0	1	0
M5	17	1.2	15	1.4	109	1	2	.10	3	.20	0	1	0	0	0	1
M6	12	0.9	13	0.9	88	3	1	.11	2	.17	1	0	0	0	1	0
M7	13	1.5	14	0.9	97	1	1	.07	3	.26	0	1	1	0	1	1
M8	19	2.5	20	1.7	85	3	5	.25	4	.19	1	0	0	0	1	0
M9	14	1.1	16	1.4	86	3	2	.16	3	.21	0	1	1	0	0	1
R1	18	1.0	19	1.1	93	2	2	.13	5	.27	0	1	1	0	0	1
R2	13	1.0	14	1.2	92	3	3	.19	4	.27	0	1	1	0	0	1
R3	20	1.2	22	1.5	92	1	3	.16	4	.21	0	1	1	0	0	1
R4	19	1.0	19	0.9	103	3	3	.17	5	.28	0	1	1	0	0	1
R5	23	1.3	21	1.4	107	3	3	.11	6	.32	0	1	1	0	0	1
R6	24	1.8	21	1.5	113	3	4	.18	5	.25	0	1	1	0	0	1
R7	23	1.2	23	1.4	100	1	4	.17	5	.22	0	1	1	0	0	1

[1] OTU symbols from Table 1 (column 1), characters as in Table 2.

[2] The TEM data for A4, A5, G3, and M2 were taken from the other collection of the same species (Table 1). The TEM data for A6 were taken from the *Pires 1281* collection.

considerable distortion within Gynotrocheae (Fig. 70). Relationships within this tribe are clarified by including component III, which accounts for an additional 13.0% of the total variation (Fig. 71). Component III also reveals marked divergence between *Anisophyllea disticha* (A1) and the other Anisophylleaceae OTUs.

OTUs are distributed across component I based on overall size, tectum thickness, collumellae height, and other characters (Table 5). Thus the larger grains of Anisophylleaceae and Rhizophoreae are to the right (Fig. 70), and the smaller Gynotrocheae pollen is to the left. Anisophylleaceae and Rhizophorea OTUs separate along component II because of differences in sculpture, shape, and other characteristics (Table 5).

TABLE 4. *Summary of data in Table 3 for Anisophylleaceae and each tribe of Rhizophoraceae.*[1]

OTU	Characters															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
AA	26	2.0	20	1.7	133	0	1	.05	3	.15	0	$\underline{1}$	0	$\underline{0}$	0	$\underline{1}$
GG	14	1.4	12	1.1	119	3	4	.27	2	.19	1	$\underline{1}$	0	0	1	$\underline{1}$
MM	17	1.4	17	1.3	104	3	3	.14	3	.20	$\underline{0}$	$\underline{1}$	$\underline{0}$	0	$\underline{1}$	$\underline{1}$
RR	20	1.2	20	1.3	100	3	3	.16	5	.26	0	1	1	0	0	1

[1] AA = Anisophylleaceae, GG = Gynotrocheae, MM = Macarisieae, RR = Rhizophoreae. All measurement characters have been averaged. For binary (SEM) characters, the predominant state is given and underlined to indicate one or more exceptions within the family or tribe. For multistate characters 6 and 33, the median is given.

TABLE 3. *Continued.*

Characters																
17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
0	1	0	0	0	0	1	.58	.18	.15	.38	.13	.46	.14	.30	.10	0
0	0	0	1	0	0	0	.47	.28	.23	.34	.14	.38	.23	.28	.11	0
0	0	0	1	0	0	0	.68	.28	.23	.43	.12	.45	.19	.28	.08	0
0	0	1	0	0	0	0	.37	.36	.19	.27	.07	.35	.34	.25	.07	0
0	0	0	1	0	0	0	.41	.46	.15	.09	.14	.37	.42	.08	.13	0
0	0	0	1	0	0	0	.71	.28	.26	.98	.18	.33	.13	.46	.08	0
0	0	0	0	0	1	0	.16	.08	.11	.20	.14	.28	.14	.34	.24	0
0	0	0	0	0	1	0	.25	.05	.11	.26	.23	.32	.06	.33	.29	0
0	0	1	1	0	0	0	.27	.05	.07	.14	.13	.46	.08	.24	.22	1
0	0	0	0	0	1	0	.28	.06	.14	.26	.22	.34	.07	.32	.27	0
0	0	1	0	0	0	0	.16	.07	.08	.12	.13	.33	.15	.25	.27	1
0	0	1	0	0	0	0	.36	.09	.19	.51	.08	.35	.09	.49	.08	2
0	0	0	1	1	0	0	.27	.09	.10	.30	.07	.37	.12	.41	.10	2
0	0	0	1	0	0	0	.20	.11	.12	.15	.08	.37	.20	.28	.15	0
0	0	1	0	0	0	0	.40	.07	.11	.43	.09	.40	.07	.43	.09	2
0	0	1	0	0	0	0	.30	.08	.14	.31	.10	.38	.10	.39	.13	1
0	0	1	0	0	0	0	.30	.10	.11	.30	.07	.39	.13	.39	.09	2
0	0	1	1	0	0	0	.17	.08	.08	.20	.05	.34	.16	.40	.10	2
0	0	1	0	0	0	0	.54	.19	.13	.77	.05	.35	.12	.50	.03	2
1	0	0	1	1	0	0	.31	.12	.11	.37	.01	.38	.15	.46	.01	2
1	0	0	1	1	0	0	.31	.11	.14	.35	.03	.39	.14	.44	.04	0
1	0	0	1	1	0	0	.17	.08	.11	.26	.09	.28	.13	.43	.15	0
1	0	0	1	1	0	0	.40	.12	.12	.59	.14	.32	.10	.47	.11	0
1	0	1	1	1	0	0	.36	.13	.19	.56	.05	.33	.12	.51	.05	0
1	0	0	1	1	0	0	.35	.21	.27	.57	.03	.30	.18	.49	.03	0
1	0	0	1	1	0	0	.51	.19	.22	.41	.06	.44	.16	.35	.05	0
1	0	1	0	0	0	0	.38	.14	.19	.46	.11	.35	.13	.42	.10	0

The minimum spanning tree interconnects Gynotrocheae OTUs with two short and two long links (Fig. 71). The short connections are *Carallia eugenioides* (G2) to *C. brachiata* (G1) and *Gynotroches axillaris* (G4) at distances of 0.630 and 0.636, respectively. *Pellacalyx* cf. *saccardianus* (G5) joins *C. brachiata* (G1) and *Crossostylis grandiflora* (G3) at distances of 1.035 and 1.023.

Connections within Macarisieae average 0.793, but only one OTU (*Dactylopetalum sessiliflorum*, M5) links with more than two other OTUs within the tribe. The congeneric OTUs *Sterigmapetalum heterodoxum* (M8) and *S. obovatum* (M9) are separated by a distance of 1.377. *Sterigmapetalum obovatum* (M9) is actually more similar (0.603) to *Bruguiera gymnorrhiza* (R1) than to any OTU of its own tribe.

Most Rhizophoreae are directly linked to *Bru-*

TABLE 4. *Continued.*

Characters																
17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
0	$\underline{0}$	$\underline{0}$	$\underline{1}$	0	0	$\underline{0}$	.54	.31	.20	.42	.13	.39	.24	.28	.10	0
0	0	$\underline{0}$	$\underline{0}$	0	$\underline{1}$	0	.22	.06	.10	.20	.17	.35	.10	.30	.26	0
$\underline{0}$	0	$\underline{1}$	$\underline{0}$	$\underline{0}$	0	0	.32	.10	.12	.37	.07	.38	.13	.42	.09	2
1	0	$\underline{0}$	$\underline{1}$	$\underline{1}$	0	0	.35	.14	.18	.46	.07	.34	.14	.44	.08	0

TABLE 5. *Character loadings from principal components analysis.*[1]

Direction	Loadings	I	II	III
+	.80–.89		13	
	.70–.79	1, 3, 26	10, 17, 21	16
	.60–.69	9, 20, 24, 25	6, 31	12
	.50–.59		9	22, 28, 32
−	.80–.89	11, 15		
	.70–.79		5	
	.60–.69	8, 32		
	.50–.59	6	25, 28	14, 18, 23, 33

[1] Numbers under each component refer to characters outlined in Table 2. Only characters with loadings greater than 0.5 are shown.

guiera gymnorrhiza (R1), with two exceptions (R5 and R7) which are two links away. The links within Rhizophoreae are the shortest of any tribe, averaging 0.639. In a similar manner, all Anisophylleaceae OTUs are joined to *Anisophyllea obtusifolia* (A3) but at much longer distances (lower similarity) than those within Rhizophoreae. Even discounting *A. disticha* (A1), links within Anisophylleaceae average 0.923, higher than any tribe of Rhizophoraceae. A1 joins A3 from a distance of 1.796, the longest link on the minimum spanning tree. *Anisophyllea disticha* is actually more similar to three Macarisieae OTUs than to *Combretocarpus rotundatus* (A4), the next closest OTU within Anisophylleaceae. The closer Macarisieae OTUs are *Cassipourea elliptica* (M3), *Comiphyton gabonense* (M4), and *Dactylopetalum sessiliflorum* (M5).

Intertribal links are shorter than many intratribal connections. *Blepharistemma membranifolia* (M2), for example, is more similar to R1 (0.702) than to either M3 (0.833) or M9 (0.718). Likewise, *Macarisia ellipticifolia* (M6) is more similar to G5 (0.819) than to either M1 (0.906) or M4 (0.850).

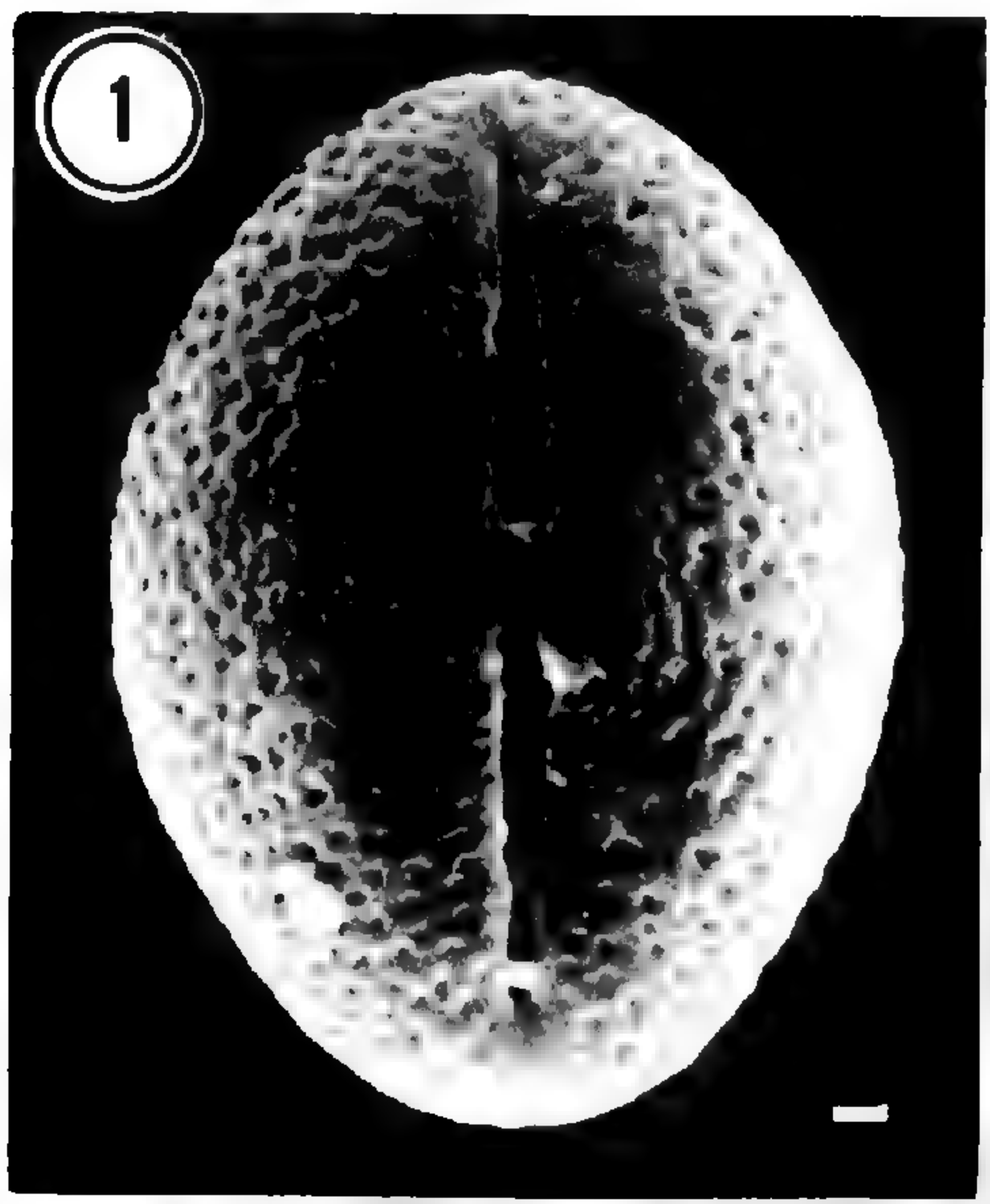
The phenetic gap between Anisophylleaceae and Rhizophoraceae is spanned by a link between *Combretocarpus rotundatus* (A4) and *Dactylopetalum sessiliflorum* (M5) at a distance of 0.913. Although this is greater than intertribal connections within Rhizophoraceae, it is shorter than several links within Anisophylleaceae.

→

FIGURES 1–12. *Scanning electron micrographs of Anisophylleaceae (1–9) and Macarisieae (10–12) pollen.—1.* Anisophyllea laurina, *lateral view, surface punctate.—2.* A. buttneri, *polar view.—3.* A. obtusifolia. *Portion of mesocolpium showing punctate surface.—4.* A. disticha, *lateral view. This species differs from the others in having a striate surface.—5.* Poga oleosa, *polar view.—6.* Polygonanthus amazonicus, *polar view.—7, 8.* Combretocarpus rotundatus.*—7. Polar view.—8. Sublateral view of a dicolporate, syncolpate grain.—9.* Polygonanthus amazonicus, *lateral view.—10.* Comiphyton gabonense, *polar view. The surface is punctate in the mesocolpia but psilate at the poles and mesocolpial margins.—11.* Sterigmapetalum heterodoxum, *lateral view, psilate surface.—12.* S. obovatum, *portion of a mesocolpium showing a punctate–rugulate surface. Scale bars = 1 µm.*

FIGURES 13–23. *Scanning electron micrographs of Macarisieae pollen.—13.* Macarisia lanceolata, *polar and lateral views. The surface is psilate at the pole and on the margins of the mesocolpia, and punctate–rugulate on the mesocolpia.—14.* M. ellipticifolia, *subpolar view. The surface is psilate and slightly punctate.—15.* M. humbertiana, *lateral view. Surface rugulate, becoming smoother near the colpi.—16.* M. pyramidata, *polar view.—17.* Blepharistemma membranifolia, *lateral view.—18.* Cassipourea afzelii, *lateral view, surface punctate.—19.* C. guianensis, *lateral view. The surface is punctate but not as coarse as in Figure 18.—20.* Dactylopetalum sessiliflorum, *lateral view.—21.* Cassipourea gummiflora *var.* verticillata, *polar view.—22.* Anopyxis kleineana, *lateral view. The surface is psilate; the outline of the large endoaperture is visible.—23.* A. ealeaensis, *lateral view. Scale bars = 1 µm unless otherwise indicated.*

FIGURES 24–35. *Scanning electron micrographs of Rhizophoreae (24–29) and Gynotrocheae (30–35) pollen.—24.* Rhizophora mangle, *lateral view, surface punctate–rugulate.—25.* R. mucronata, *lateral view.—26.* R. stylosa, *lateral view.—27.* Ceriops tagal, *polar view.—28.* Bruguiera gymnorrhiza, *lateral view.—29.* Kandelia candel, *lateral view. Note the outline of the endoaperture.—30.* Gynotroches axillaris, *lateral view. The colpus membrane and the margins of the mesocolpia have a granular–spinulate surface; the rest of the grain has psilate–punctate surface.—31.* Crossostylis grandiflora, *lateral view.—32.* Pellacalyx *cf.* saccardianus, *lateral view.—33.* Carallia eugenioides, *polar view.—34.* C. eugenioides, *lateral view. The surface is psilate–punctate with granular–spinulate mesocolpial margins and colpial membranes.—35.* C. brachiata, *lateral view. Similar to Figure 34 but fewer granules–spinules. Scale bars = 1 µm.*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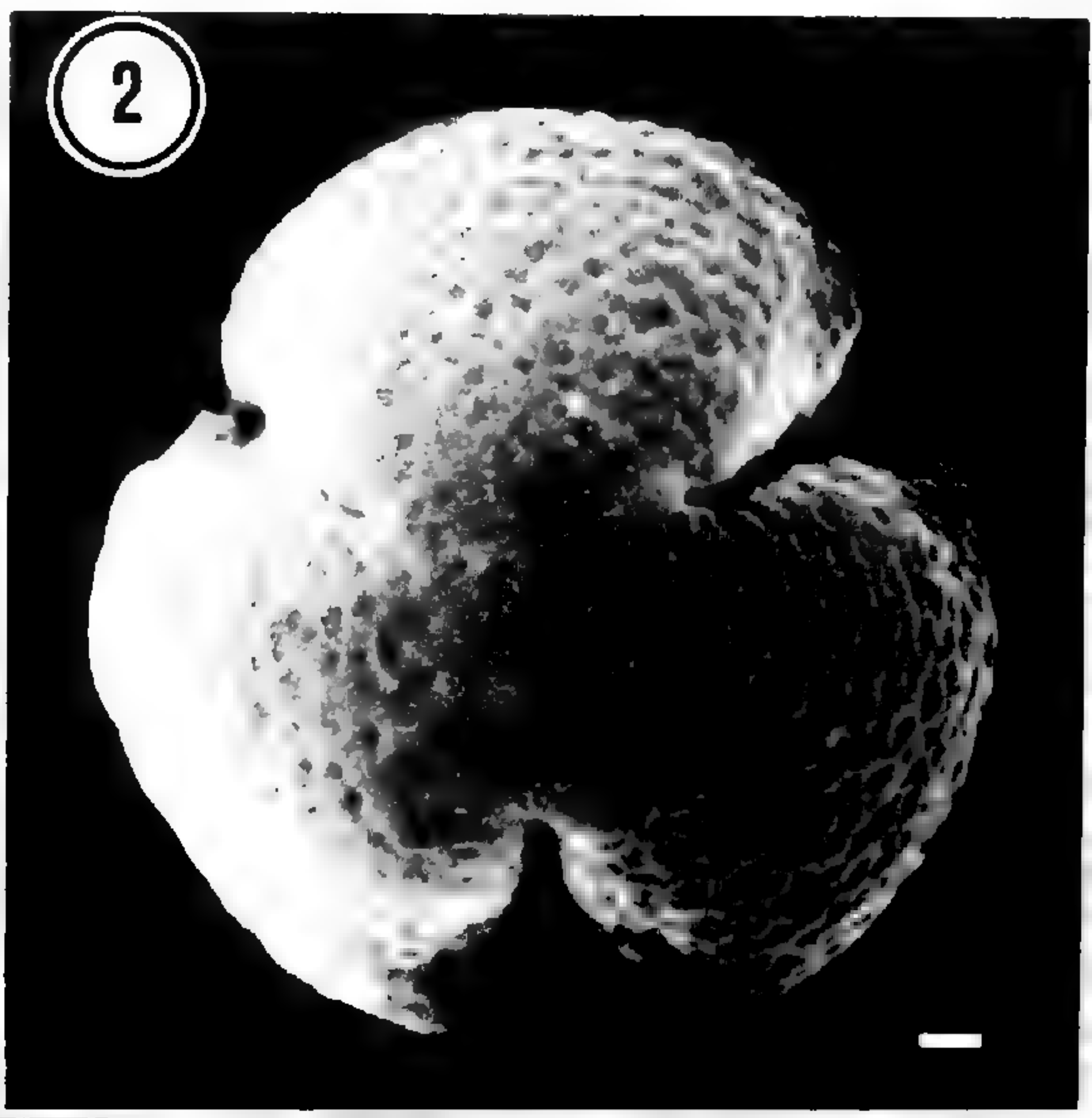
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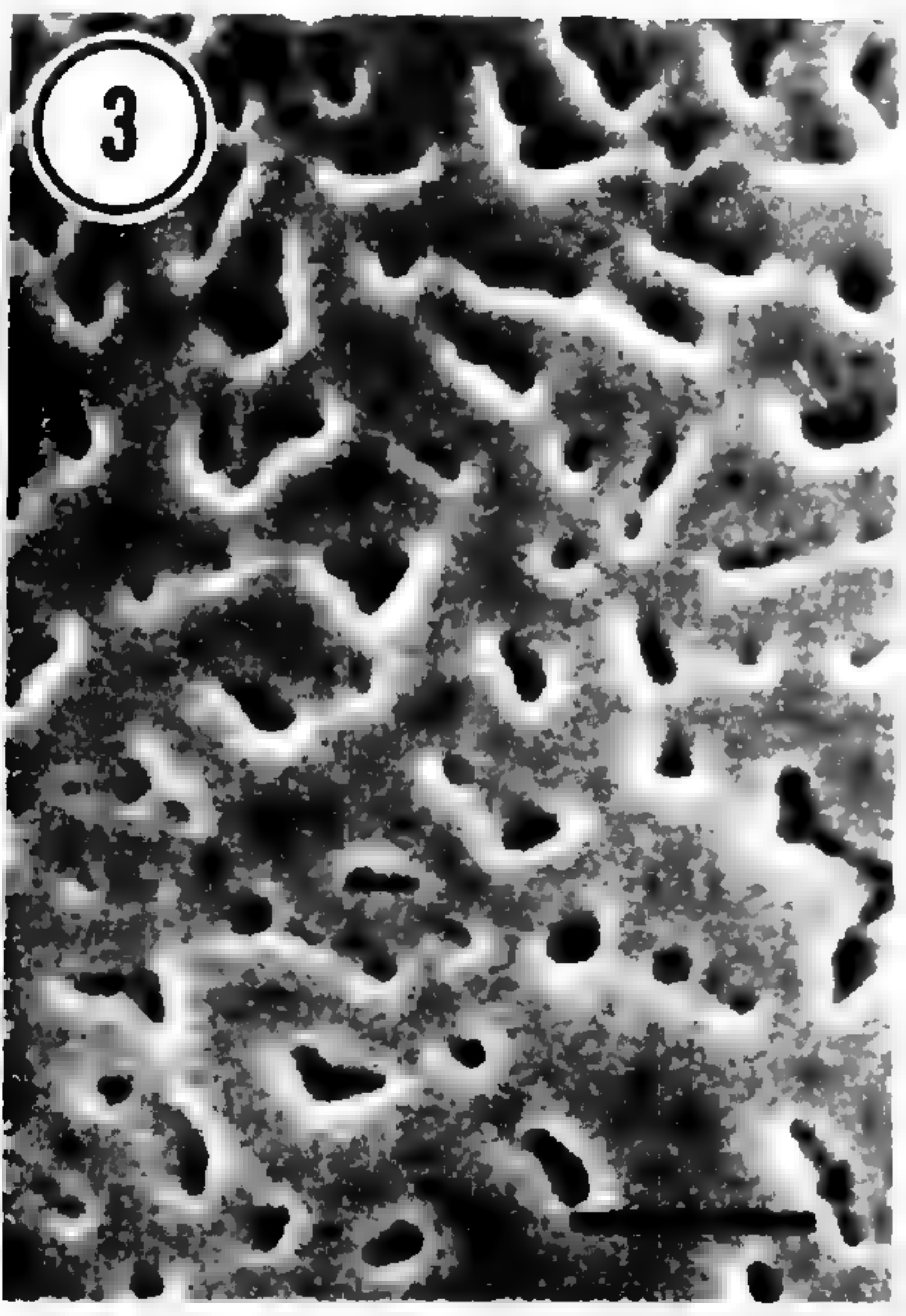
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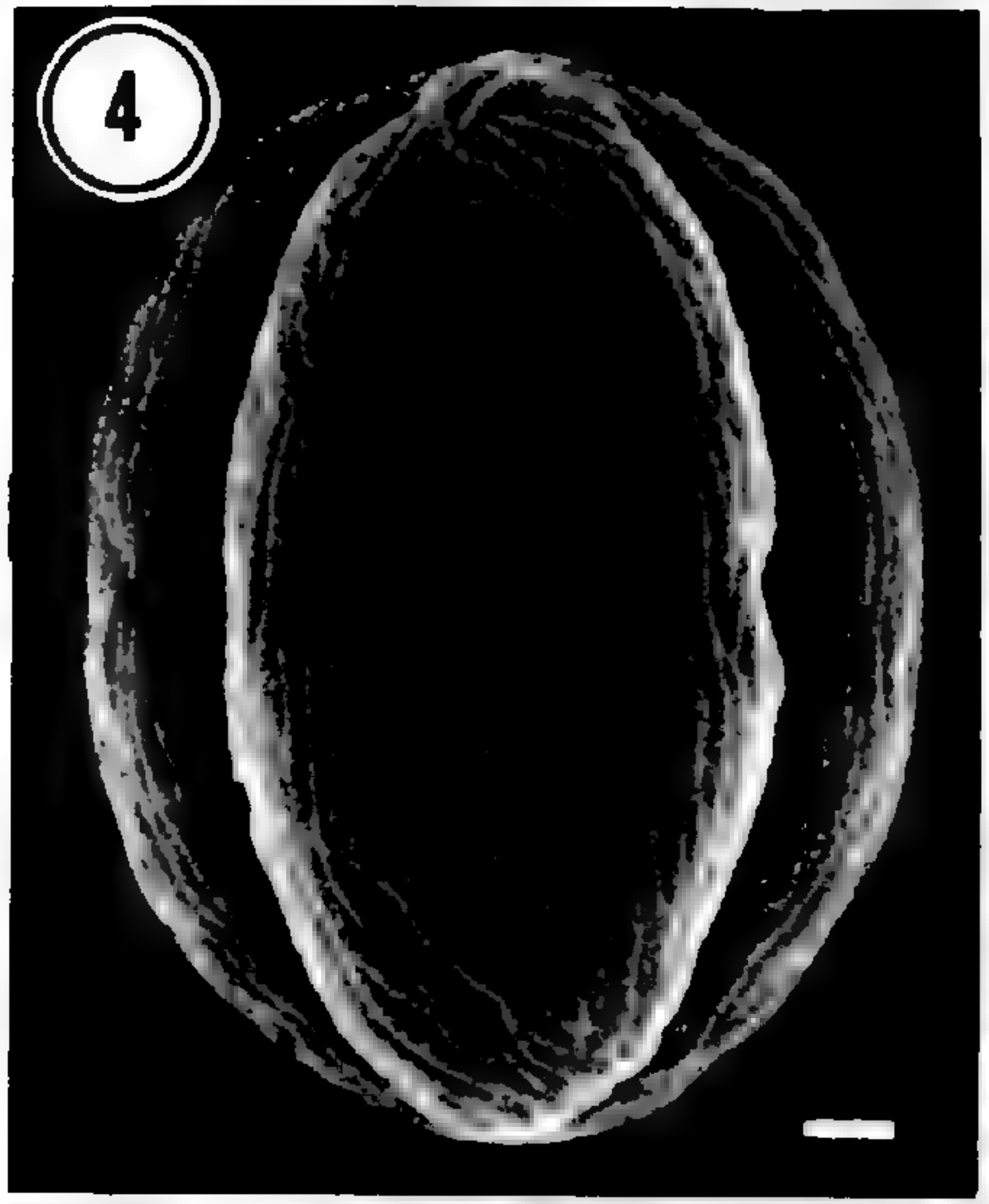
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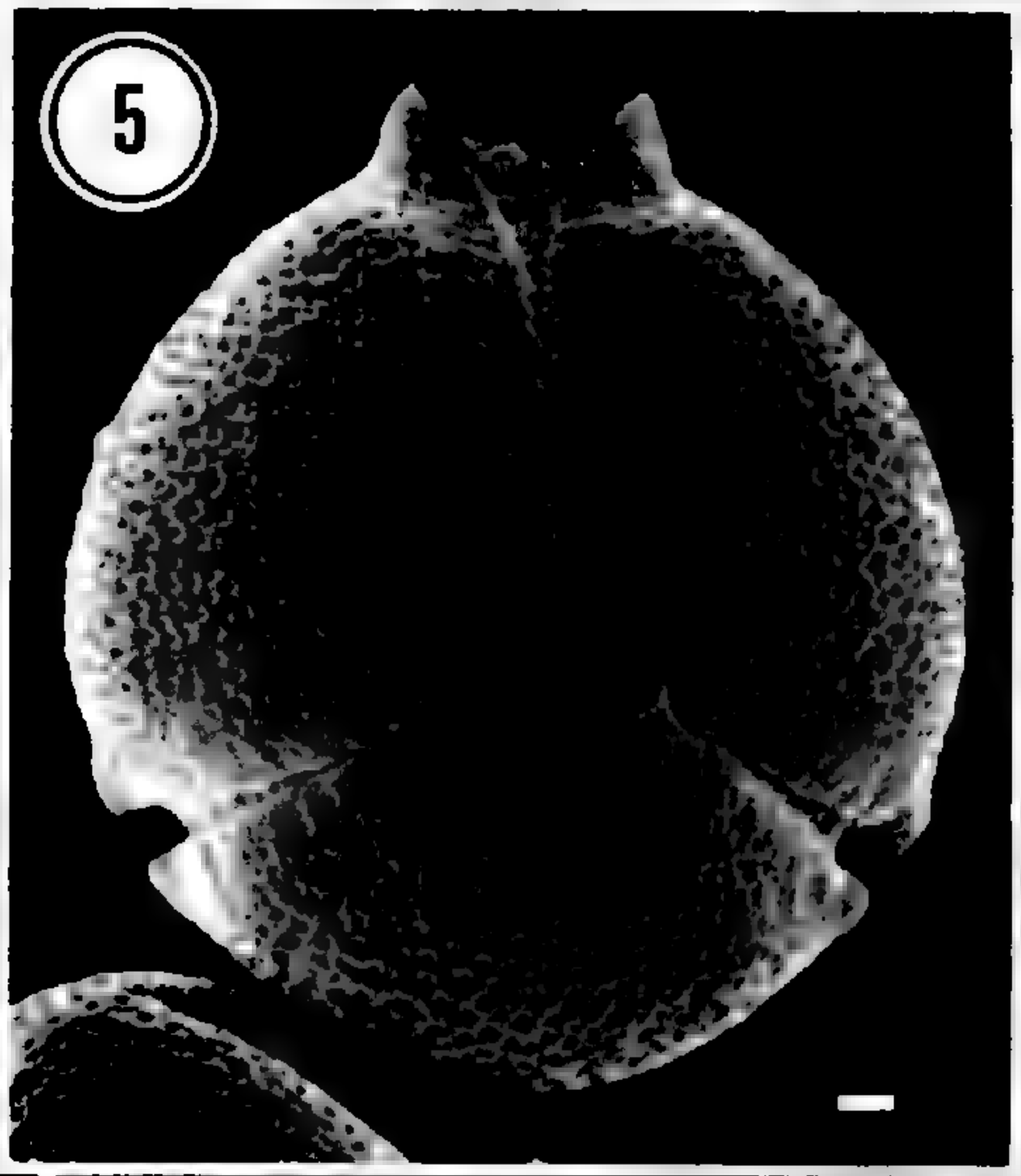
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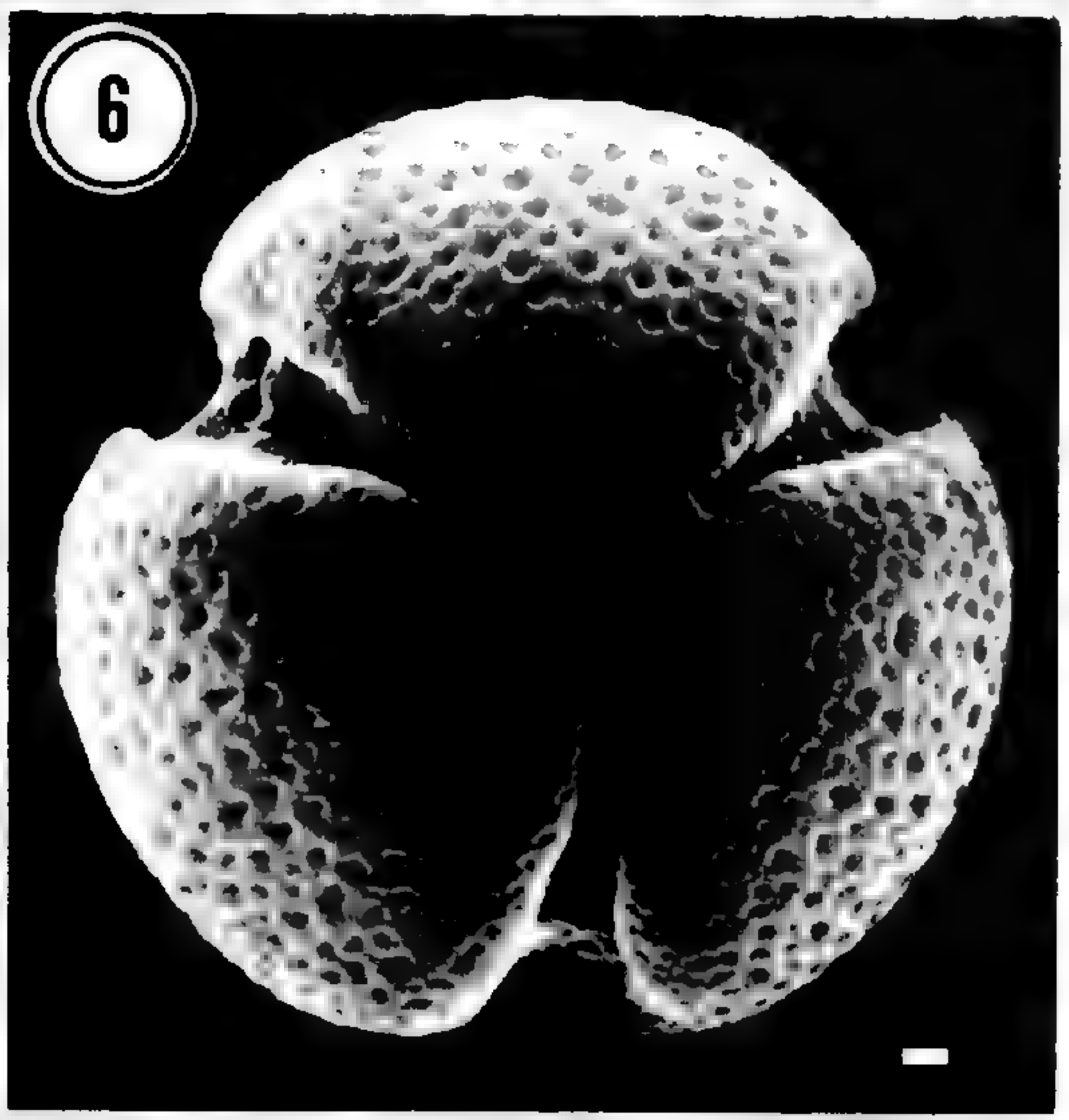
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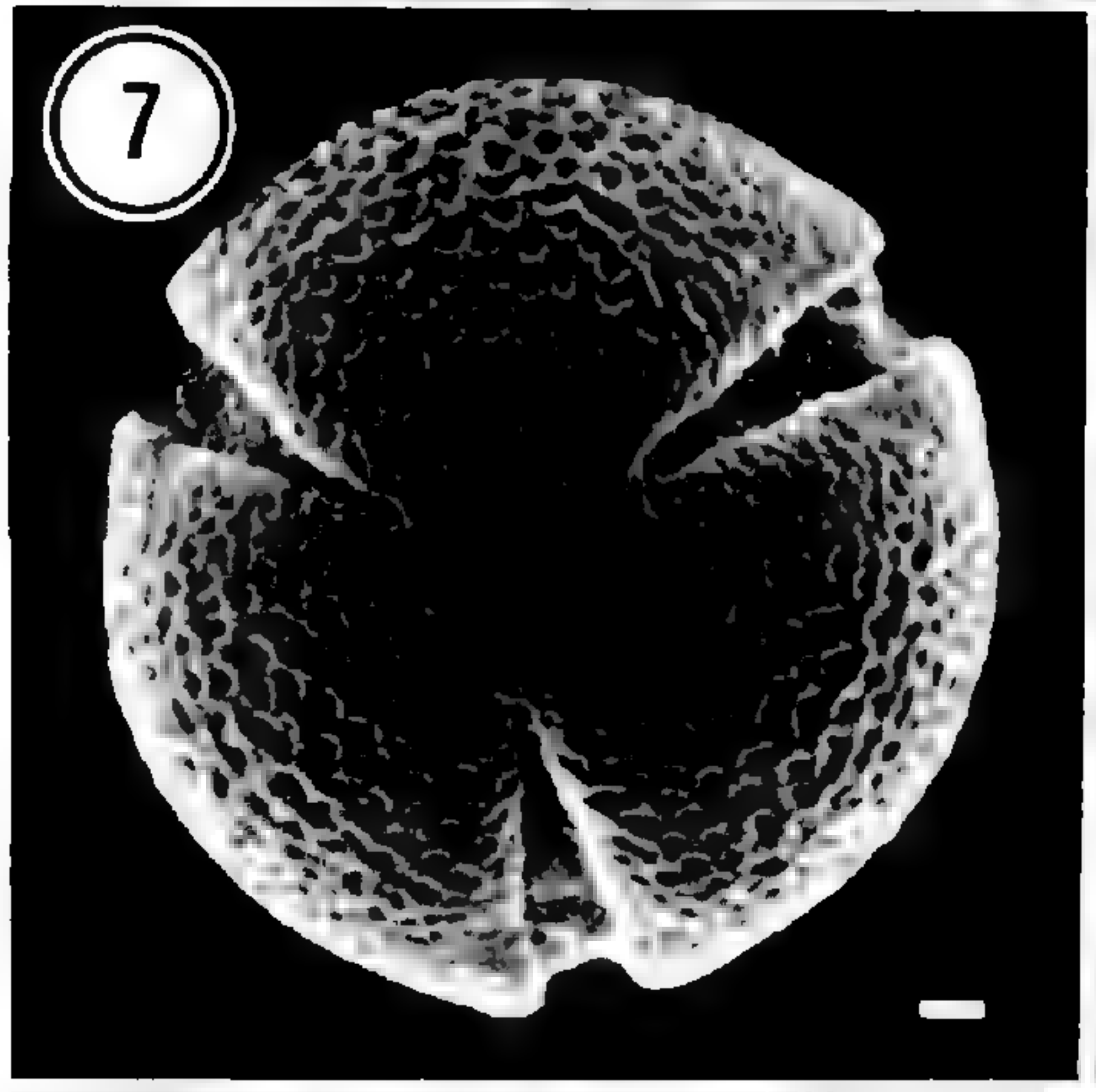
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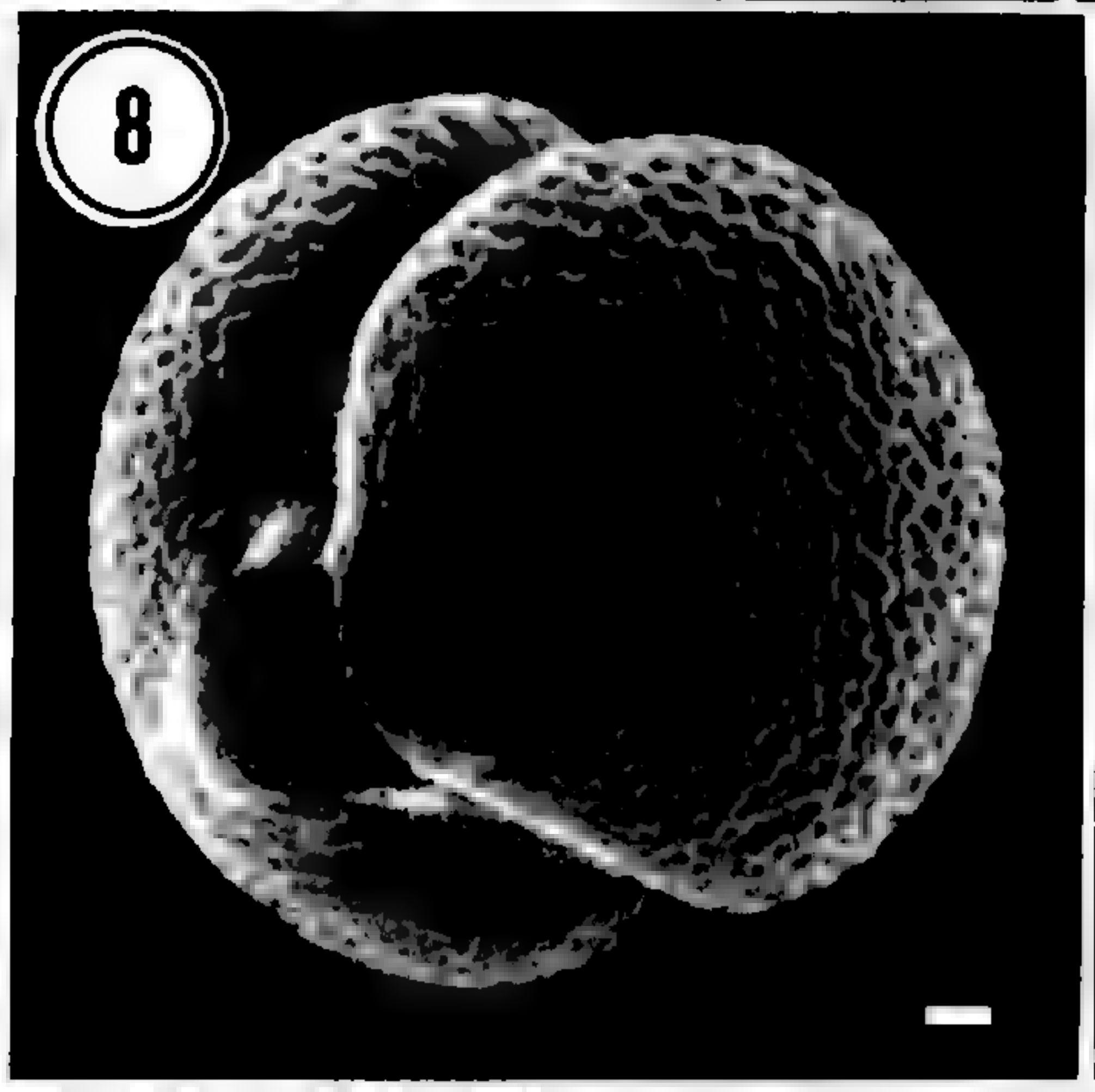
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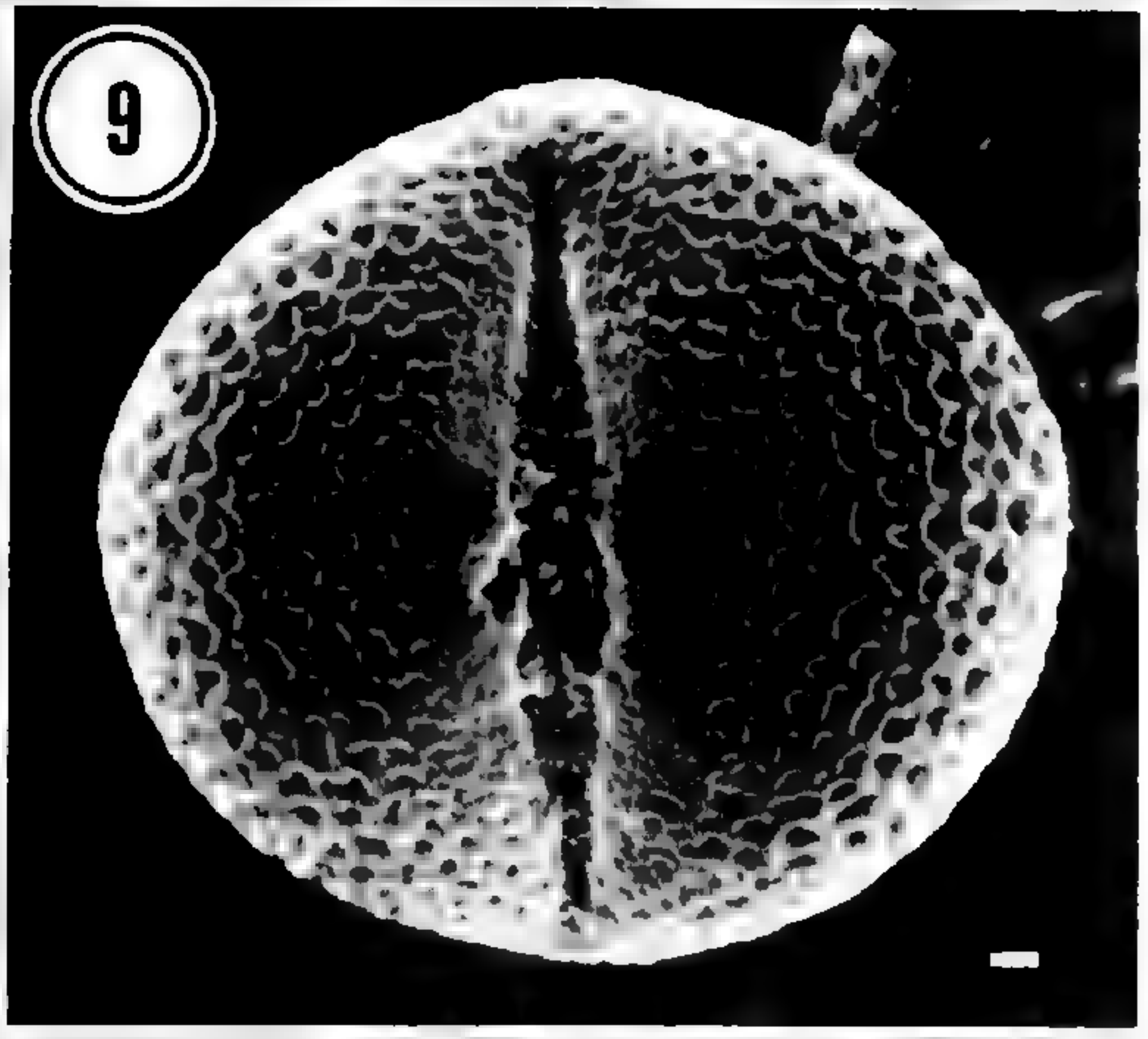
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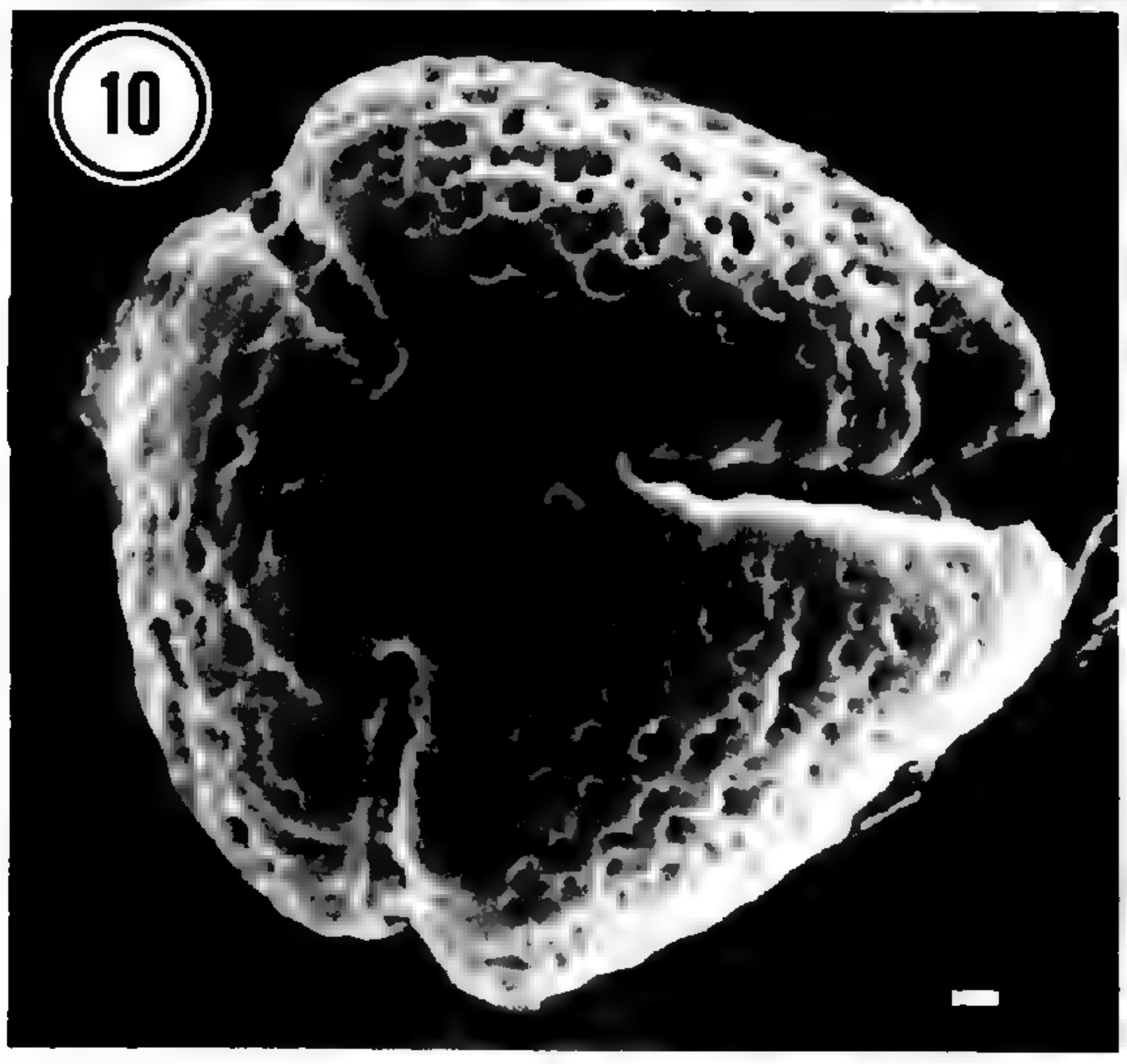
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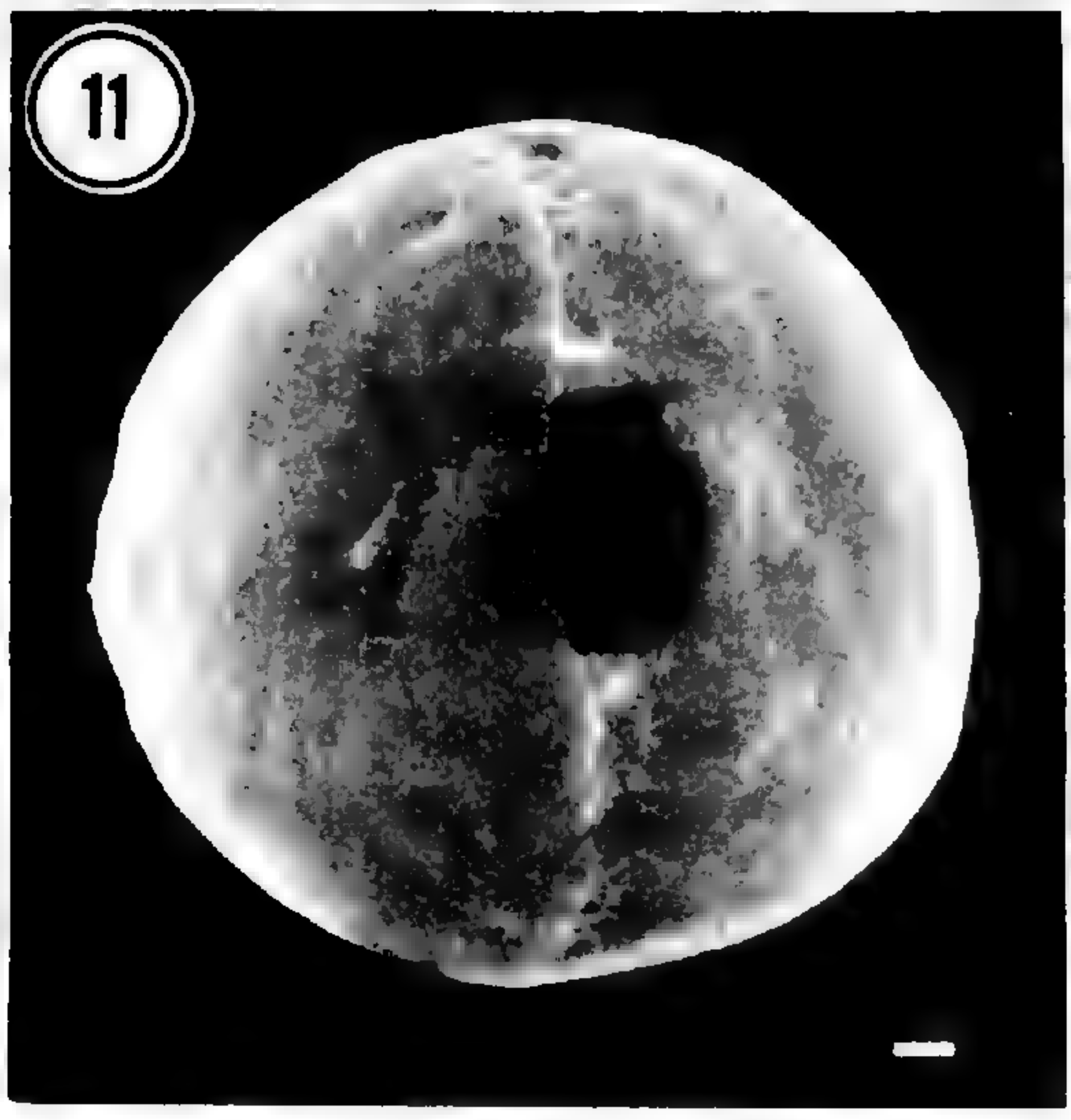
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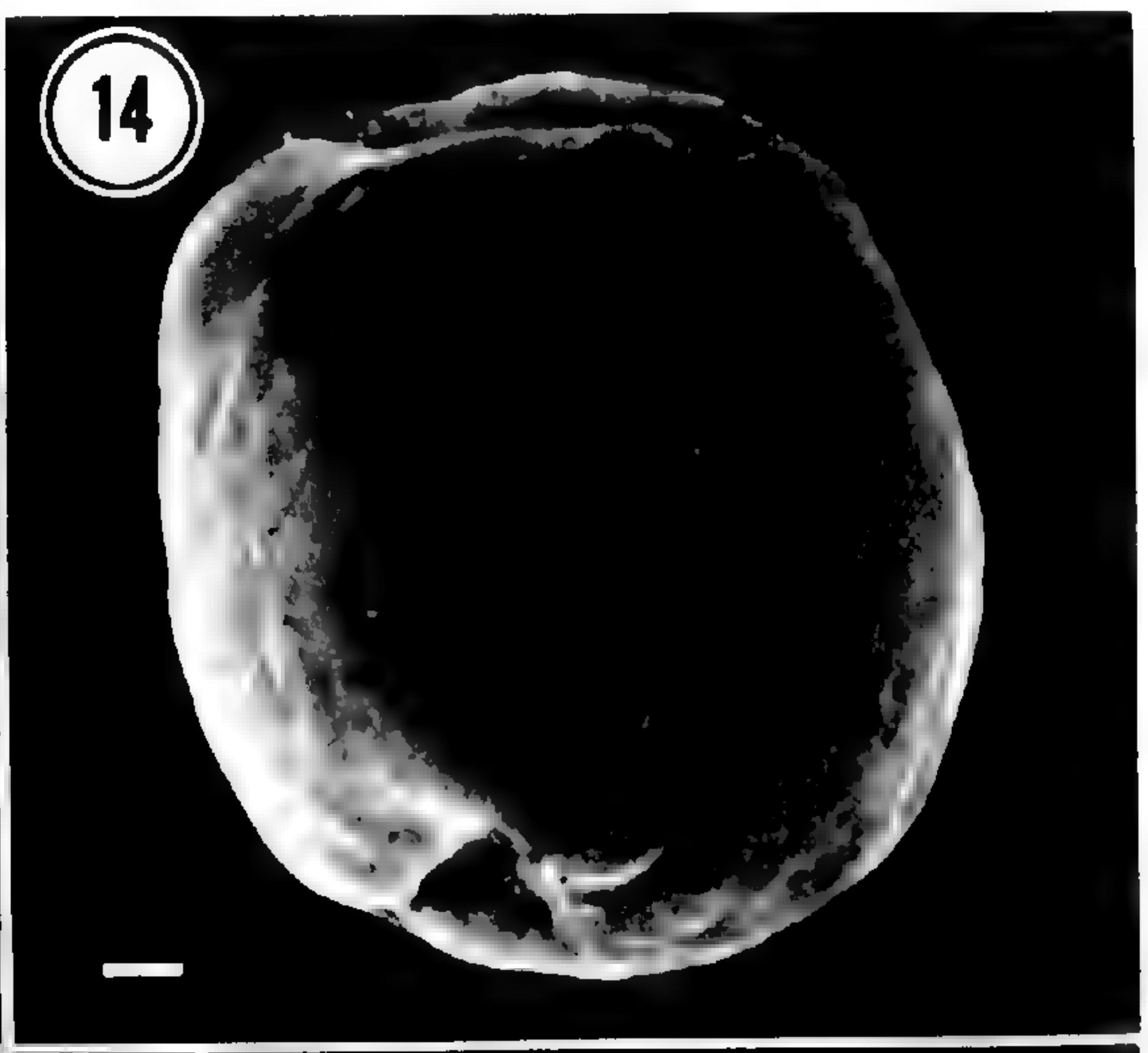
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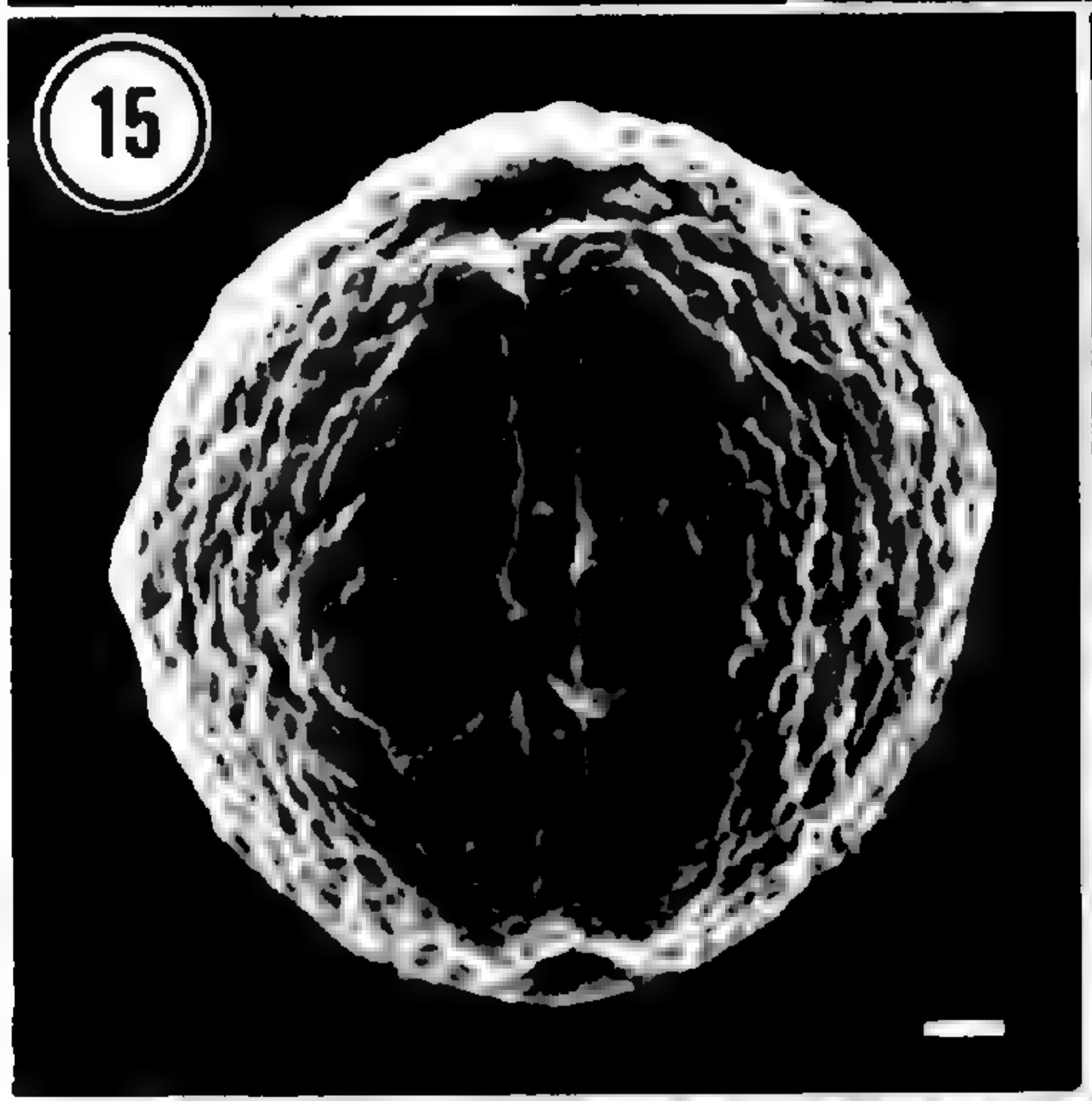
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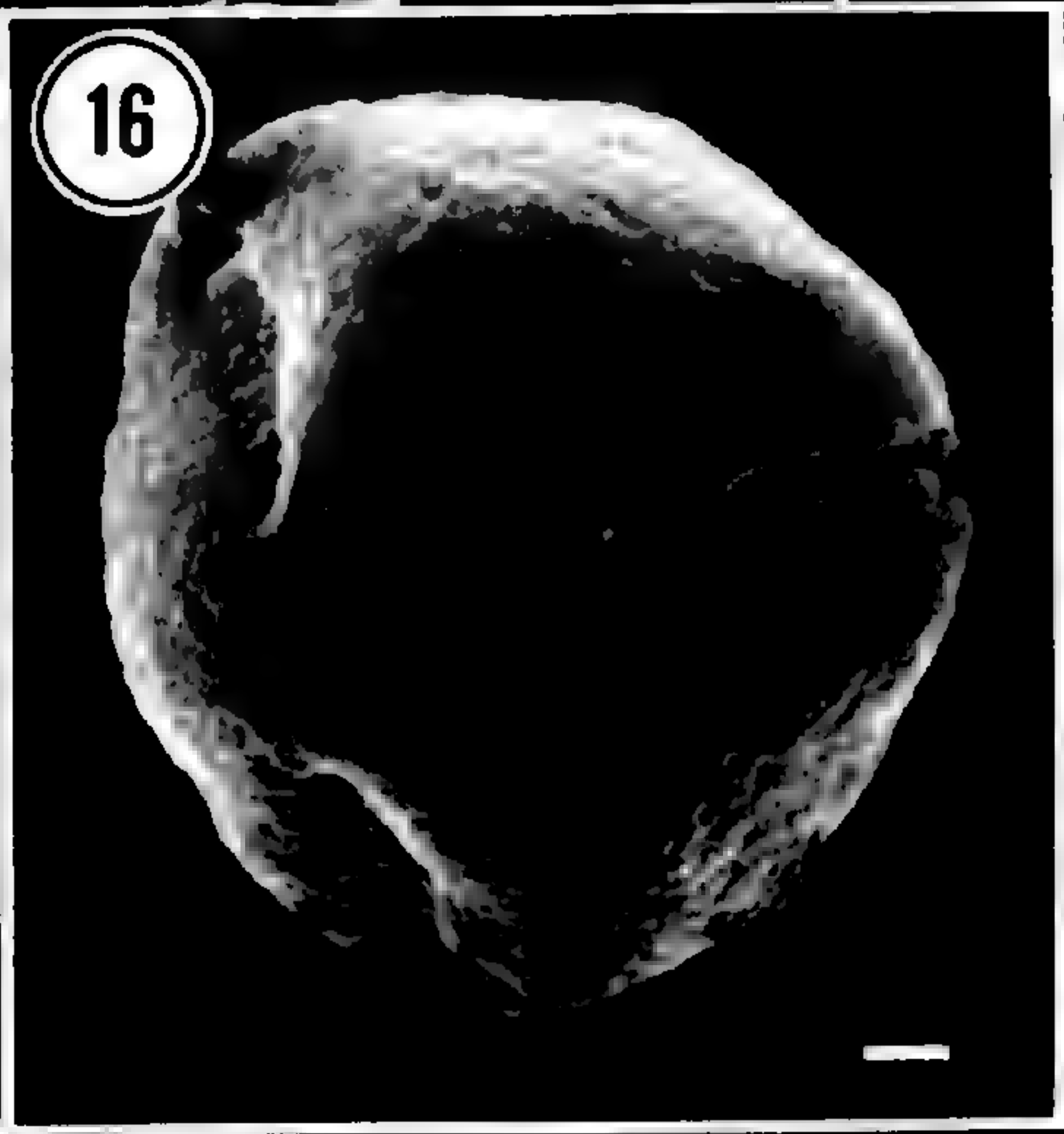
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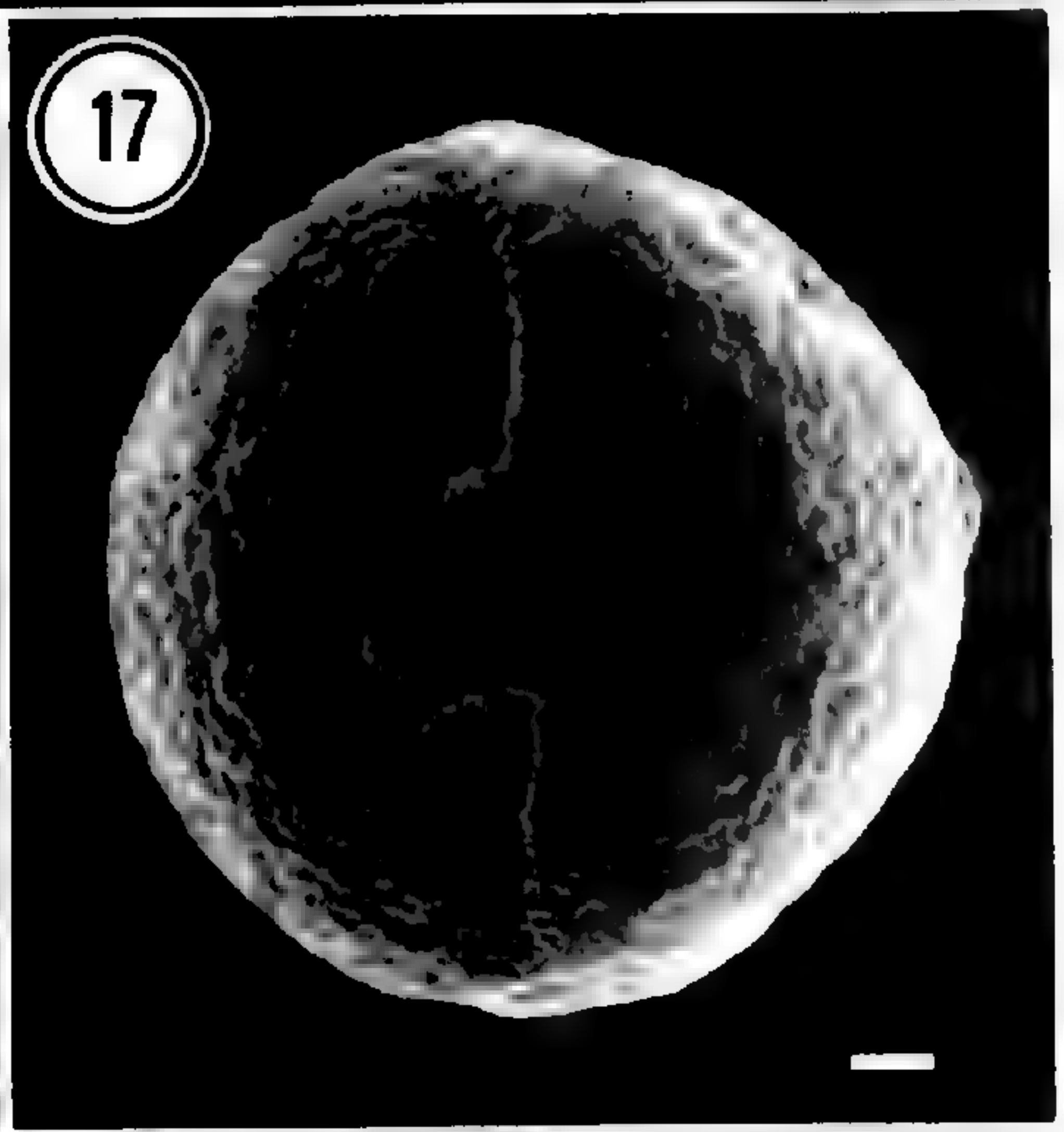
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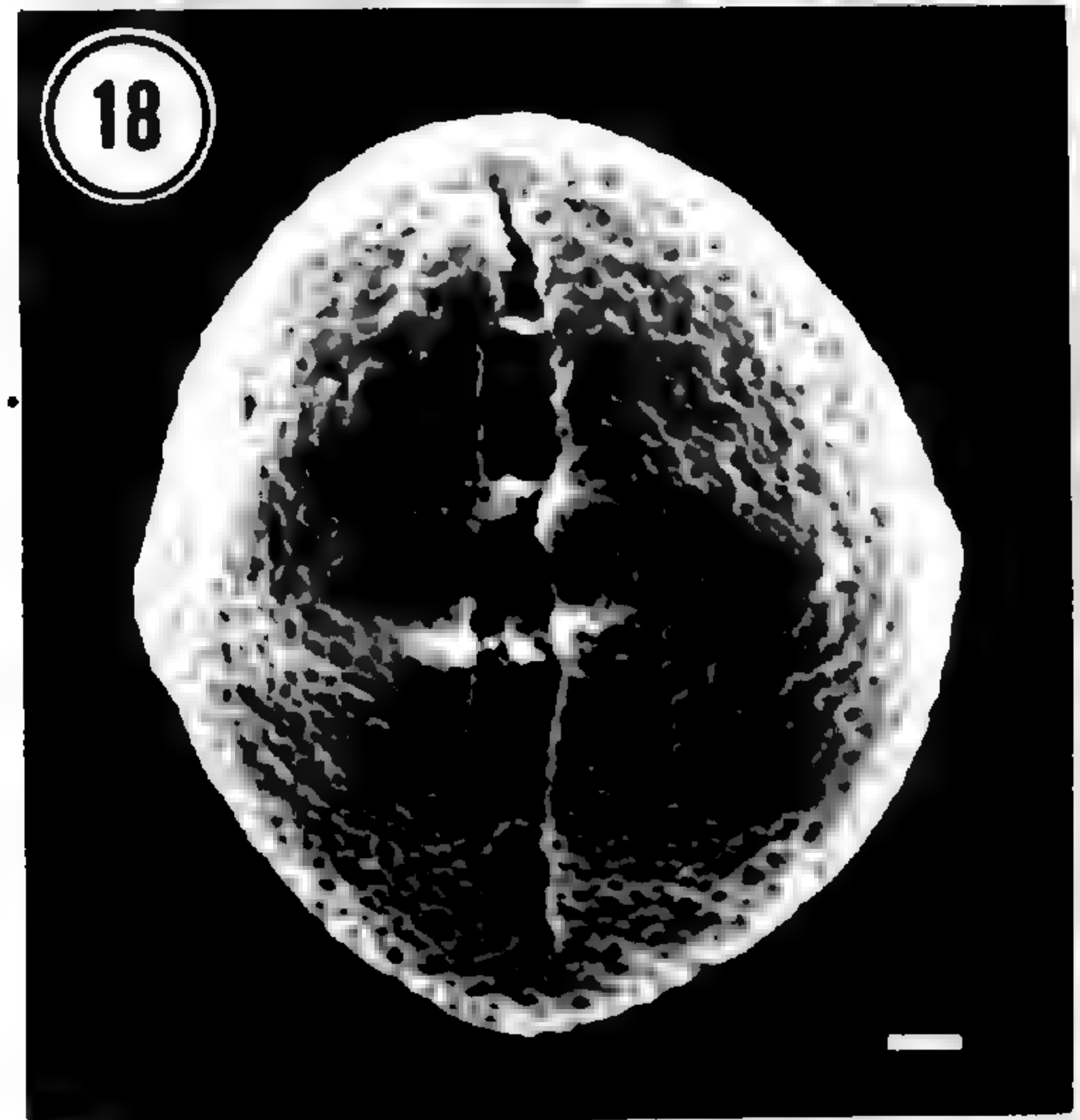
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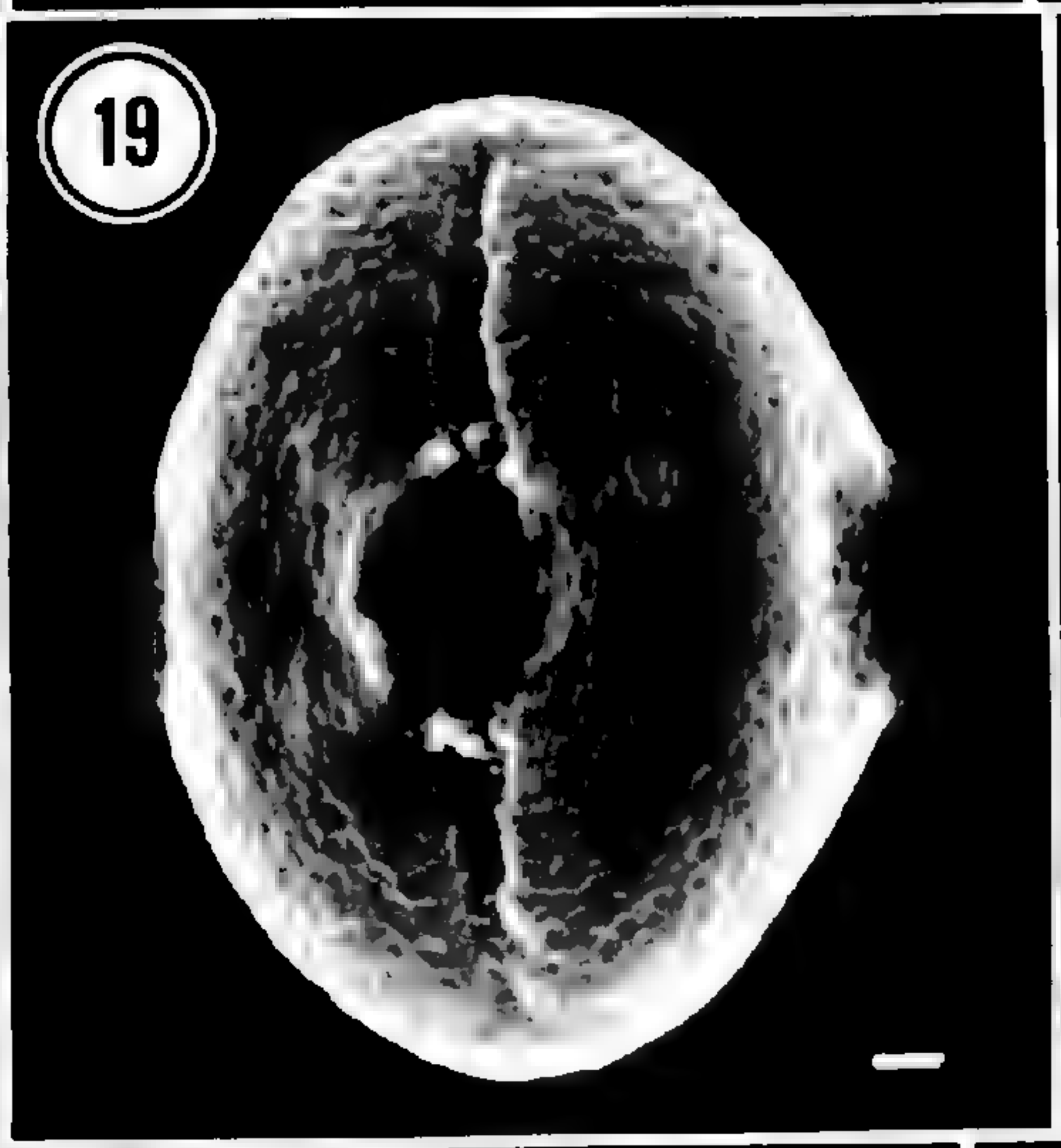
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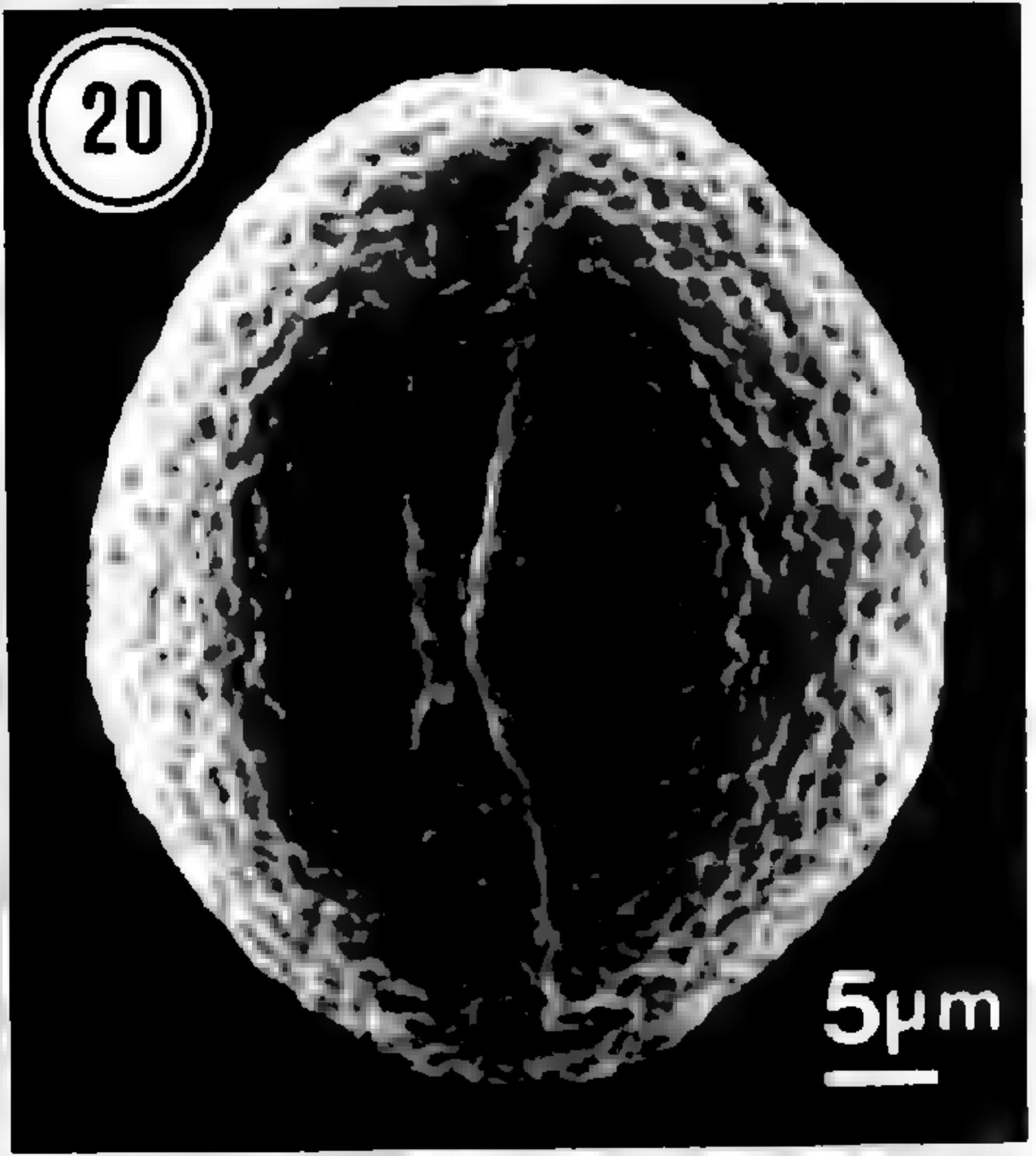
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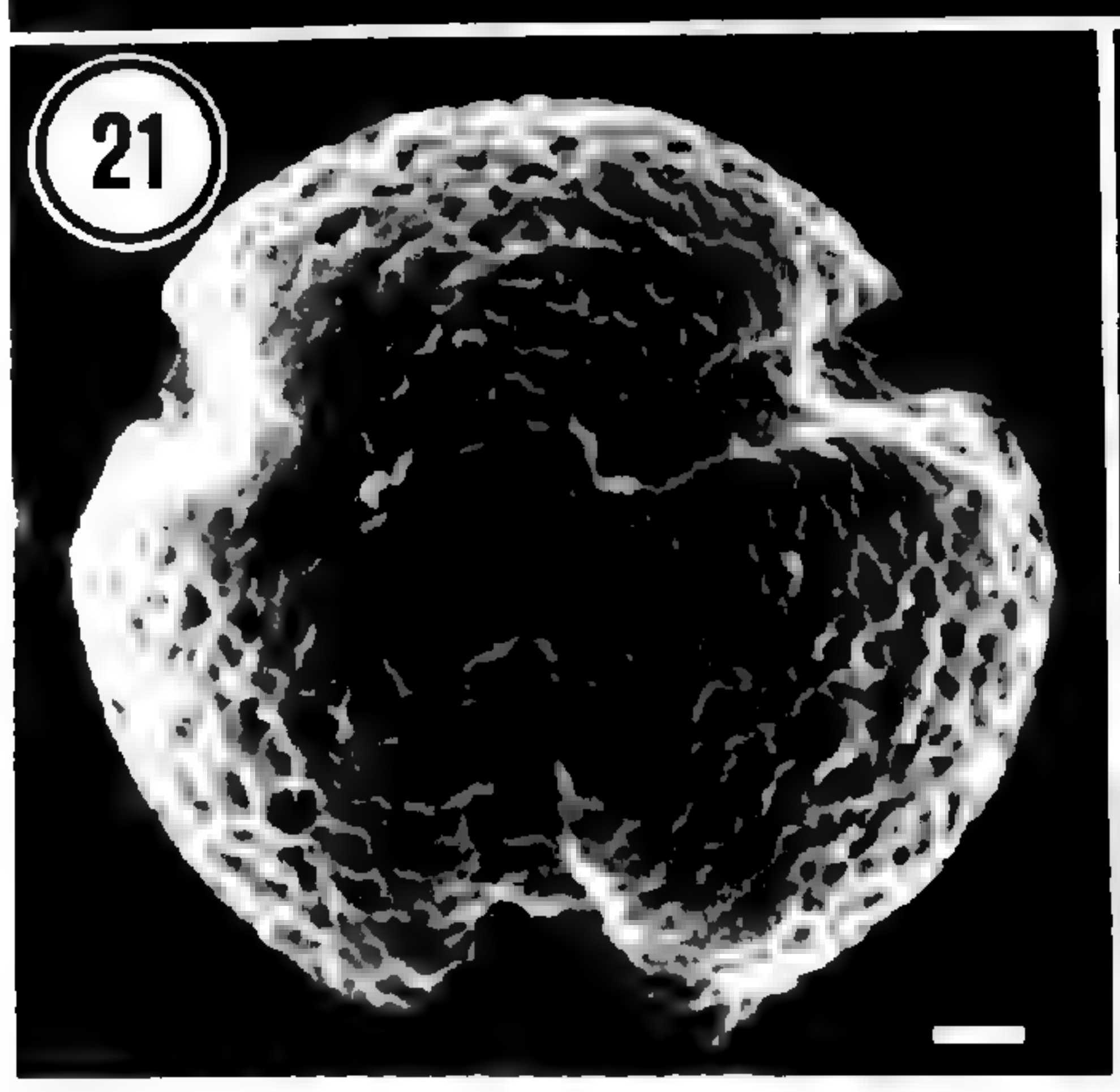
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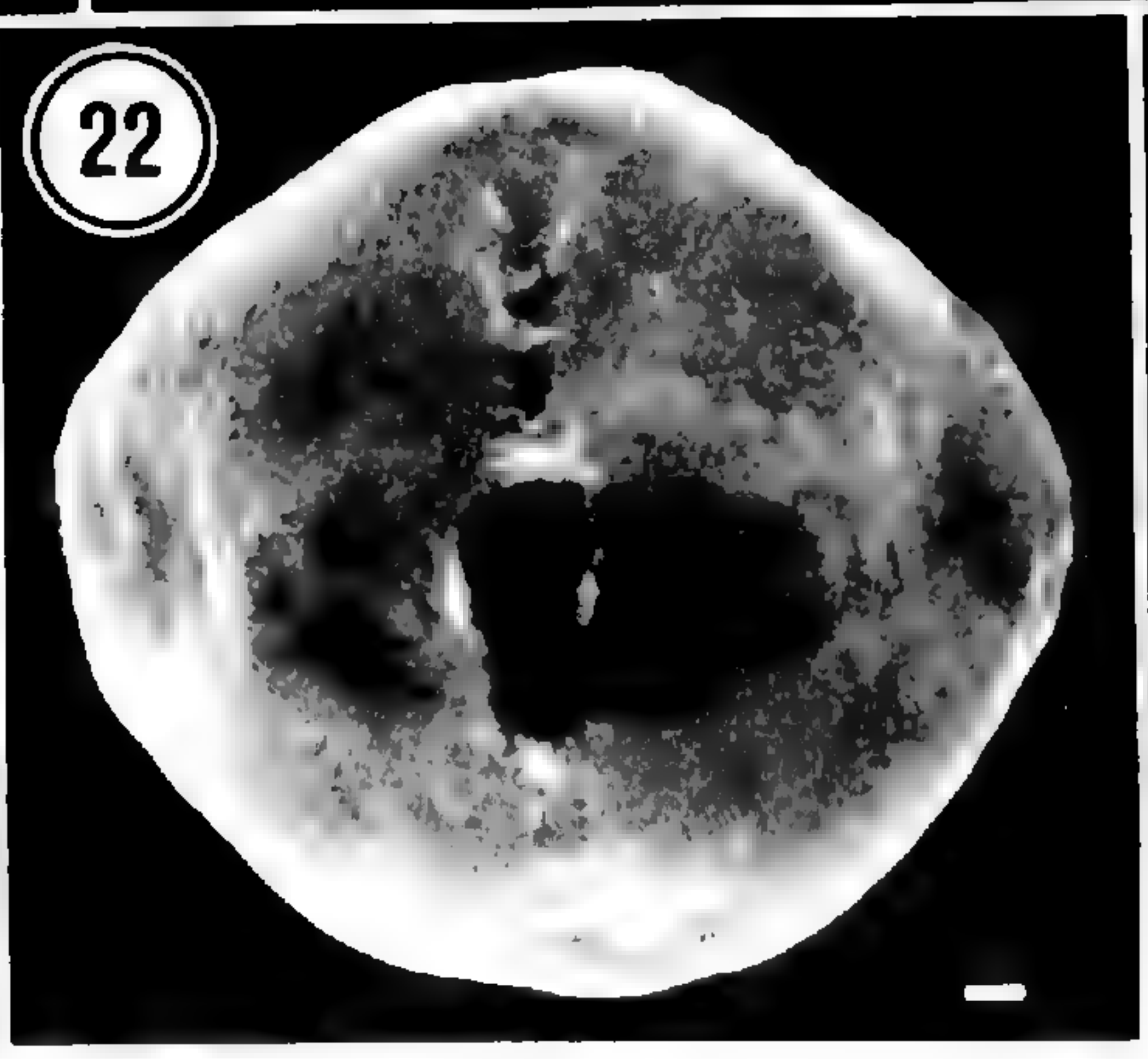
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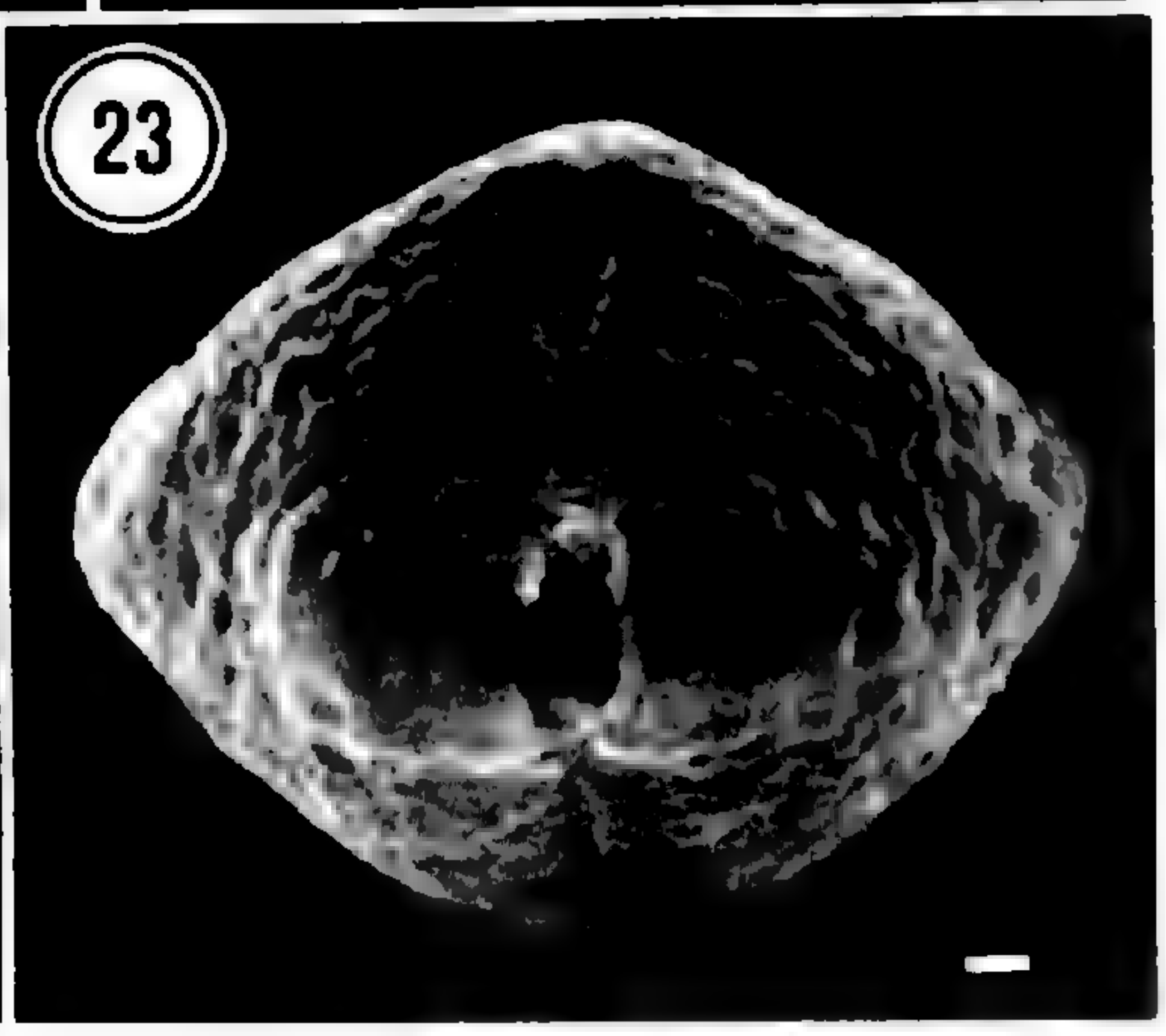
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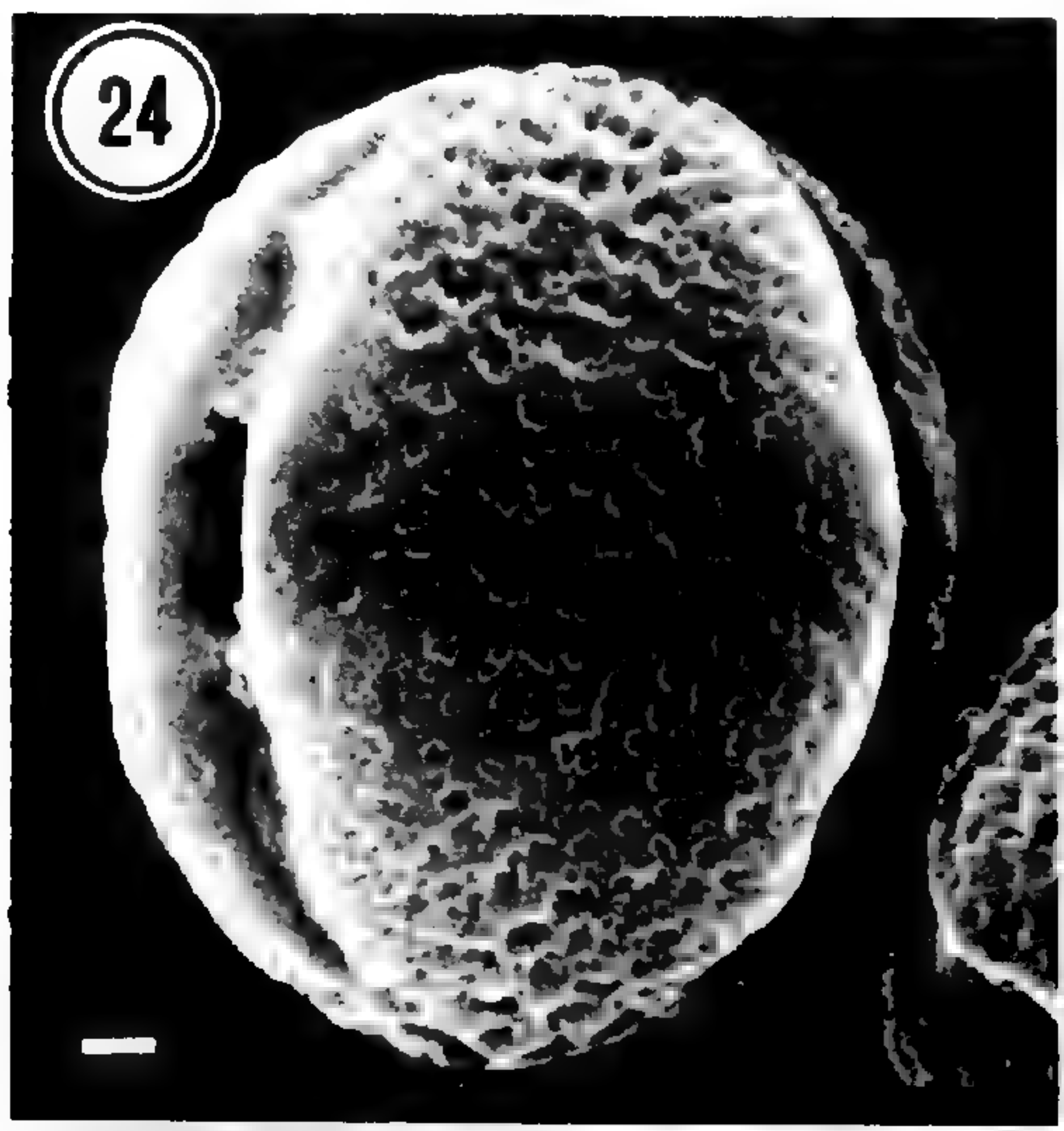
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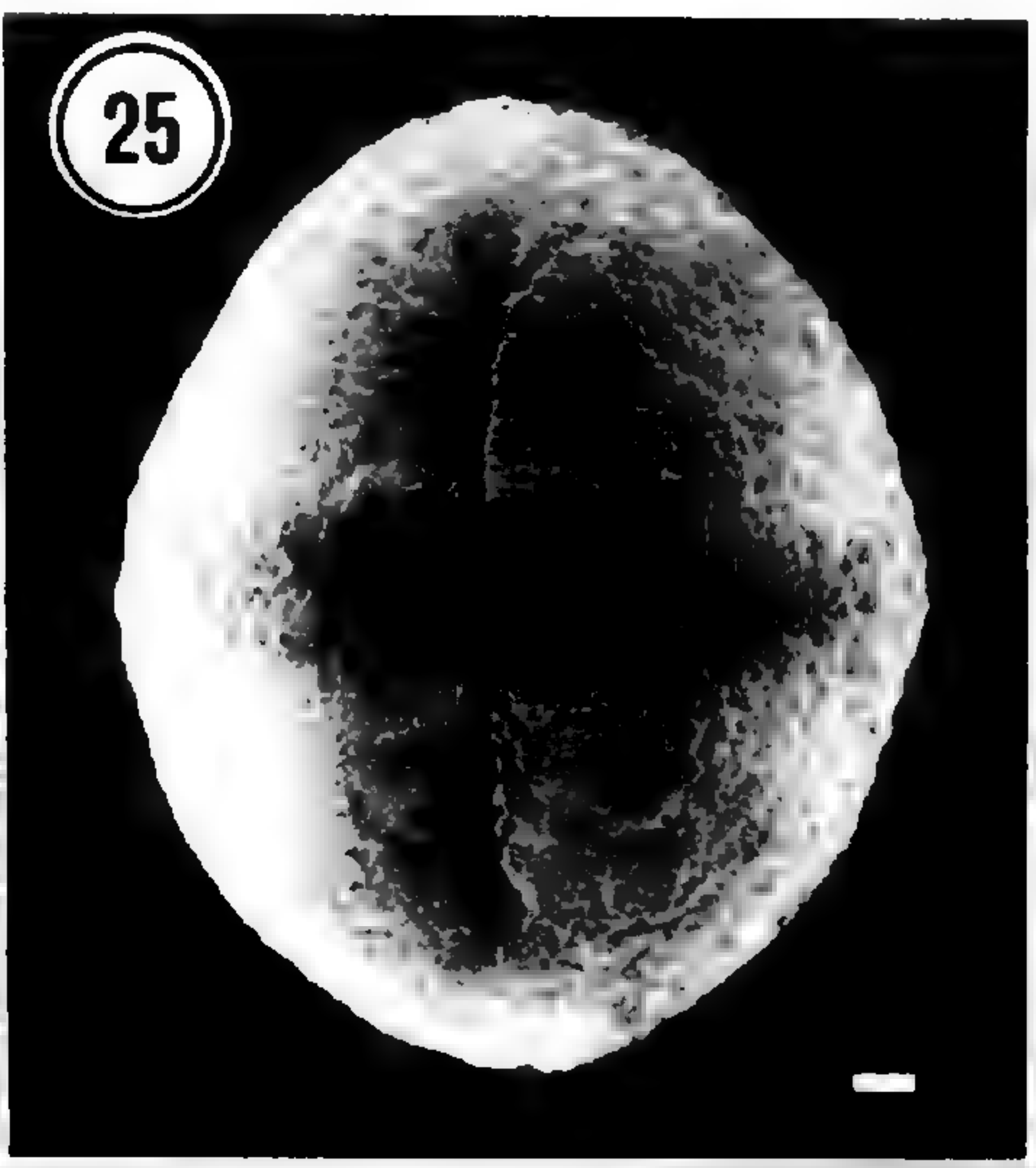
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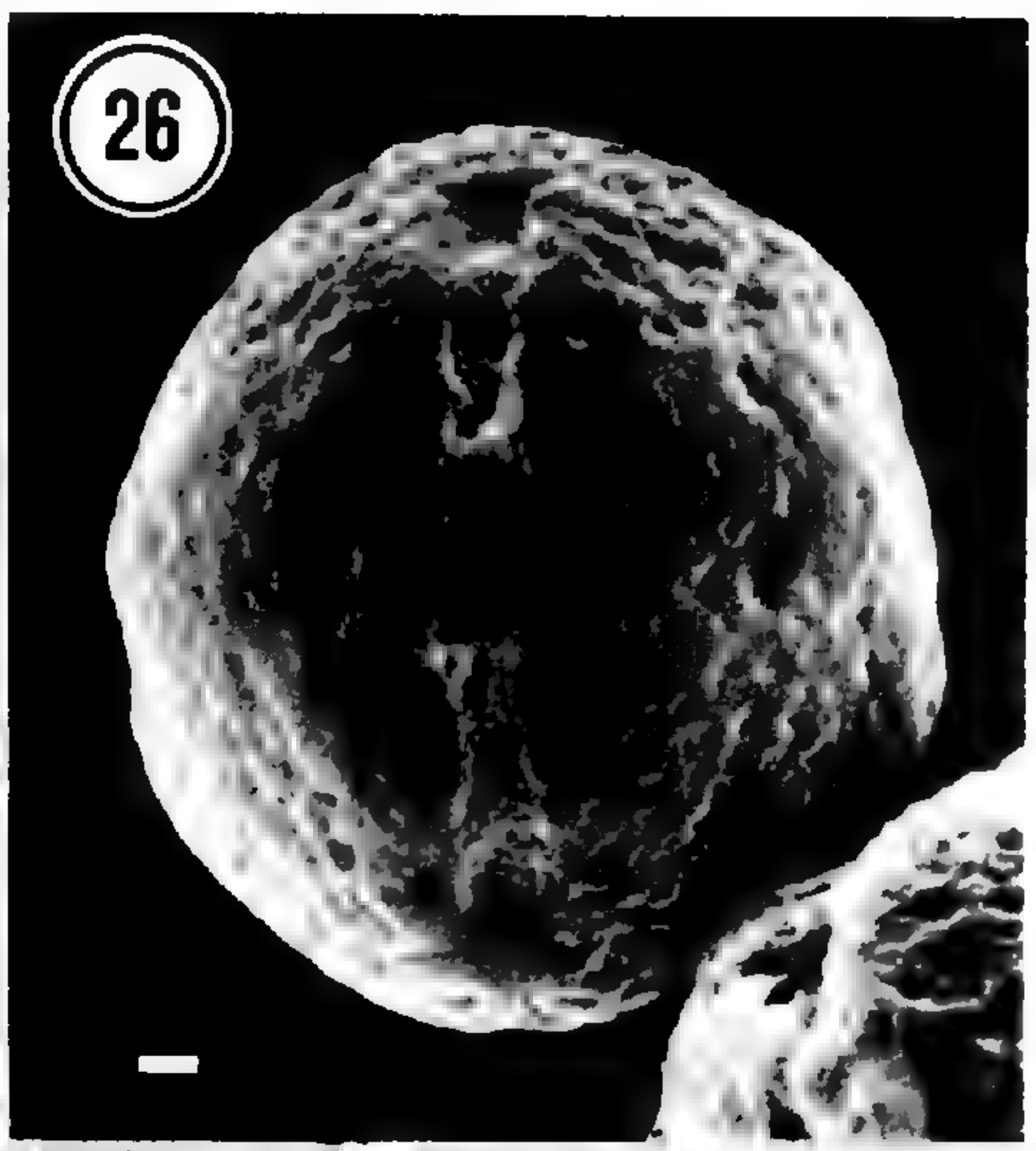
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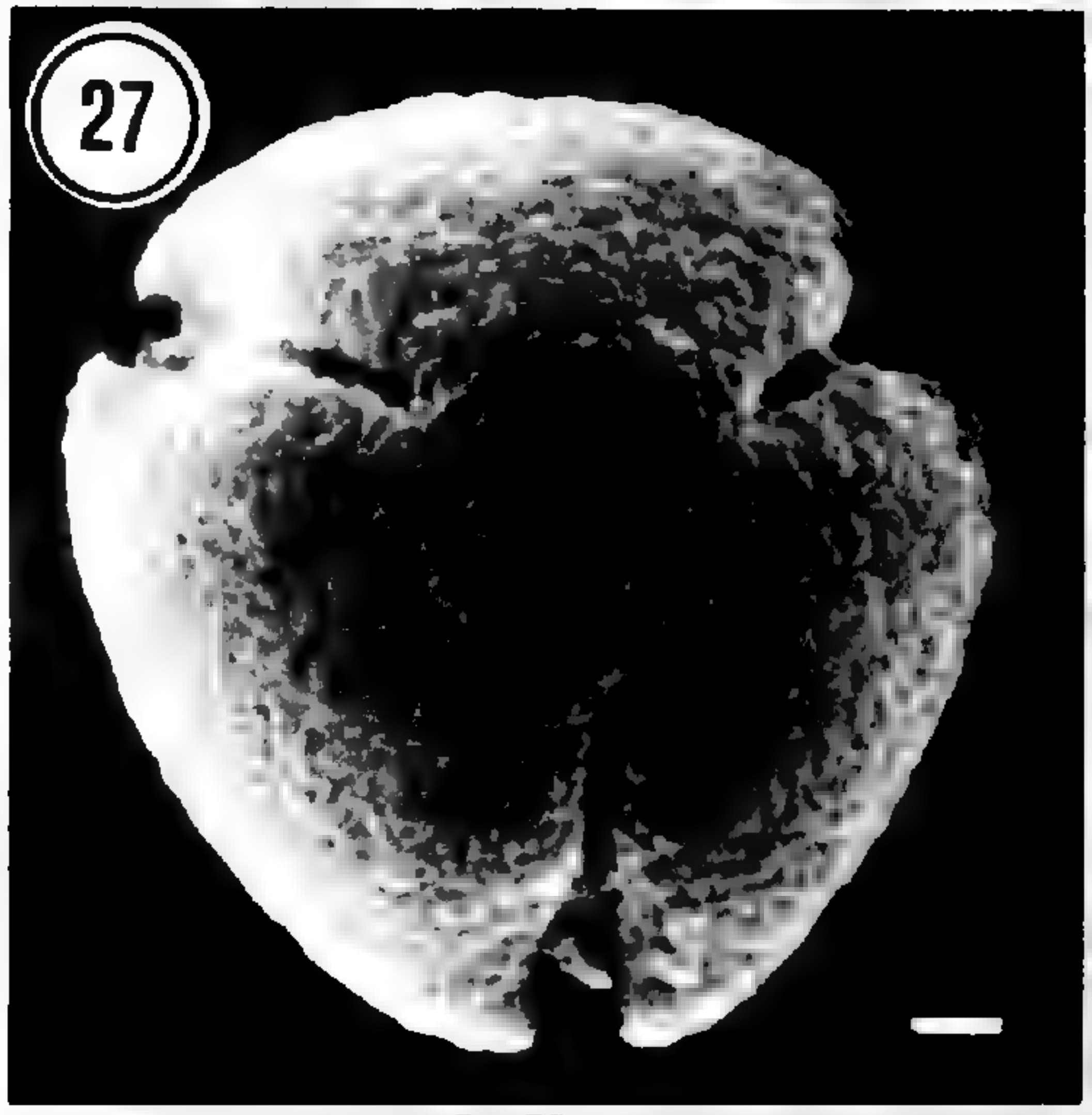
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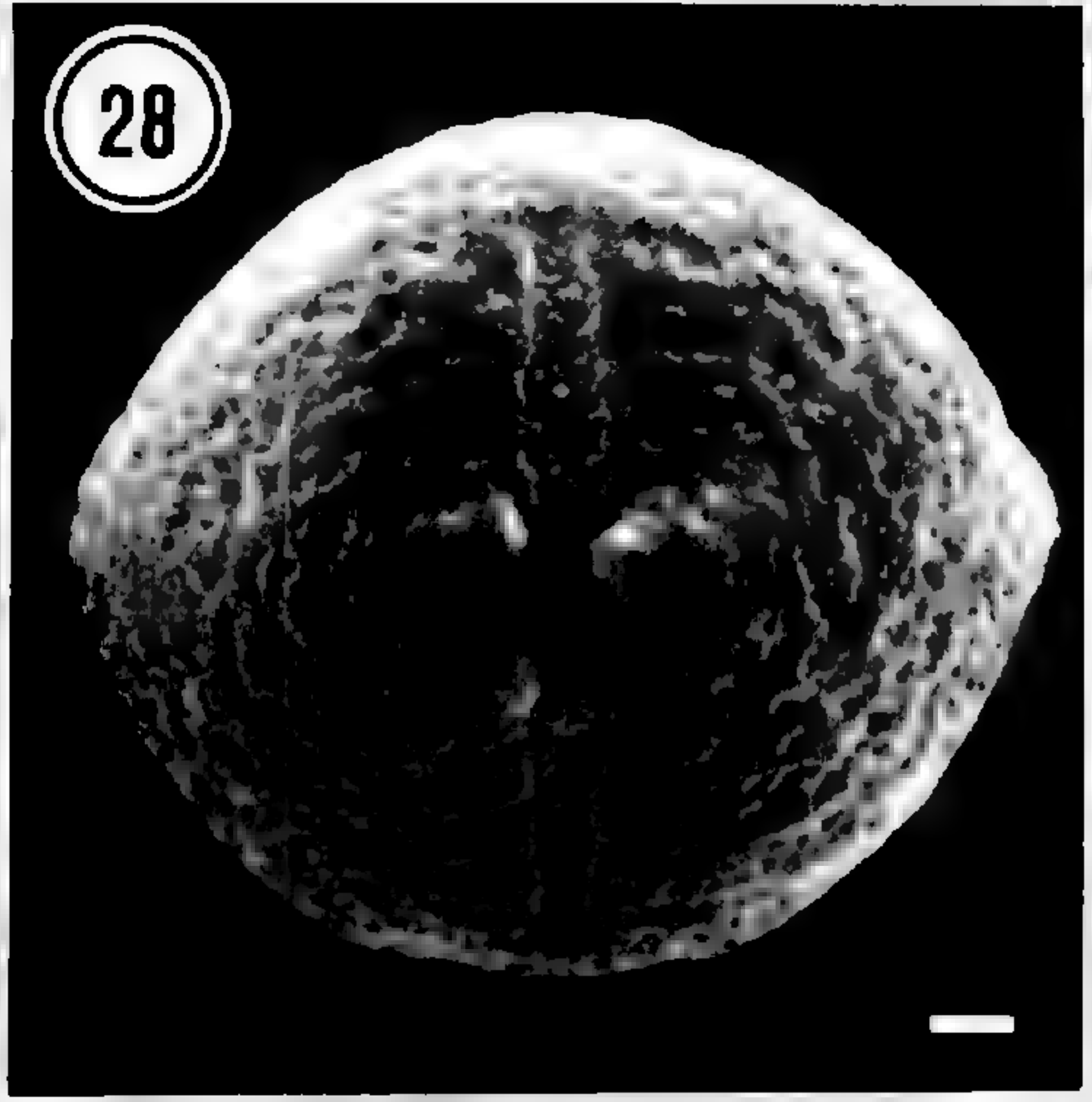
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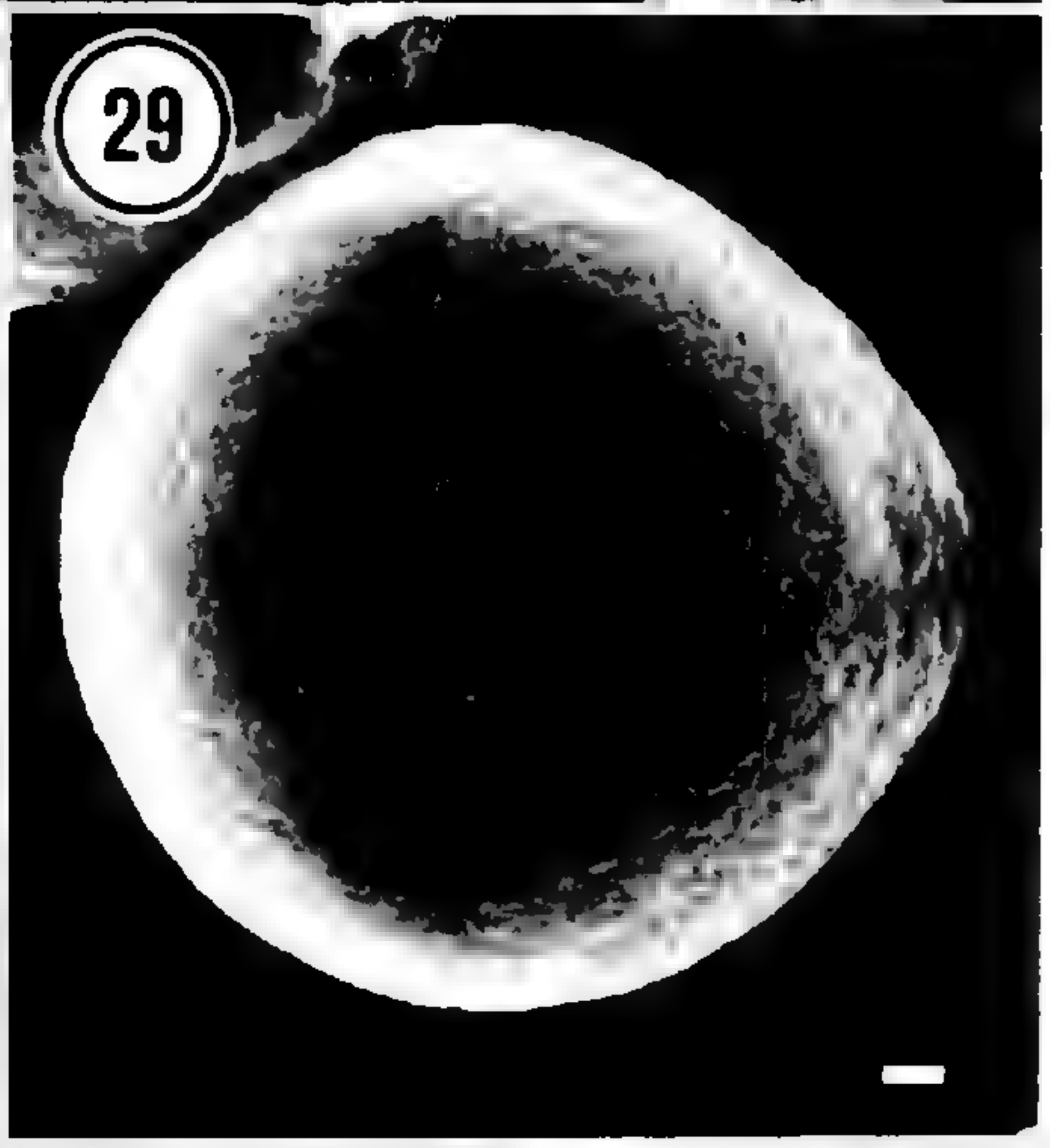
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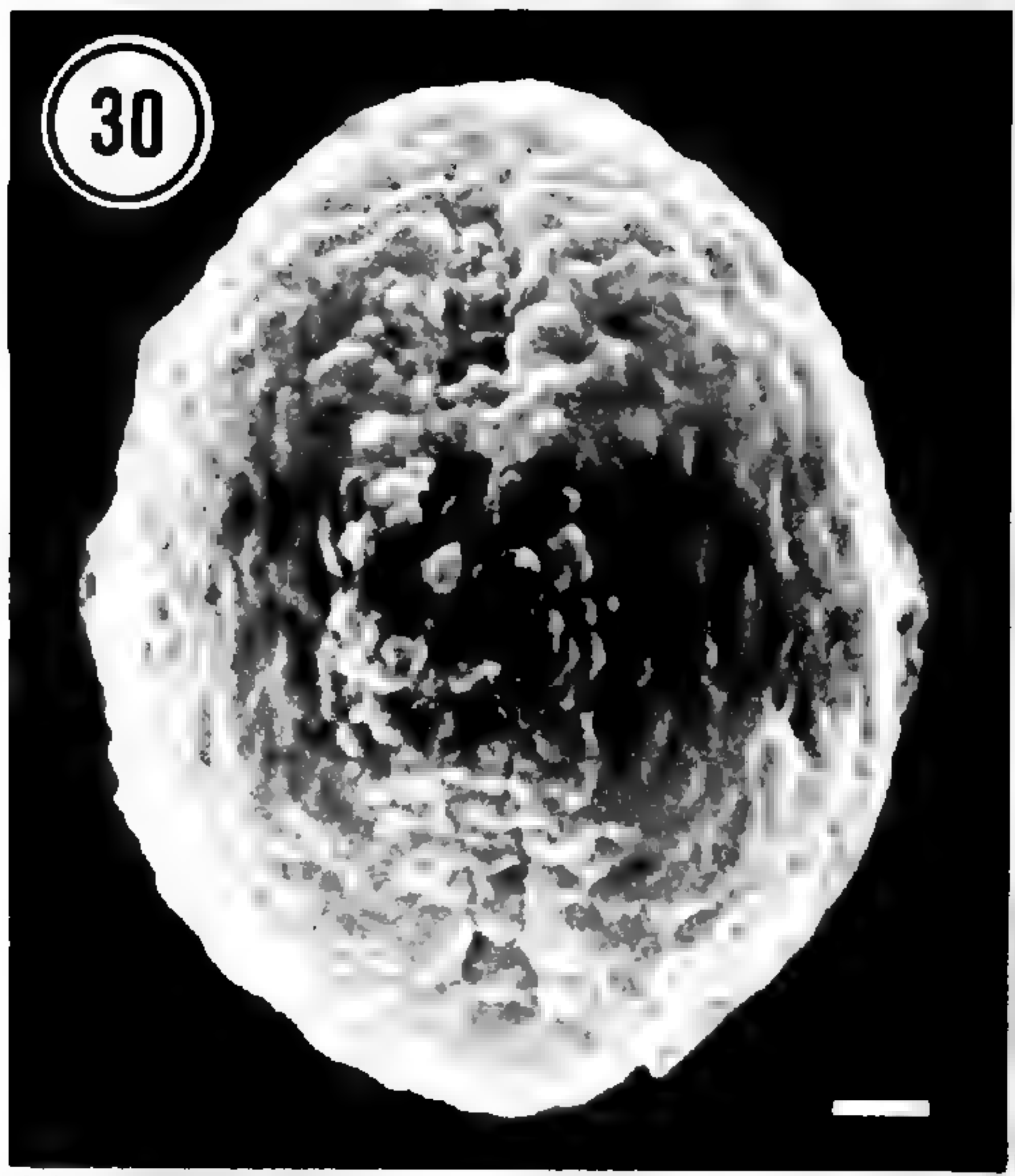
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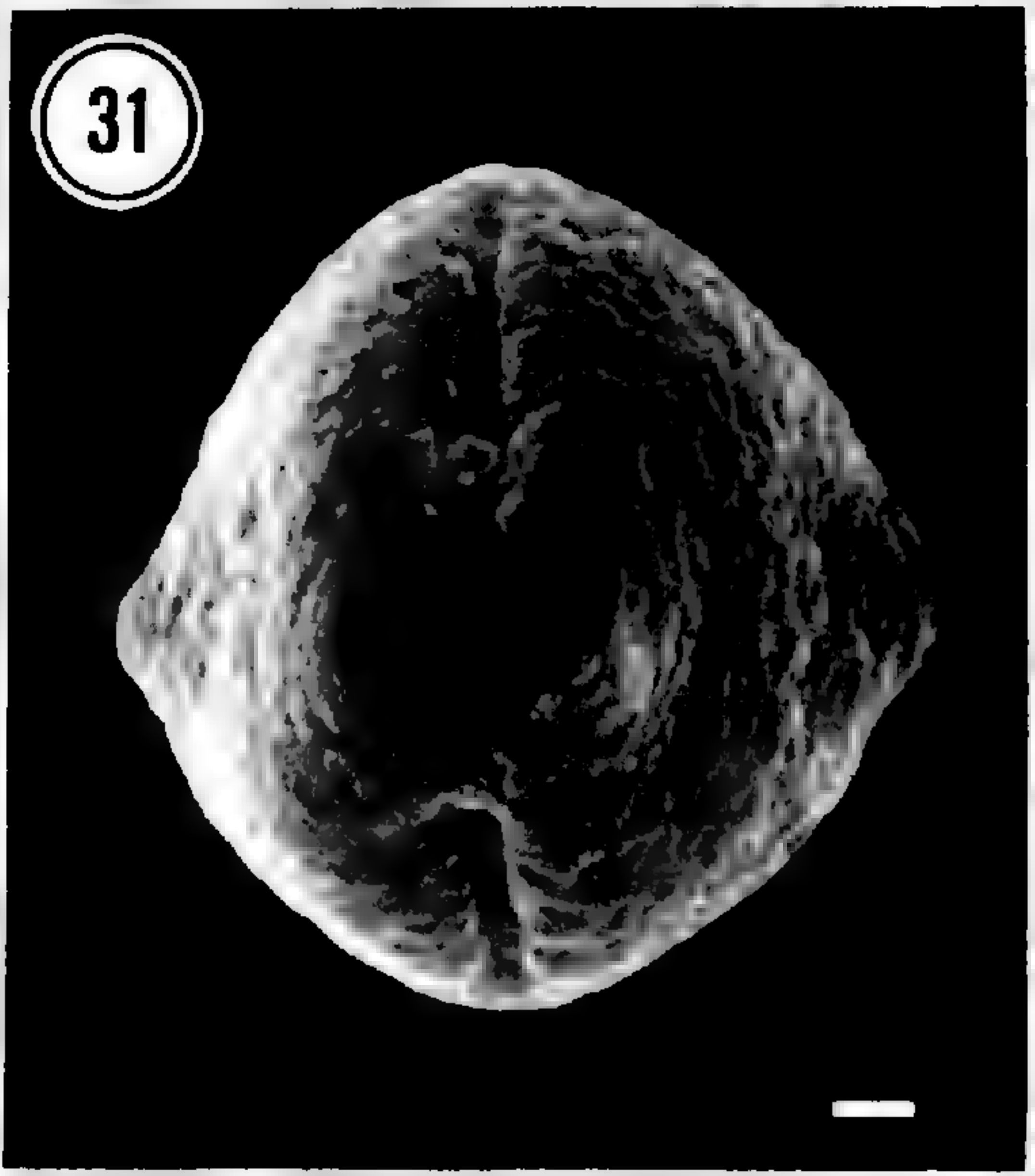
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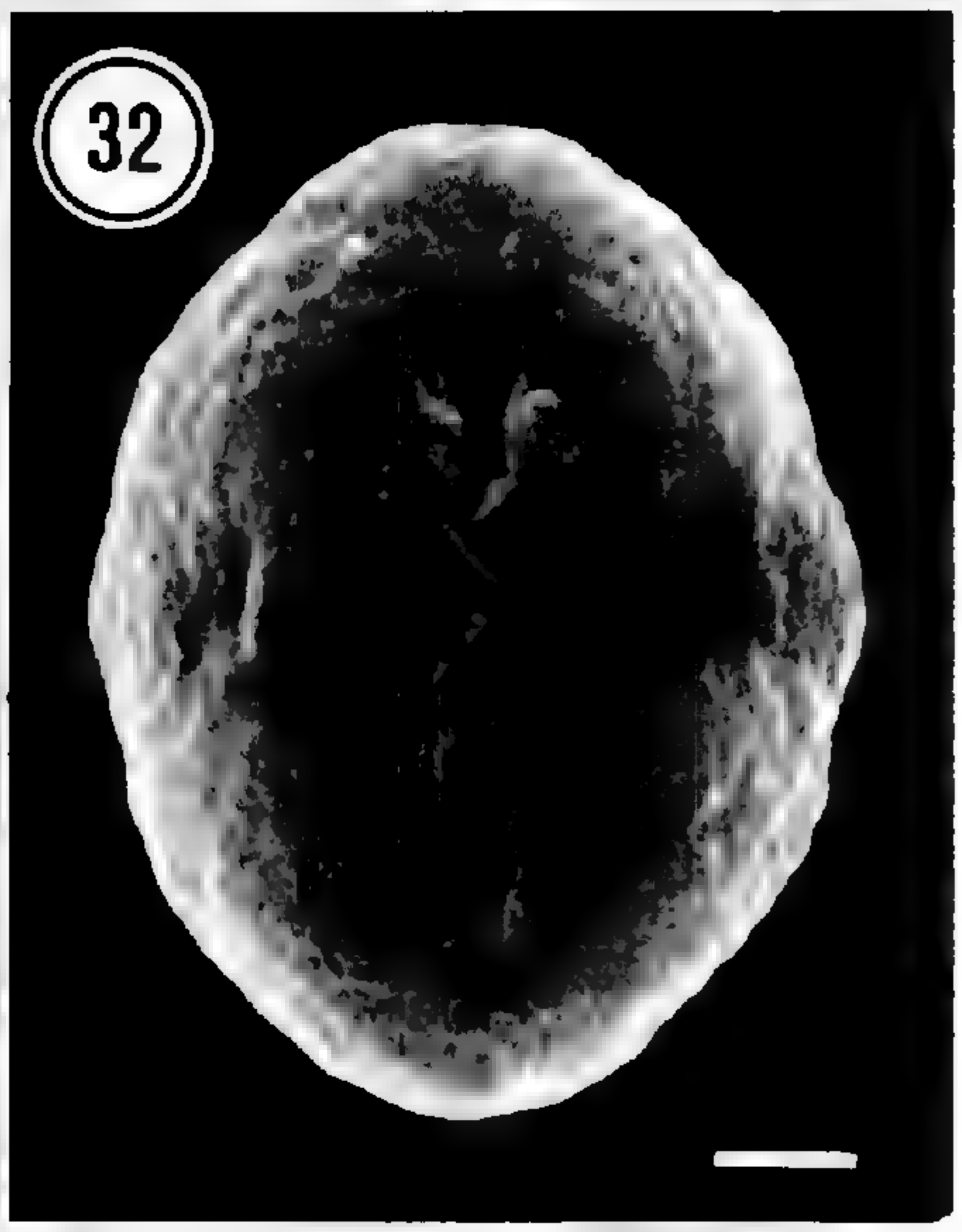
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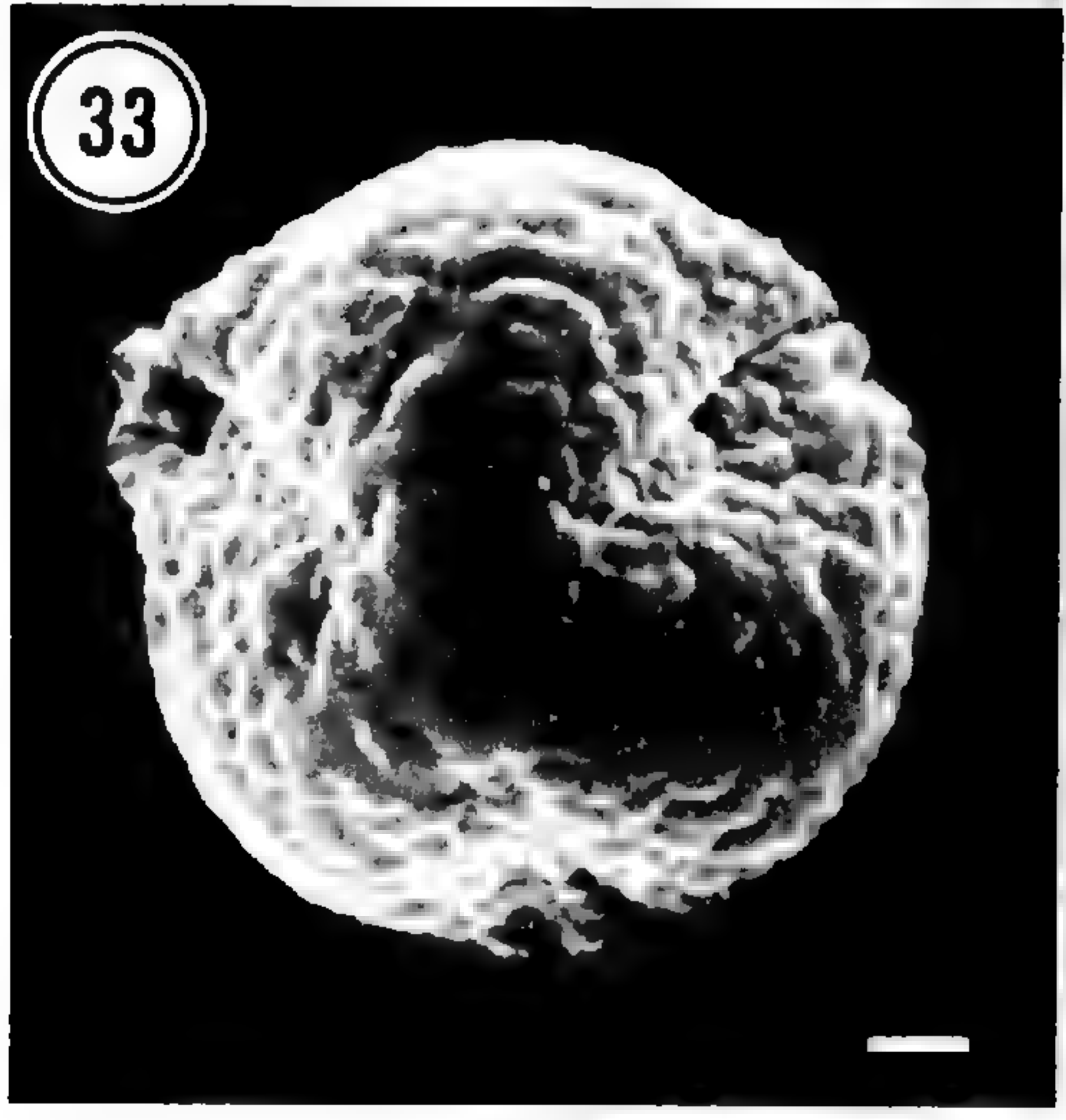
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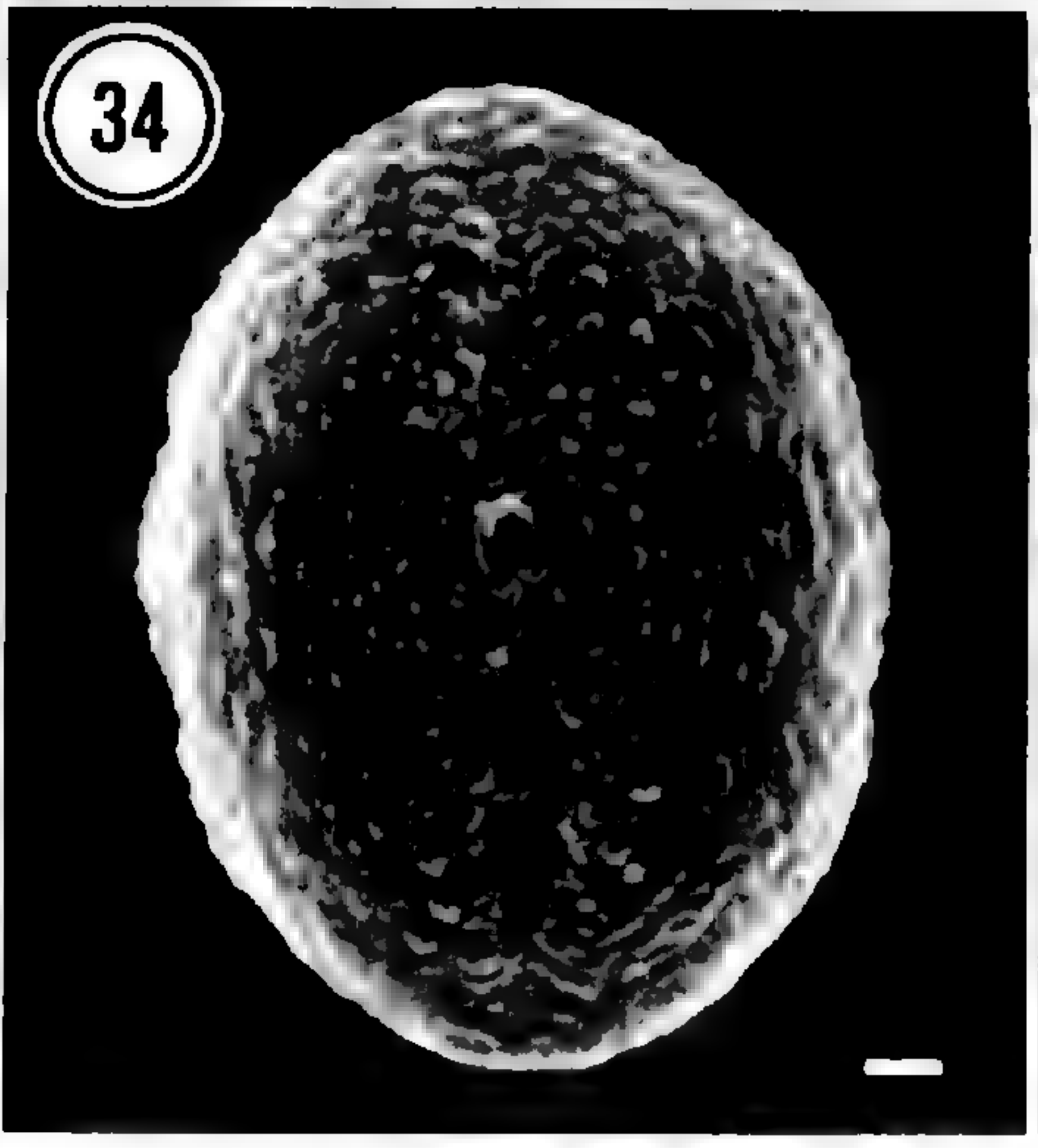
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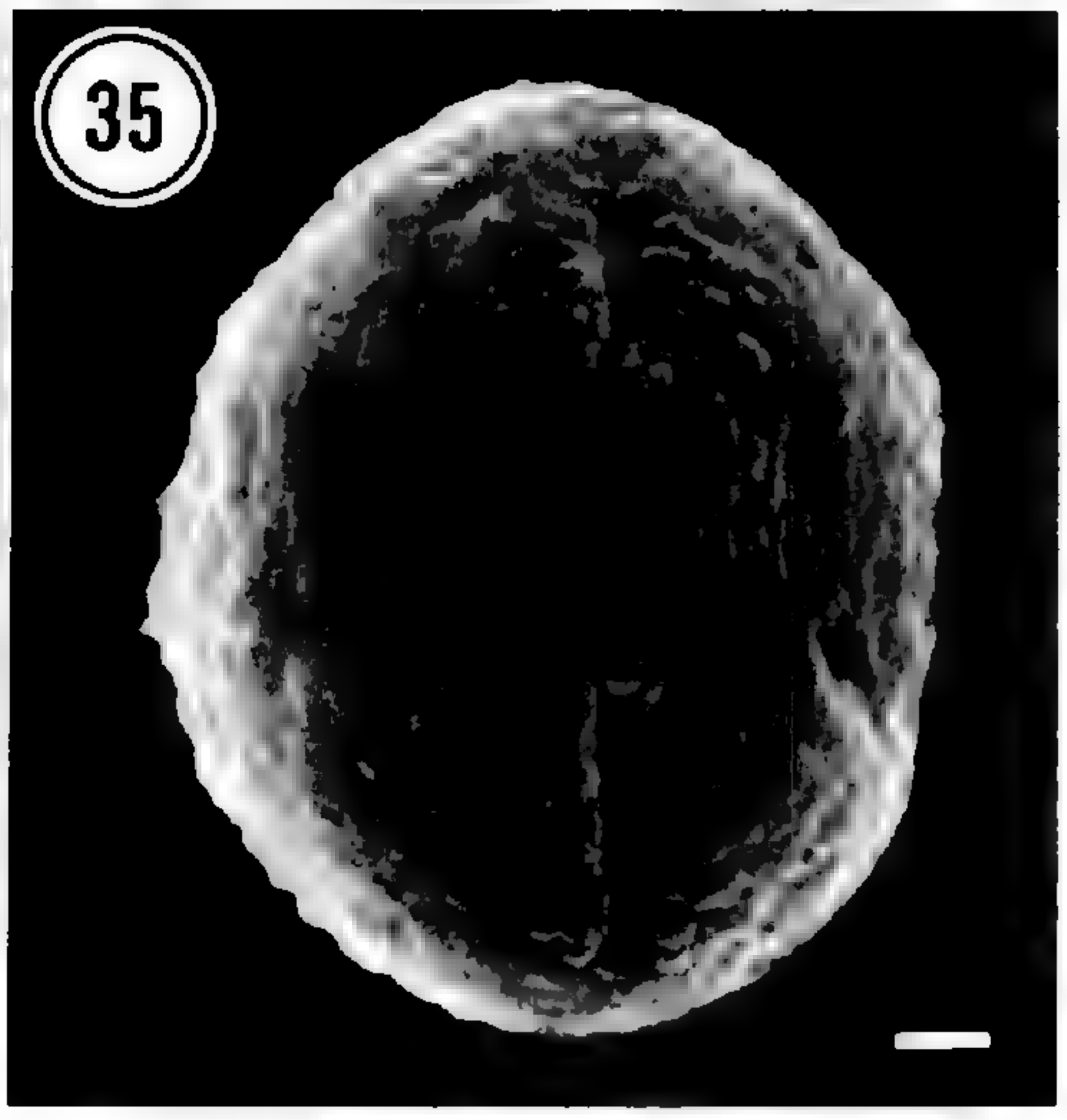
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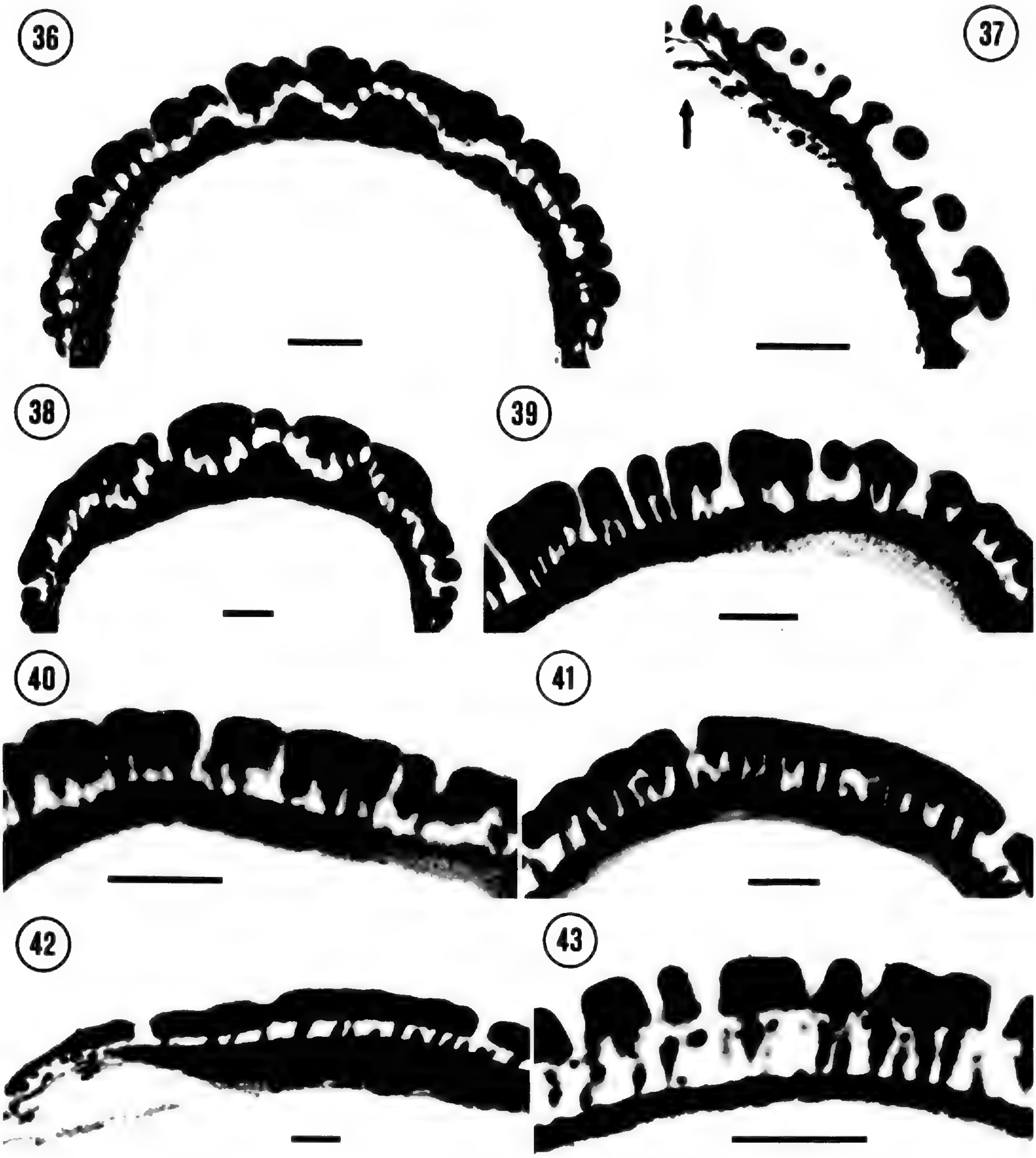
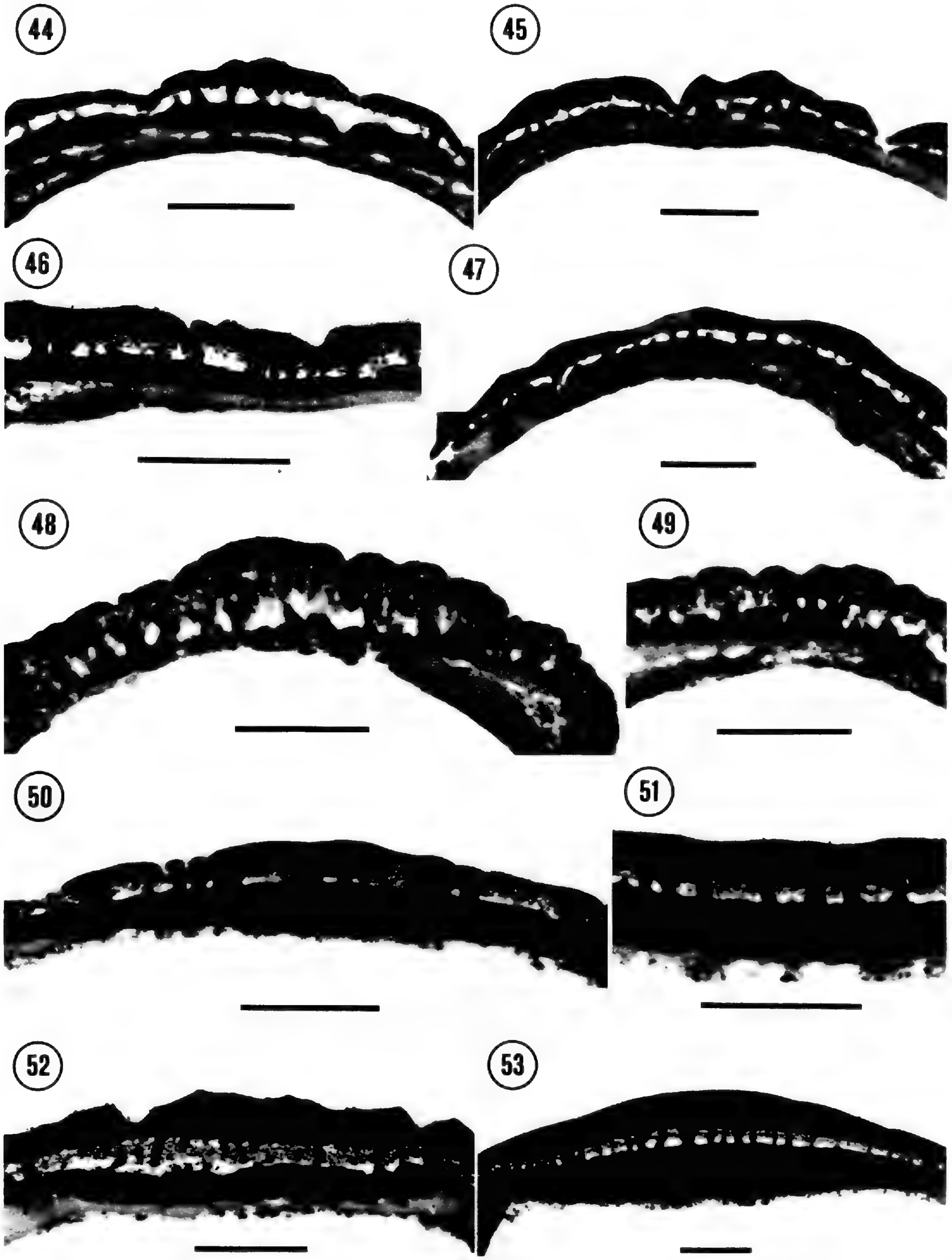


FIGURES 36–43. *Transmission electron micrographs of Anisophylleaceae pollen.—36.* Anisophyllea disticha. *In the center of the mesocolpium the columellae layer is undulating and the corresponding foot layer shows "hills" and "valleys." Toward the colpi the foot layer becomes thin and the columellae are straight. The outer margin of the tectum appears lobed due to perpendicularly sectioned striae.—37.* Combretocarpus rotundatus. *Section of a mesocolpium near an endoaperture (arrow). The tectum is incomplete, the columellae simple, the foot layer uniform, and the endexine disrupted.—38, 39.* Anisophyllea obtusifolia. *The undulating columellae (as in Fig. 38) are present only in some areas of the grain, possibly near the equator. In other sections, the middle part of the mesocolpium also has straight columellae (as in Fig. 39, to the left).—40.* A. fallax. *The tectum is thick and incomplete, the columellae thin and short, and the foot layer and endexine uniform.—41.* A. laurina. *The columellae are well developed.—42.* Polygonanthus amazonicus. *The foot layer is thick and tapering toward the endoaperture (left).—43.* Poga oleosa. *The tectum is incomplete and thick; the columellae are tall, becoming granular distally; the foot layer is thin; and the endexine is thicker than the foot layer and is uniform. Scale bars = 1 μm.*



FIGURES 44–53. *Transmission electron micrographs of Gynotrocheae (44–49) and Macarisieae (50–53) pollen.—44.* Carallia brachiata *and 45.* C. eugenioides. *In both, the tectum is thin, the columellae are short and unbranched, the foot layer is uneven in thickness and the endexine is uniform but has long, narrow gaps in Figure 44.—46.* Crossostylis grandiflora. *A thin granular layer is present just below the tectum. The endexine is thicker and has irregular open spaces near a colpus (left).—47.* Gynotroches axillaris. *The exine is similar to that in* Carallia.*—48.* Pellacalyx pustulata. *The tectum is thin, the short columellae are extensively branched, and the foot layer is thin and irregular. A line separates the foot layer from the endexine. The latter becomes very thick near the colpus, where it has a large, irregular gap.—49.* P. *cf.* saccardianus. *The exine is similar*

DISCUSSION

Lack of endoaperture fusion is the only feature of Anisophylleaceae pollen that does not overlap variation within Rhizophoraceae. Therefore, the phenetic gap between the two families results from the combined effects of many characters. With LM, for example, Anisophylleaceae OTUs have the highest or lowest average (or median) in 8 of 10 characters (1, 2, 4–8, and 10) and the same high average as Rhizophoreae for character 3. Anisophylleaceae OTUs also have the highest or lowest average for six TEM characters (24–26, 29–31) and the second highest average for characters 27 and 28. Also with TEM, Anisophylleaceae pollen can be separated from Gynotrocheae by a much lower endexine thickness ratio, and from Macarisieae by lack of intercolumellar granulation.

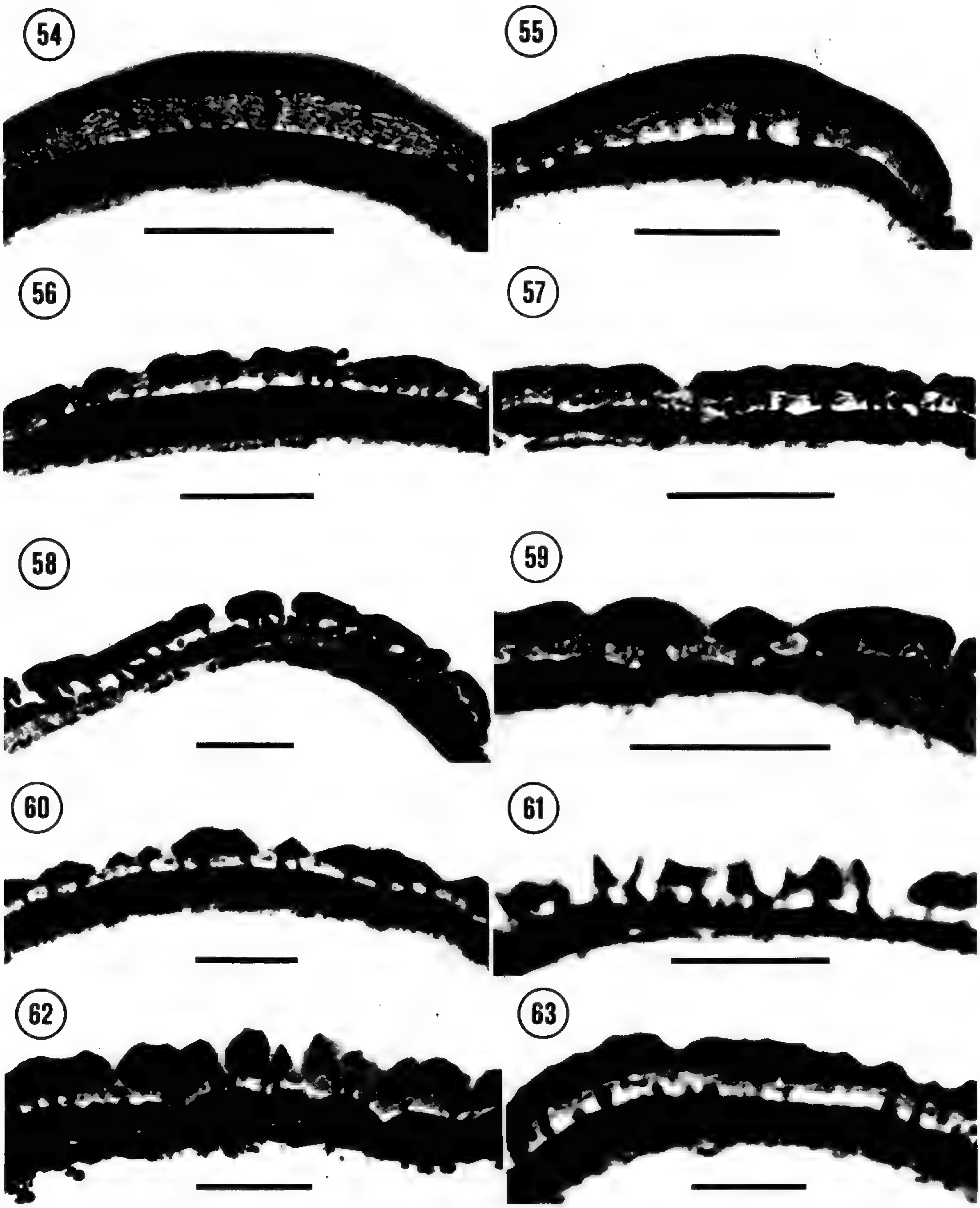
SEM analysis reveals the punctate-only sculpture of four Anisophylleaceae OTUs. *Combretocarpus rotundatus* (A4) differs slightly by having psilate mesocolpial margins. The striate sculpture of *Anisophyllea disticha* (A1) is strikingly different from any other in this study and is primarily responsible for isolating *A. disticha* along component III. In contrast, punctate pollen within Rhizophoraceae is usually psilate–punctate or punctate–rugulate. Exceptions include *Cassipourea elliptica* (M3), which is punctate-only, and *Dactylopetalum sessiliflorum* (M5), which has the same SEM character states as *C. rotundatus* (A4). The similarity in exine sculpture between *D. sessiliflorum* and *C. rotundatus* partially accounts for their connection on the minimum spanning tree.

Pollen of Anisophylleaceae can therefore be distinguished from Rhizophoraceae by the following combination of character states: larger polar axis and breadth, greater variation in polar axis and breadth, higher P/E ratio (in the subprolate–prolate range), narrow or nonexistent endoapertures, lack of endoaperture fusion, relatively small polar area (including some syncolpate grains), punctate sculpture, thicker tectum, taller and wider columellae, the highest tectum thickness and columellae height ratios, the lowest foot layer ratio, a low endexine ratio, and absence of intercolumellar granulation. These results agree with separate familial status for Anisophylleaceae. On the other hand, Anisophylleaceae, even without *Anisophyllea disticha* (A1), is a relatively variable taxon with longer average links on the minimum spanning tree than the tribes of Rhizophoraceae.

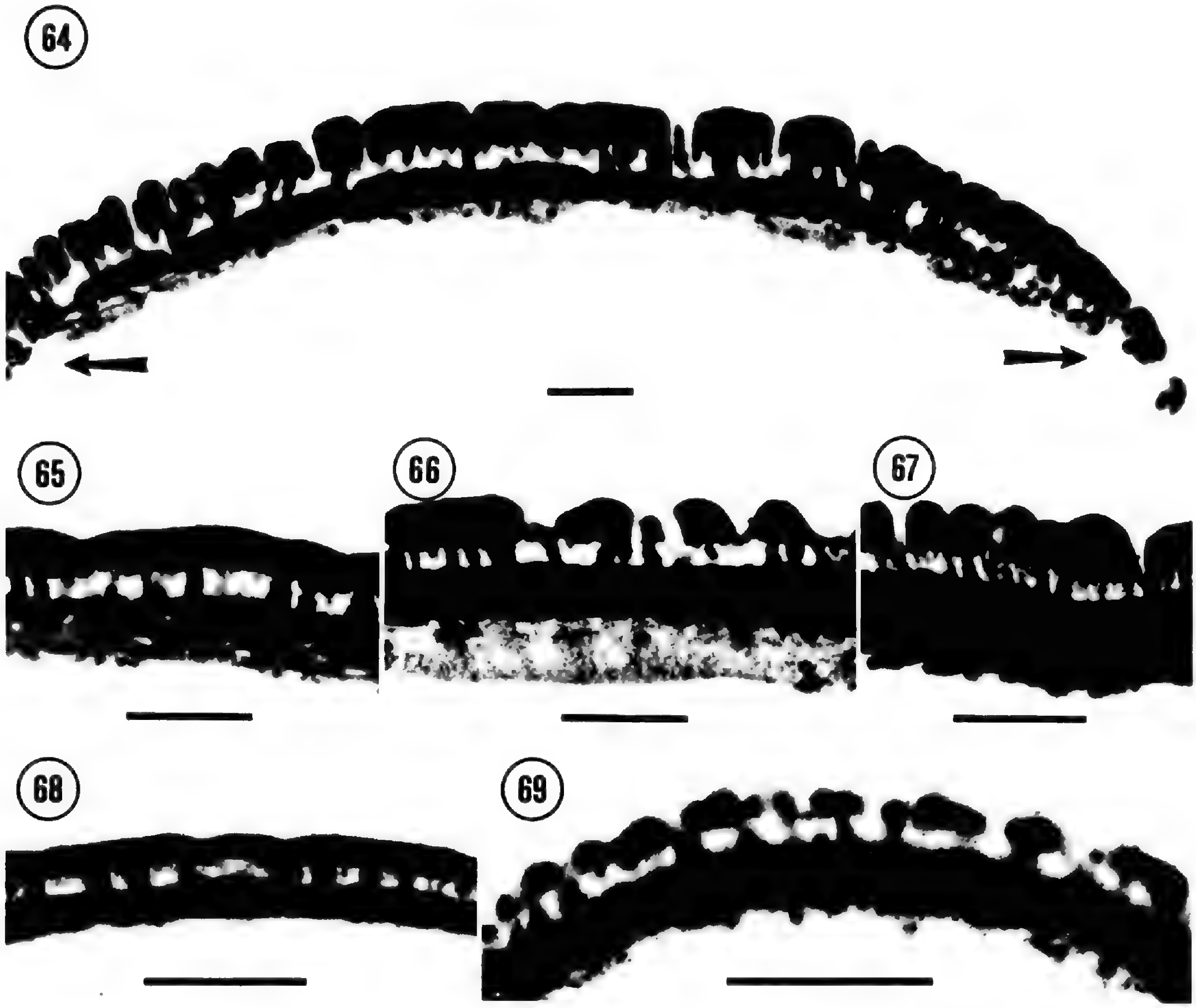
Pollen of Gynotrocheae, Macarisieae, and Rhizophoreae can be generally characterized, but these tribes cannot be separated based on palynological evidence. Characteristics generally distinguishing pollen grains of Rhizophoreae from those of Macarisieae and Gynotrocheae are larger size, lower P/E ratios (averaging 100), greater distances between colpal ends, higher polar area indexes, punctate–rugulate sculpture, thicker tecta, taller and wider columellae, and thicker foot layers. At the opposite end of the continuum are Gynotrocheae with the smallest grains, highest P/E ratios (average 119), psilate–punctate sculpture, highest endoapertural indexes, lowest foot layer ratios, and highest endexine ratios. Results of the phenetic analysis are not consistent with the proposed separation of *Crossostylis grandiflora* (G3) from Gynotrocheae (see other symposium papers, this volume). In both the ordination and minimum spanning tree, *C. grandiflora* is located within the group of Gynotrocheae OTUs.

Macarisieae OTUs are widely distributed in phenetic space, partly because of the many exceptions to the predominant SEM character states. There is essentially no phenetic gap between Macarisieae and either Rhizophoreae or Gynotrocheae. Macarisieae is also most similar to Anisophylleaceae. In many measurements and ratios, the Macarisieae average is between Rhizophoreae and Gynotrocheae, including polar axis and breadth, P/E ratio, distance between colpal ends, polar area index, tectum and foot layer thickness, height and width of columellae, columellar height ratio, and foot layer and endexine thickness ratios. Macarisieae pollen is also characterized by the presence of intercolumellar granulation. Only two OTUs outside Macarisieae, *Crossostylis grandiflora* (G3) and *Pellacalyx* cf. *saccardianus* (G5), have this feature, and only one Macarisieae OTU, *Cassipourea elliptica* (M3), lacks granulation.

←
to that in Figure 48 but no line is evident.—50. Anopyxis ealeaensis. *The narrow columellae layer has a granular matrix. The foot layer is very thick.—51.* A. kleineana. *The exine is similar to that of the previous species, but the endexine is highly disrupted.—52.* Sterigmapetalum obovatum. *The granular matrix is well developed, and the columellae are cut obliquely.—53.* S. heterodoxum. *The distinct granular layer is present below the tectum. The foot layer is very thick; the endexine is thin and disrupted in the mesocolpium but is well developed below the colpi. Scale bars = 1 μm.*



FIGURES 54–63. *Transmission electron micrographs of Macarisieae pollen.—54.* Macarisia lanceolata. *Middle part of a mesocolpium. Note that the intercolumellar spaces are filled with a granular matrix.—55.* M. ellipticifolia. *Mesocolpium near a colpus (on the right).—56.* M. humbertiana. *Foot layer quite thick, and endexine granular due to proximity of circular endoaperture.—57.* M. pyramidata. *In 55, 56, and 57 the granular layer (matrix) is not as extensive as in 54.—58.* Cassipourea elliptica. *An oblique section showing part of a mesocolpium near a colpus (to the right). Here the endexine is greatly thickened and is granular on the left due to the proximity of an endoaperture.—59.* Blepharistemma membranifolia. *Granular matrix present, endexine thin or absent except near the colpus, where it is very thick (to the right).—60.* Dactylopetalum sessiliflorum. *Middle part of a mesocolpium; a thin granular layer below the tectum.—61.* D. zenkeri. *Incomplete tectum suggests a reticulate or meshlike surface.—62.* Comiphyton gabonense. *Columellae layer is narrow and has some granules below the tectum.—63.* Petalodactylis obovata. *Exine similar to those in 55, 56, and 57. Scale bars = 1 μm.*



FIGURES 64–69. *Transmission electron micrographs of Rhizophoreae pollen.*—*64.* Rhizophora mucronata (9947), section of an entire mesocolpium. Tectum incomplete, columellae simple, and foot layer uniform. Endexine is granular in the mesocolpium, probably due to the vicinity of the circular, fused endoapertures. Near the open endoapertures (arrows) the foot layer and endexine are absent.—65. R. stylosa. *Tectum complete; endexine very thick.*—*66.* R. mangle. *Tectum incomplete in some areas; the thick granular endexine is probably due to the circular endoaperture.*—*67.* Kandelia candel. *Note the massive endexine. Columellae appear to become granular distally.*—*68.* Bruguiera gymnorrhiza. *A few granules, similar to those described for Macarisieae, are present in the intercolumellar spaces. The thin endexine is difficult to distinguish.*—*69.* Ceriops tagal. *Tectum incomplete, foot layer very thick, and endexine thin and disrupted. Scale bars = 1 µm.*

CONCLUSION

Principal components analysis using palynological data clearly separates Anisophylleaceae from Rhizophoraceae and supports the hypothesis of separate familial status for Anisophyllaceae. If Macarisieae pollen data were not considered, Rhizophoreae and Gynotrocheae OTUs would also form discrete phenetic groups. Including Macarisieae pollen data changes this picture to one of continuous phenetic variation from Rhizophoreae through Macarisieae to Gynotrocheae.

The majority of pollen morphological characteristics in Anisophylleaceae and Rhizophoraceae occur in a broad range of families throughout the angiosperms. Therefore, it was not possible within the limits of this study to suggest relationships with other taxa. It seems particularly significant that neither family we investigated can be connected to Myrtales on palynological grounds. Light and ultrastructural data on Myrtales pollen (Patel et al., 1985) are generally comparable to data in this study. The colporoidate or fused endoapertures possessed by Anisophylleaceae or Rhizophoraceae have no counterpart in Myrtales, however, and the pseudocolpi of Myrtales pollen do not correspond to features of either Anisophylleaceae or Rhizophoraceae pollen.

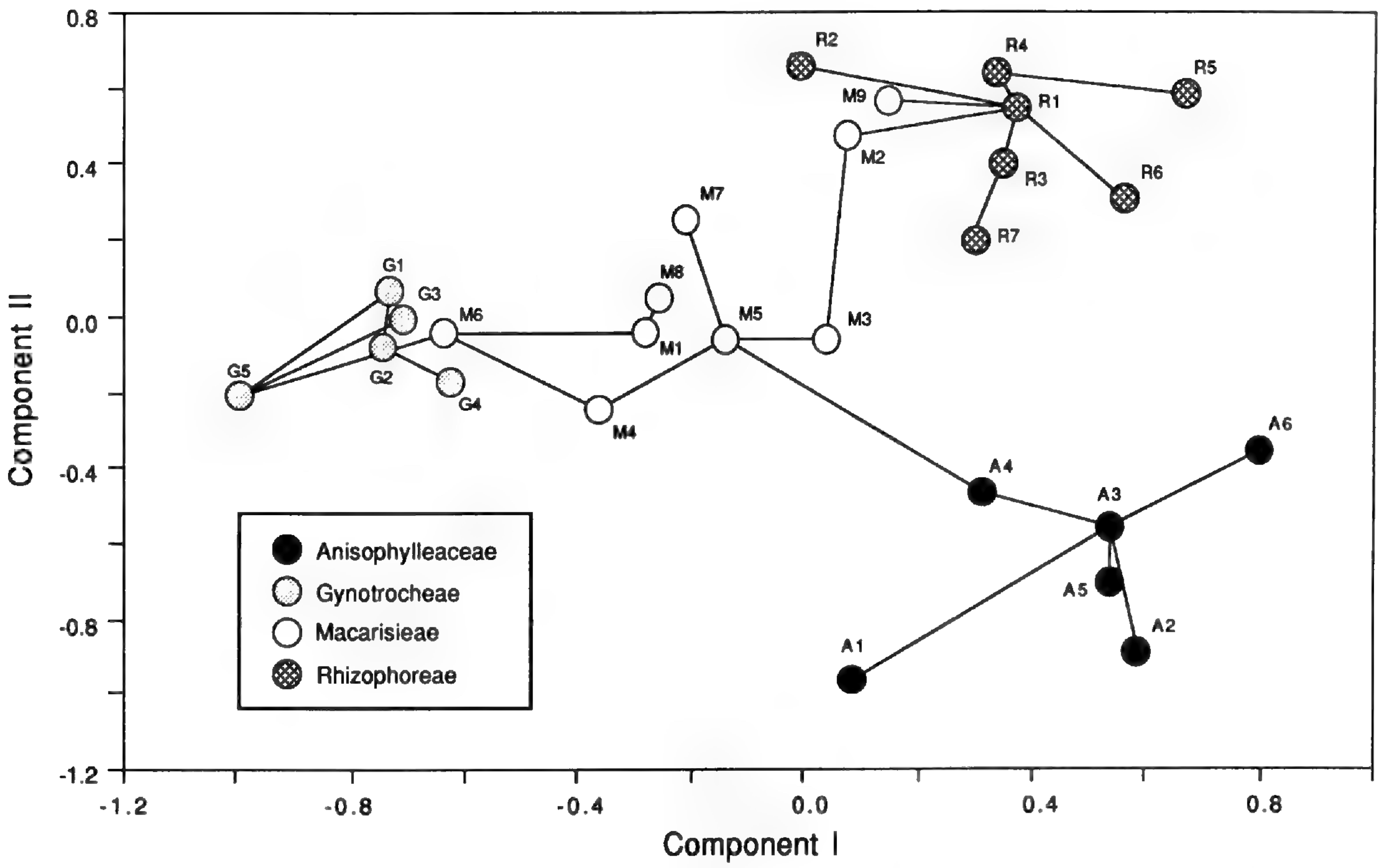


FIGURE 70. *Projection of 27 OTUs onto the first two principal components (data from Table 3). Percent of total variation explained is 25.5 for component I and 20.7 for component II. The superimposed minimum spanning tree was calculated from an average taxonomic distance matrix.*

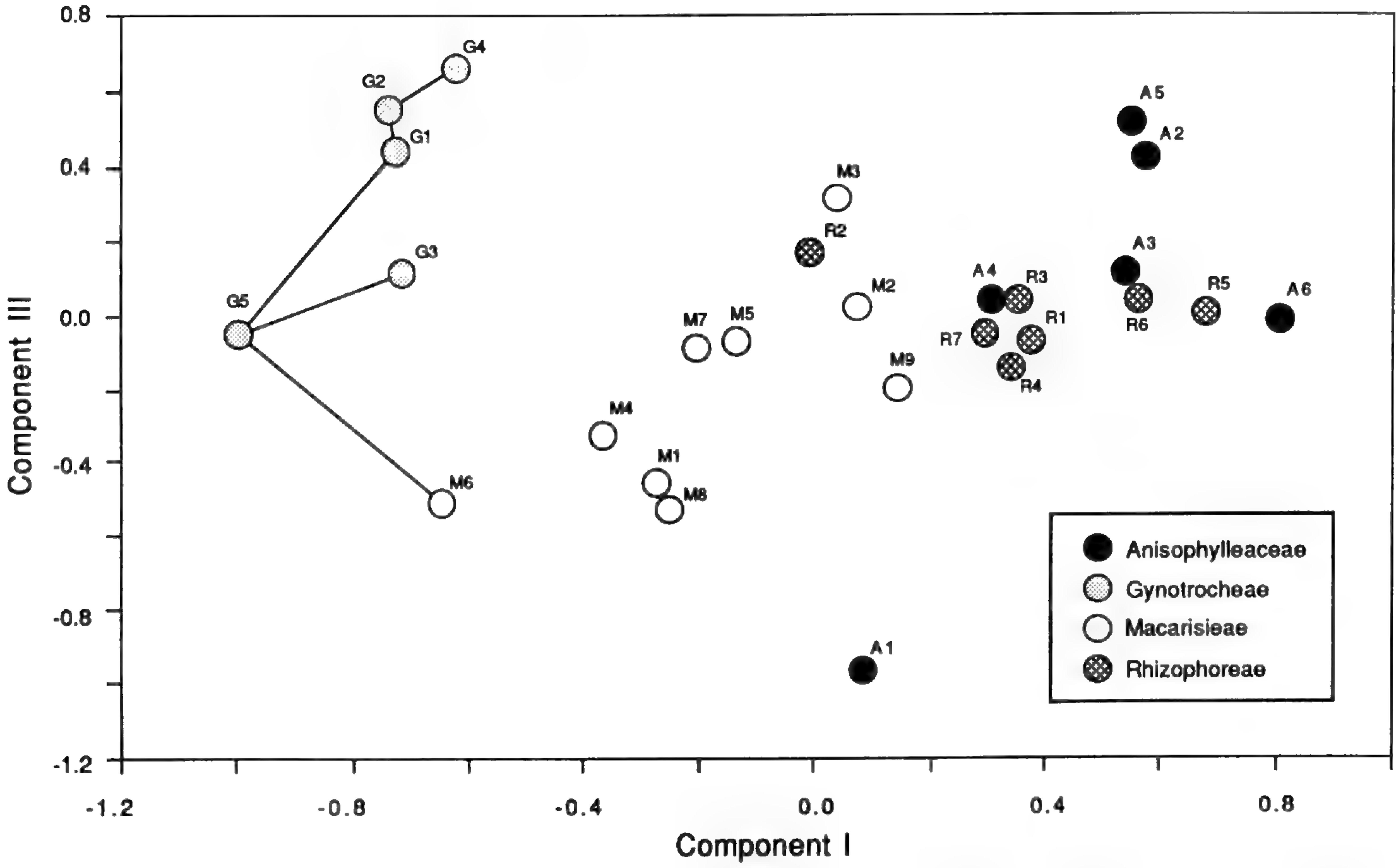


FIGURE 71. *Projection of same 27 OTUs (Fig. 70) onto principal components I and III. Percent of variation expressed by component III is 13.0. A partial minimum spanning tree has been included to clarify relationships within Gynotrocheae.*

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SIEVE-ELEMENT PLASTIDS AND SYSTEMATIC RELATIONSHIPS OF RHIZOPHORACEAE, ANISOPHYLLEACEAE, AND ALLIED GROUPS[1]

H.-Dietmar Behnke[2]

ABSTRACT

One hundred fifty-five species of 41 families belonging to the proposed ordinal composition around and including the families Rhizophoraceae and Anisophylleaceae have been studied with respect to their sieve-element plastids. The great majority of taxa, including the Anisophylleaceae, contain S-type plastids. P-type sieve-element plastids were found in Humiriaceae, Rhizophoraceae, and Erythroxylaceae (all with specific subtype-P5), and (with P-forms not readily assigned to a specific subtype) in Eucryphiaceae, Neuradaceae, Oxalidaceae (s.l.), Rhabdodendraceae, and part of Zygophyllaceae. A critical evaluation of sizes and specific contents of their sieve-element plastids negates close relationships between Rhizophoraceae and Anisophylleaceae, integrates the Rhizophoraceae in the Geraniales, but is not able to suggest a position for the Anisophylleaceae. Within the Geraniales the family sequence Humiriaceae (form-P5cs plastids)–Erythroxylaceae (P5c)–Rhizophoraceae (P5c) is proposed to be paralleled by another P-type containing sequence Lepidobotryaceae (S-type)–Hypseocharitaceae (S)–Oxalidaceae (S, Pc)–Averrhoaceae (Pcfs), both being linked to the S-type Linaceae s.l. Sieve-element data do not support the inclusion of Rhizophoraceae in the Celastrales; however, such data corroborate the exclusion of the new celastralean family Elaeocarpaceae from the Malvales. Among the taxa proposed by Dahlgren, Anisophylleaceae would be best placed in vicinity to the S-type families of the Rosales, not in close association to P-type Neuradaceae. The presence of P-type sieve-element plastids in Zygophyllaceae, Neuradaceae, and Humiriaceae is reported here for the first time.

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The family Rhizophoraceae is distinct from other dicotyledon taxa by the formation of rather extraordinary P-type sieve-element plastids (Behnke, 1982a). Their specific form-P5c plastids contain some twenty more or less rectangular protein crystals—i.e., an accumulation of proteins to a degree found nowhere else in P-type plastids—and were originally reported for seven species of the family and an additional four species of the Erythroxylaceae. A closely related form-P5cf (containing protein filaments in addition to the crystals) was found in the family Cyrillaceae (*Cliftonia* and *Cyrilla*). These unique subtype-P5 plastids raised questions about the systematic position of the three families (Behnke, 1982a) and initiated further research on sieve-element plastids and other characters.

A first study of the distribution of types of sieve-element plastids of Myrtales and allied groups (an association of taxa into which the family Rhizophoraceae had been placed most commonly) revealed that (1) all core families of the Myrtales and all of those closely related contained S-type plastids, and (2) within the Rhizophoraceae (an additional seven species were investigated) the two genera *Anisophyllea* and *Combretocarpus* also contained S-type plastids (Behnke, 1984). This gave support to various efforts to separate the tribe Anisophylleeae from the Rhizophoraceae and to erect the family Anisophylleaceae (Cronquist, 1981; Dahlgren, 1983; Tobe & Raven, 1987).

The present additional report on sieve-element plastids in Rhizophoraceae, Anisophylleaceae, and allies is an extension of the previous investigations taking also into account all the higher taxa, i.e., ordinal compositions and their associates, to which the two families have been affiliated (see Dahlgren, this volume).

MATERIALS AND METHODS

One hundred fifty-five species of 41 families, all proposd by Dahlgren (this volume) for placement around Rhizophoraceae and Anisophylleaceae were investigated (see Table 1).

Living material recently removed from the plant or shipped within a few days under special care is a prerequisite for a fixation of sieve elements and the eventual investigation of their plastids with the transmission electron microscope. Thin hand sections were made with a razor blade from preferably young herbaceous shoots or end parts of tree branches less than 1 cm in diameter. The sections were immersed into a fixing solution containing formaldehyde and glutaraldehyde and processed according to standard methods (see Behnke, 1982b). Material made available by collections at original locations was sent to Heidelberg either fresh (causing a delay of up to a week between sampling and start of fixation) or as formaldehyde/glutaraldehyde prefixed hand sections (causing an equally long delay between primary and postfixation).

RESULTS

A SHORT OUTLINE OF CHARACTERS OF SIEVE-ELEMENT PLASTIDS USED TO CHARACTERIZE THE TAXA INVESTIGATED

Sieve-element plastids are separated into two *types* by presence (P-type) or absence (S-type) of protein crystals and/or filaments, while starch grains may or may not be present. *Subtypes* of P-type sieve-element plastids are identified by any unmistakable feature of their protein inclusions, e.g., the subtype-P5 by a high number of generally rectangular protein crystals. *Forms* of sieve-element plastids are defined by any combination of the three inclusions: c = protein crystals, f = protein filaments, s = starch grains, e.g., P5cf. In addition, all sieve-element plastids within a family will be characterized by their average diameter and average amount of protein vs. starch content (Table 2), both calculated from the respective data of the different species listed in Table 1.

Recent studies of the sieve-element plastids of the Acanthaceae (Behnke, 1986a) and within all families of the Magnoliidae (Behnke, 1988)—the latter for the first time taking into account diameters and quantitative data of the plastids—resulted in a general model for the interrelationships between the different forms of plastids. It was concluded that at least in these groups, P-type plastids may have derived from S-type plastids (for details see Behnke, 1988, but compare with Behnke, 1981).

In his summary statement of Rhizophoraceae and Anisophylleaceae and their systematic relationships, Dahlgren (this volume) proposes a revised classification and lists the ordinal composition around each of the two families. The following description of the sieve-element plastids in these taxa follows his sequence of families.

DISTRIBUTION OF THE DIFFERENT SIEVE-ELEMENT PLASTIDS AMONG THE FAMILIES GROUPED AROUND RHIZOPHORACEAE

Zygophyllaceae (ZYG; Fig. 1: *Guaiacum, Larrea*). Five species in four genera investigated, one with P-type, the others with S-type plastids. Plastid diameter is 1.2 μm. *Larrea divaricata* contains form-Pcs sieve-element plastids with two protein crystals of different diameters (0.4 and 0.3 μm) and different crystal spacing. There are about five typically disc-shaped starch grains in addition. The S-type plastids of other species studied contain up to ten starch grains of different diameters and shapes, including typically disc-shaped ones.

In this family the plastids of the mature sieve element are often disrupted, making it impossible to record some protein crystals. Therefore, after the detection of P-type plastids in both collections of *Larrea* (Table 1), all species have been studied once more.

Nitrariaceae (NIT; Fig. 1: *Nitraria*). This monogeneric family, represented here by *Nitraria retusa*, contains S-type plastids with characteristics slightly different from those of ZYG, i.e., with a diameter of 1.0 μm and about five more or less globular starch grains.

Peganaceae (PEG; Fig. 1: *Peganum*). *Peganum harmala* likewise contains S-type plastids with a diameter of 1.2 μm and about five starch grains.

Balanitaceae (BLT; Fig. 1: *Balanites*). Two species investigated in the monogeneric family both contain S-type plastids with about ten globular starch grains. Plastid diameters are 1.7 μm in one and 1.1 μm in the other (Table 1).

Vivianiaceae (VIV; Fig. 1: *Caesarea*). *Caesarea albiflora* contains S-type plastids with up to five typically disc-shaped starch grains. Plastid diameter is 1.1 μm. (See also Behnke & Mabry, 1977.)

Geraniaceae (GER; Fig. 1: *Pelargonium*). Five species in three genera investigated, all with S-type plastids. There are about five disc-shaped starch grains within a plastid, the average diameter of which is 1.2 μm (range 1.0–1.6 μm). (See also Behnke & Mabry, 1977.)

Ledocarpaceae (LDC; Fig. 1: *Wendtia*). *Wendtia gracilis* contains small S-type plastids (diameter 0.9 μm) with a few starch grains of variable sizes. The plastids appear distinctly different from those of the Geraniaceae.

Ixonanthaceae (IXO; Fig. 2: *Ixonanthes*). The two species of *Ixonanthes* investigated contain S-type plastids of an average diameter of 1.1 μm and with an average of ten small and large, more or less globular starch grains.

Humiriaceae (HOU; Fig. 2: *Humiria*, *Endopleura*, *Sacoglottis*). Four species in three genera investigated: all with P5cs sieve-element plastids. This form is characterized by numerous (average more than ten) irregular to rectangular protein crystals and about ten small starch grains. The average measurements are: plastid diameter 1.2 μm and protein crystals 0.3 μm.

Hugoniaceae (HUG; Fig. 2: *Indorouchera*). The two species investigated represent two genera, and both contain S-type plastids with about ten starch grains, among them one or two large ones. The average plastid diameter is 1.1 μm.

Erythroxylaceae (ERX; Fig. 2: *Erythroxylum*). The four species of *Erythroxylum* investigated are characterized by P5c sieve-element plastids. This highly specific form contains about ten up to 0.7 μm large rectangular protein crystals (and no starch), which are densely packed within the comparatively small plastids (diameter 1.1 μm). (See also Behnke, 1982a.)

Linaceae (LIN; Fig. 2: *Linum*). Three species in two genera investigated, all containing S-type plastids with an average of about five starch grains (often including a large globular one), which may disintegrate into small particles. The average plastid diameter is 1.2 μm (range 1.0–1.5 μm).

Lepidobotryaceae (LPB; Fig. 2: *Lepidobotrys*). The monotypic *Lepidobotrys staudtii* contains S-type plastids with up to ten starch grains disintegrated into small particles. The plastid diameter is 1.2 μm.

Oxalidaceae (OXL; Fig. 3: *Averrhoa*, *Oxalis*, *Sarcotheca*). Twelve species in five genera investigated. Sieve-element plastids not uniform: two types including three different forms occur in the family.

Averrhoa and *Sarcotheca* contain form-Pcfs plastids with an average diameter of 1.1 μm. This P-form, not specified to belong to a distinct P-subtype, contains protein filaments (f), two rectangular or cubic protein crystals (c) up to 0.4 μm in diameter, and about five globular starch grains (s), of which one may be very large.

Oxalis (8 species tested) is characterized by very small (average diameter 0.8 μm) form-Pc sieve-element plastids with two protein crystals, a very prominent (diameter about 0.5 μm) cubical one and a second, smaller one.

Biophytum and *Hypseocharis* contain S-type plastids of different sizes and different starch contents (see Table 1 and Behnke, 1982c).

Form-Pcfs and -Pc sieve-element plastids (and/or -Pcs not found in the Oxalidaceae) are reported in other dicots, e.g., in Vitaceae, Rhabdodendraceae, Connaraceae, Eucryphiaceae, Acanthaceae, Gunneraceae (Behnke 1974, 1976a, 1982c, 1985, 1986a, b), and Neuradaceae (see below).

TABLE 1. *Sieve-element plastid data of the investigated species. Family = families recognized by Dahlgren (this volume), family acronyms after Weber (1982); D'1989 = number of family in Dahlgren (in press) and family acronym if different from "family"; Herbarium = deposit of vouchers. The following data characterize the sieve-element plastids: Type (and form); DIA = diameter in µm; N = number of protein crystals; PMA = maximum diameter of protein crystals in µm; SN = average number of starch grains. "Publication" refers to previous works of the author.*

Family	D'1989	Species	Origin of Material	Herbarium	Type	DIA	N	PMA	SN	Publication
ZYG	236	*Guaiacum coulteri* A. Gray	BG-HEID	HEID	S	1.2	0	0	8	
ZYG	236	*Guaiacum officinale* L.	BG-B, -HEID	GH-B, HEID	S	1.3	0	0	8	
ZYG	236	*Larrea divaricata* Cav.	Mexico, Ulrich, BG-HEID	HEID	Pcs	1.1	2	0.4	5	
ZYG	236	*Porlieria hygrometa* Ruiz. & Pav.	BG-CP		S	1.2	0	0	8	
ZYG	236	*Zygophyllum* sp.	BG-HEID	HEID	S	1.5	0	0	5	
NIT	238	*Nitraria retusa* Aschers.	Israel, *J. Aronson*		S	1.0	0	0	6	
PEG	237	*Peganum harmala* L.	BG-E		S	1.2	0	0	5	
BLT	244	*Balanites aegyptiaca* Delile	BG-L	HEID	S	1.7	0	0	10	
BLT	244	*Balanites angolensis*	BG-CP		S	1.1	0	0	10	
VIV	240	*Caesarea albiflora* Cambess.	Brazil, *A. Schultz*	HEID	S	1.1	0	0	5	(1977)
GER	239	*Erodium malachoides* Willd.	Italy, *H.D.B. 830407*	HEID	S	1.0	0	0	5	
GER	239	*Erodium manescavii* Coss.	BG-HEID	HEID	S	1.1	0	0	5	
GER	239	*Geranium cinereum* Cav.	BG-HEID	HEID	S	1.1	0	0	5	
GER	239	*Geranium sanguineum* L.	BG-HEID	HEID	S	1.2	0	0	5	
GER	239	*Pelargonium tetragonum* (L.f.) L'Herit. ex Ait.	BG-HEID	HEID	S	1.6	0	0	8	(1977)
LDC	241	*Wendtia gracilix* Meyen	Chile, *R. Rodriguez & J. Grau 2164*	CONC	S	0.9	0	0	3	
BBS	242	*Biebersteinia multifida* DC.	Armenia, USSR, *Gabrielian*	HEID	S	1.1	0	0	2	
IXO	248	*Ixonanthes grandiflora* Hochr.	BG-BO	HEID	S	1.3	0	0	10	
IXO	248	*Ixonanthes reticulata* Jack.	Sabah, *H.D.B. & Lee 830721*	HEID	S	1.0	0	0	10	
HOU	246	*Endopleura* sp.	Brazil, *B. Nelson 1566*	MO	P5cs	1.2	10	0.3	15	
HOU	246	*Humiria balsamifer*	Brazil, *B. Nelson*	HEID	P5cs	1.3	20	0.3	5	
HOU	246	*Sacoglottis* sp.	Brazil, *B. Nelson 1506*	MO, HEID	P5sc	0.9	6	0.2	8	
HOU	246	*Sacoglottis trichogyna* Cuatr.	Costa Rica, *M. H. Grayum 7662*	MO, HEID	P5cs	1.3	10	0.3	8	
HUG	245 LIN	*Hugonia mystax* L.	Sri Lanka, *Gunatilleke*	HEID	S	1.0	0	0	10	
HUG	245 LIN	*Indorouchera grifffithiana* H. Hallier	BG-BO	HEID	S	1.1	0	0	10	
ERX	249	*Erythroxylum coca* Lam.	BG-HEID	HEID	P5c	1.1	10	0.6	0	(1984)
ERX	249	*Erythroxylum novo-granatense* (Morris) Hieron	BG-HEID	HEID	P5c	1.3	10	0.5	0	(1984)
ERX	249	*Erythroxylum pulchrum* A. St. Hil.	BG-RB, *Kubitzki*		P5c	1.1	10	0.7	0	(1984)

TABLE 1. *Continued.*

Family	D'1989	Species	Origin of Material	Herbarium	Type	DIA	N	PMA	SN	Publication
ERX	249	*Erythroxylum suberosum* A. St. Hil.	Brazil, *I. S. Gottsberger*	BOTU, UB	P5c	1.1	10	0.4	0	(1984)
LIN	245	*Linum dolomiticum* Borb.	BG-HEID		S	1.0	0	0	3	
LIN	245	*Linum flavum* L.	BG-HEID	HEID	S	1.2	0	0	8	
LIN	245	*Reinwardtia cicanoba* (Buch.-Ham. ex D. Don) Hara	BG-K	HEID	S	1.5	0	0	5	
LPB	250	*Lepidobotrys staudtii* Engl.	Cameroon, *D. Thomas & E. Martin 478*	MO, HEID	S	1.2	0	0	10	
OXL	251	*Averrhoa carambola* L.	BG-HEID	HEID	Pcfs	1.0	2	0.4	3	(1982c)
OXL	251	*Biophytum sensitivum* (L.) DC.	BG-HEID, -BONN	HEID	S	0.8	0	0	3	(1982c)
OXL	251	*Hypseocharis pimpinellifolia* Remy	BG-CP		S	1.3	0	0	15	(1982c)
OXL	251	*Oxalis acetosella* L.	Heidelberg, *H.D.B. 790413*	HEID	Pc	0.8	2	0.4	0	(1982c)
OXL	251	*Oxalis carnosa* Mol.	BG-HEID	HEID	Pc	0.8	2	0.5	0	(1982c)
OXL	251	*Oxalis crenata* Jacq.	BG-HEID	HEID	Pc	0.8	2	0.5	0	(1982c)
OXL	251	*Oxalis deppei* Lodd. ex Sweet	BG-HEID	HEID	Pc	0.8	2	0.5	0	(1982c)
OXL	251	*Oxalis gigantea* Baun.	BG-SBBG		Pc	1.0	2	0.5	0	(1982c)
OXL	251	*Oxalis rhombifolia* Jacq.	BG-MJG		Pc	0.8	2	0.5	0	(1982c)
OXL	251	*Oxalis stricta* L.	BG-HEID		Pc	0.8	2	0.4	0	(1982c)
OXL	251	*Oxalis valdiviensis* Barbeoud	BG-HEID		Pc	0.9	2	0.5	0	
OXL	251	*Sarcotheca diversifolia* H. Hallier	Sabah, *H.D.B. & Lee 830722*	HEID	Pcfs	1.2	2	0.3	5	
CEL	256	*Canotia holacantha* Torr.	BG-DES	HEID	S	1.1	0	0	5	
CEL	256	*Catha edulis* Forsk.	BG-HEID		S	1.3	0	0	5	
CEL	256	*Celastrus buxifolius* L.	BG-HEID		S	1.3	0	0	10	
CEL	256	*Celastrus orbiculatus* Thunb. var. *punctatus*	BG-HEID	HEID	S	1.4	0	0	5	
CEL	256	*Elaeodendron shaerophyllum* Presl.	BG-K		S	1.1	0	0	5	
CEL	256	*Euonymus fortunei* (Turcz.) Hand.-Mazz.	BG-HEID	HEID	S	1.6	0	0	10	
CEL	256	*Goupia* sp.	Brazil, *B. Nelson*	HEID	S	1.6	0	0	12	
CEL	256	*Hippocratea comosa* Sw.	BG-HEID		S	1.8	0	0	5	
CEL	256	*Loeseneriella ritchardii* R. Wilczek	BG-P	HEID	S	1.0	0	0	0	
CEL	256	*Peritassa campestris* (Cambess.) A. C. Smith	Brazil, *I. S. Gottsberger*	BOTU, UB	S	1.4	0	0	10	
CEL	256	*Pterocelastrus tricuspidatus* Walp.	BG-K	HEID	S	1.0	0	0	5	
CEL	256	*Putterlickia pyracantha* Endl.	BG-SBBG		S	1.4	0	0	5	

TABLE 1. *Continued.*

Family	D'1989	Species	Origin of Material	Herbarium	Type	DIA	N	PMA	SN	Publication
CEL	256	*Salacia uregaensis* R. Wilczek	BG-BONN		S	1.0	0	0	5	
CEL	256	*Siphonodon australis* Benth.	BG-NSW		S	1.1	0	0	10	
ELC	258	*Aceratium dasyphyllum* A. C. Smith	BG-BO	HEID	S	1.2	0	0	5	
ELC	258	*Aristotelia chilensis* (Mol.) Stuntz	BG-BONN	HEID	S	1.4	0	0	5	
ELC	258	*Crinodendron patagua* Mol.	BG-BONN	HEID	S	1.1	0	0	5	
ELC	258	*Elaeocarpus acronodia* Blume	BG-BO	HEID	S	1.7	0	0	10	
ELC	258	*Elaeocarpus ganitrus* Roxb.	Hawaii, Waimea-Arboretum		S	1.6	0	0	10	
RHZ	257	*Bruguiera gymnorrhiza* Lam.	BG-B	GH-B	P5c	1.2	20	0.5	0	(1982a)
RHZ	257	*Bruguiera sexangula* Lour.	BG-CP		P5c	—	20	0.4	0	(1982a)
RHZ	257	*Carallia brachiata* Merrill	QLD, *R. Tracey 281278*		P5c	1.3	20	0.4	0	(1982a)
RHZ	257	*Cassipourea barteri* (Hook. f.) N. E. Br.	BG-BR	HEID	P5c	1.5	20	0.4	0	
RHZ	257	*Cassipourea elliptica* (Sw.) Poir.	Costa Rica, *Juncosa 260879*	DUKE, HEID	P5c	1.5	20	0.5	0	(1984)
RHZ	257	*Cassipourea killipii* Cuatrecasas	Columbia, *Juncosa 2540*	JAUM, COL, MO, HEID	P5c	1.2	20	0.4	0	(1984)
RHZ	257	*Ceriops tagal* C. B. Robinson	QLD, *G. J. Muller*	HEID	P5c	1.3	20	0.6	0	(1984)
RHZ	257	*Crossostylis biflora* Forst.	BG-E		P5c	1.3	20	0.3	0	(1982a)
RHZ	257	*Crossostylis grandiflora* Brogn. & Gris.	New Caledonia, *Juncosa 2009814*	DUKE, HEID	P5c	1.3	20	0.3	0	(1984)
RHZ	257	*Kandelia rheedii* Wight & Arn. (= *R. stylosa*)	QLD, *R. Tracey 281278*		P5c	1.4	20	0.3	0	(1982a)
RHZ	257	*Rhizophora* cf. *conjugata* L.	BG-BONN		P5c	1.5	20	0.3	0	(1982a)
RHZ	257	*Rhizophora mangle* L.	BG-HEID	HEID	P5c	1.4	20	0.3	0	(1982a)
RHZ	257	*Sterigmapetalum heterodoxum* Steyerm. & Liesner	Venezuela, *Berry & Wingfield 4304*	HEID	P5c	1.4	20	0.3	0	(1984)
CUN	163	*Aphanopetalum resinosum* Endl.	BG-K	HEID	S	1.2	0	0	6	
CUN	163	*Caldcluvia paniculata* D. Don.	BG-DUSS		S	1.0	0	0	8	(1985)
CUN	163	*Cunonia capensis* L.	BG-BR	HEID	S	1.3	0	0	10	
CUN	163	*Schizomeria ovata* D. Don	NSW, *H.D.B. 810819*		S	1.2	0	0	0	
CUN	163	*Weinmannia trichosperma* Cav.	BG-DUSS		S	1.1	0	0	5	
BAU	164	*Bauera rubioides* Andr.	NSW, *H.D.B. 810817*, BG-K		S	0.8	0	0	5	
BNL	165	*Brunellia costaricensis* Standley	Costa Rica, *Barringer 2931*	F, CR	S	1.3	0	0	10	
BNL	165	*Brunellia* sp.	Ecuador, *Balslev 62509*		S	1.7	0	0	10	
BNL	165	*Brunellia standleyana* Cuatr.	Costa Rica, *Poveda 3315a*	CR	S	1.2	0	0	10	

TABLE 1. *Continued.*

Family	D'1989	Species	Origin of Material	Herbarium	Type	DIA	N	PMA	SN	Publication
DVS	166	*Davidsonia pruriens* F. Muell.	BG-NSW		S	1.4	0	0	10	
ECR	167	*Eucryphia billardieri* Spach.	BG-K		Pc	0.7	2	0.4	0	(1985)
ECR	167	*Eucryphia cordifolia* Cav.	BG-DUSS	HEID	Pc	0.6	2	0.3	0	(1985)
ECR	167	*Eucryphia glutinosa* (Poepp. et Endl.) Baill.	BG-DUSS	HEID	Pc	0.6	2	0.2	0	(1985)
ECR	167	*Eucryphia lucida* Druce	BG-K		Pc	0.6	2	—	0	(1985)
ECR	167	*Eucryphia* ×*nymansensis* Bausch.	BG-K	HEID	Pc	0.6	2	0.3	0	
CRO	185	*Crossosoma bigelovii* S. Wats.	*A. C. Gibson*, BG-RSA	RSA	S	1.7	0	0	10	
CRO	185	*Crossosoma californicum* Nutt.	BG-RSA, -SBBG	RSA	S	1.8	0	0	10	
CRO	185	*Forsellesia nevadensis* (Gray) Greene	Arizona, *A. C. Gibson*		S	1.0	0	0	0	
ROS	180	*Alchemilla xanthochlora* Rothm.	BG-HEID		S	0.9	0	0	5	
ROS	180	*Dryas suedermannii* Süderm.	BG-HEID	HEID	So	0.8	0	0	0	
ROS	180	*Duchesnea indica* (Andr.) Focke	BG-HEID	HEID	So	0.9	0	0	0	
ROS	180	*Filipendula ulmaria* (L.) Maxim.	BG-CP		So	0.8	0	0	0	
ROS	180	*Fragaria vesca* L.	BG-HEID	HEID	S	0.9	0	0	1	
ROS	180	*Geum rivale* L.	BG-HEID	HEID	So	0.6	0	0	0	
ROS	180	*Kerria japonica* (L.) DC.	Heidelberg, *H.D.B. 780821*	HEID	S	1.4	0	0	5	
ROS	180	*Lyonothamnus floribundus* A. Gray	BG-SBBG		S	1.6	0	0	10	
ROS	180	*Neviusia alabamensis* A. Gray	BG-BONN	HEID	S	1.3	0	0	5	
ROS	180	*Potentilla rupestris* L.	BG-HEID	HEID	So	0.8	0	0	0	
ROS	180	*Quillaja brasiliensis* Mart.	BG-HEID		So	1.1	0	0	0	
ROS	180	*Rhodotypus scandens* (Thunb.) Mak.	BG-HEID	HEID	S	1.2	0	0	10	
ROS	180	*Rosa* sp.	BG-HEID	HEID	So	1.0	0	0	0	
ROS	180	*Rubus phoenicolasius* Maxim.	BG-BONN	HEID	So	1.1	0	0	0	
ROS	180	*Sanguisorba minor* Scop.	BG-HEID	HEID	So	0.9	0	0	0	
ROS	180	*Spiraea wilsonii* Duthie	BG-HEID	HEID	S	1.0	0	0	5	
NRD	181	*Neurada procumbens* L.	Kuwait, *L. Boulos*	HEID	Pcs	1.5	1	0.4	10	
ANS	184	*Anisophyllea* cf. *purpurascens* Hutchins. & Dalz.	Cameroon, *D. Thomas 6120*	MO	S	1.2	0	0	10	
ANS	184	*Anisophyllea trapezoidales* Baill.	Sabah, *H.D.B 830721*	HEID	S	1.2	0	0	10	(1984)'
ANS	184	*Combretocarpus* cf. *motleyi* Hook. f.	Sarawak, *Sri Aman*		S	1.1	0	0	10	(1984)
ANS	184	*Poga oleosa* Schott	Cameroon, *D. Thomas 6119*	MO	S	1.3	0	0	10	
ANS	184	*Polygonanthus amazonicus* Ducke	Brazil, *B. Nelson*	MO	S	1.4	0	0	10	

TABLE 1. *Continued.*

Family	D'1989	Species	Origin of Material	Herbarium	Type	DIA	N	PMA	SN	Publication
MAL	182	*Amelanchier canadensis* (L.) Medik.	BG-HEID		S	1.0	0	0	5	
MAL	182	*Aronia prunifolia* (Marsh.) Rehder	BG-HEID	HEID	S	1.2	0	0	5	
MAL	182	*Cotoneaster frigidus* Wall. ex Lindl.	BG-HEID		S	1.2	0	0	5	
MAL	182	*Crataegus* ×*dippeliana* Lange	BG-HEID	HEID	S	1.4	0	0	5	
MAL	182	*Cydonia oblonga* Mill.	BG-HEID	HEID	S	1.3	0	0	5	
MAL	182	*Eriobotrya japonica* (Thunb.) Lindl.	BG-HEID		S	1.2	0	0	10	
MAL	182	*Malus sylvestris* Mill.	BG-HEID		S	1.6	0	0	10	
MAL	182	*Mespilus germanica* L.	BG-SIENA		S	1.0	0	0	5	
MAL	182	*Pyracantha coccinea* M. J. Roem.	Heidelberg, *H.D.B. 780821*	HEID	S	1.4	0	0	10	
MAL	182	*Pyrus communis* L.	Heidelberg, *H.D.B. 780821*		S	1.0	0	0	10	
MAL	182	*Raphiolepis indica* Lindl.	BG-HEID		S	1.0	0	0	10	
MAL	182	*Sorbus aucuparia* L.	BG-HEID	HEID	S	1.2	0	0	10	
MAL	182	*Vauquelinia californica* Sarg.	BG-SBBG		S	1.2	0	0	10	
AMY	183	*Exochorda giraldii* Hesse	BG-HEID	HEID	S	0.9	0	0	3	
AMY	183	*Prunus cerasifera* Ehrh.	BG-HEID	HEID	S	1.2	0	0	0	
AMY	183	*Prunus padus* L.	BG-HEID	HEID	S	1.0	0	0	5	
AMY	183	*Prunus scoparius* Schneider	BG-HEID		S	0.9	0	0	10	
RHB	187	*Rhabdodendron amazonicuum* (Spruce ex Benth.) Hub.	Brazil, *G. T. Prance s.n.*	NY	Pcs	1.0	1	0.3	5	(1976a)
RHB	187	*Rhabdodendron macrophyllum* (Spruce ex Benth.) Hub.	Brazil, *G. T. Prance 20187*; and *B. Nelson 1290*	MO, HEID	Pcs	1.4	1	0.2	5	(1976a)
SAX	168	*Astilbe simplicifolia* Mak.	BG-HEID	HEID	S	1.2	0	0	8	
SAX	168	*Bergenia purpurascens* (Hook. f. & Thoms.) Engl.	BG-HEID	HEID	S	1.2	0	0	5	
SAX	168	*Peltiphyllum peltatum* (Torr.) Engl.	BG-CP		S	1.6	0	0	10	
SAX	168	*Rodgersia aesculifolia* Batal	BG-BONN	HEID	S	1.4	0	0	8	
SAX	168	*Saxifraga paniculata* Mill.	BG-HEID	HEID	S	1.0	0	0	8	
SAX	168	*Tolmiea menziesii* (Pursch.) Torr. et A. Gray	BG-HEID	HEID	S	1.3	0	0	10	
PTH	168 SAX	*Penthorum sedoides* L.	N. Carolina, *A. E. Radford* and BG-HAM	NCU	S	1.2	0	0	8	
VHL	168 SAX	*Vahlia capensis* Thunb.	BG-PRE	HEID	S	1.2	0	0	10	
FCO	169	*Francoa sonchifolia* Cav.	BG-BONN, -K	HEID	S	1.4	0	0	3	
GRY	170	*Greyia sutherlandii* Hook. et Harv.	BG-BONN, -HEID	HEID	S	1.2	0	0	5	

TABLE 1. *Continued.*

Family	D'1989	Species	Origin of Material	Herbarium	Type	DIA	N	PMA	SN	Publication
BRX	171	*Brexia madagascariensis* (Lam.) Nor. ex Thou.	BG-K, -BERN		S	1.1	0	0	5	
CRS	172	*Ribes bracteosum* Dougl. ex Hook.	BG-HEID		S	1.2	0	0	10	
ITE	173	*Choristylis rhamnoides* Harv.	BG-K		S	1.3	0	0	5	
ITE	173	*Itea ilicifolia* Oliv.	BG-K	HEID	S	1.6	0	0	5	
CPH	174	*Cephalotus follicularis* Labill.	BG-M		S	1.1	0	0	5	
CRS	175	*Cotyledon orbiculatum* L.	BG-HEID	HEID	So	1.0	0	0	0	
CRS	175	*Kalanchoe laciniata* (L.) DC.	BG-HEID	HEID	So	0.9	0	0	0	
CRS	175	*Kalanchoe uniflora* (Stapf) R. Hamet.	BG-HEID	HEID	So	0.8	0	0	0	
PDS	176	*Podostemum ceratophyllum* Michx.	Georgia, *S. B. Jones;* and *D. E. Boufford 22047*	CM	S	2.3	0	0	8	

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[1] Erroneously listed in Table 1 of Behnke (1984) as PVc.

Celastraceae (CEL; Fig. 4: *Catha, Pterocelastrus*). Fourteen species in 13 genera investigated, all with S-type plastids. There are 5–10 mostly globular starch grains recorded within these plastids, but their diameter is not uniform (average: 1.3 μm; range 1.0–1.8 μm). The sieve elements of *Goupia* contain crystalline, persistent p-protein bodies, a feature that characterizes a number of different dicotyledonous taxa (see Behnke, 1981) but is not found elsewhere in Celastraceae. *Hippocratea* and *Salacia,* as well as *Siphonodon,* sometimes separated as Hippocrateaceae and Siphonodontaceae, respectively, do not differ significantly in sieve-element characters.

Elaeocarpaceae (ELC; Fig. 4: *Aristotelia, Elaeocarpus*). The five species in four genera investigated contain S-type plastids. Their sizes (1.1–1.7 μm; average 1.4 μm) and number of globular starch grains (5–10) resemble those in CEL.

Rhizophoraceae (RHZ; Fig. 5: *Cassipourea, Ceriops, Crossostylis, Rhizophora, Sterigmapetalum*). Thirteen species of eight genera investigated, all with the specific form-P5c sieve-element plastids. Twenty or more rectangular to irregular protein crystals (0.2–0.5 μm) fill the plastid interior. The average plastid diameter is 1.4 μm. In *Rhizophora* the protein crystals are irregular, only rarely showing exact rectangular outlines. It is demonstrated, at least for *R. mangle,* that during the development of a sieve-element plastid, protein accumulates first as a large granular body (see Fig. 5, lower left micrograph) and only thereafter 'crystallizes' into several distinct parts.

In this study of their sieve-element plastids, all of the tribes recognized within the family were covered. Except for the crystal outlines mentioned for *Rhizophora,* there is almost no distinction possible between the plastids of the different species. The comparatively large protein crystals depicted in *Ceriops* (Fig. 5), which come very close in size to those shown in *Erythroxylum* (Fig. 2), are not restricted to this species. Similar views could have been chosen from other Rhizophoraceae. (See also Behnke, 1982a, 1984.)

DISTRIBUTION OF THE DIFFERENT SIEVE-ELEMENT PLASTIDS AMONG THE FAMILIES GROUPED AROUND ANISOPHYLLEACEAE

Cunoniaceae (CUN; Fig. 6: *Cunonia, Weinmannia*). Five species of five genera investigated, all with S-type plastids. The diameter of the plastids is about 1.2 μm; their contents are up to

TABLE 2. *The families of the ordinal periphery around Anisophylleaceae and Rhizophoraceae arranged according to sieve-element plastid data.*

Family	Types	PSP[1]	PDIA	N	PMA	PS	SSP	SDIA	SN	SO	SODI	Dahlgren
Brunelliaceae	S						3	1.4	10			BNL 165
Davidsoniaceae	S						1	1.4	10			DVS 166
Cunoniaceae	S						5	1.2	7			CUN 163
Baueraceae	S						1	0.8	5			BAU 164
Eucryphiaceae	Pc	5	0.6	2	0.3							ECR 167
Saxifragaceae	S						6	1.3	8			SAX 168
Penthoraceae	S						1	1.2	8			PTH 168
Vahliaceae	S						1	1.2	10			VHL 168
Francoaceae	S						1	1.4	3			FCO 169
Greyiaceae	S						1	1.2	5			GRY 170
Brexiaceae	S						1	1.1	5			BRX 171
Grossulariaceae	S						1	1.2	10			GRS 172
Iteaceae	S						2	1.4	5			ITE 173
Cephalotaceae	S						1	1.1	5			CPH 174
Crassulaceae	So									3	0.9	CRS 175
Crossosomataceae	S						3	1.5	10			CRO 185
Anisophylleaceae	S						5	1.2	10			ANS 184
Rosaceae	S, So						7	1.2	6	9	0.9	ROS 180
Malaceae	S						13	1.2	8			MAL 182
Amygdalaceae	S						4	1.0	6			AMY 183
Rhabdodendraceae	Pcs	2	1.2	1	0.3	5						RHB 187
Neuradaceae	Pc	1	1.5	1	0.4	10						NRD 181
Gunneraceae	Pc	3	1.5	2	0.5	8						GNN 188
Podostemaceae	S						1	2.3	8			PDS 176
Balanitaceae	S						2	1.4	10			BLT 244
Zygophyllaceae	S, Pcs	1	1.1	2	0.4	5	4	1.3	7			ZYG 236
Nitrariaceae	S						1	1.0	6			NIT 238
Peganaceae	S						1	1.2	5			PEG 237
Geraniaceae	S						5	1.2	6			GER 239
Vivianiaceae	S						1	1.1	5			VIV 240
Ledocarpaceae	S						1	0.9	3			LDC 241
Biebersteiniaceae	S						1	1.1	2			BBS 242
Linaceae	S						3	1.2	7			LIN 245
Hugoniaceae	S						2	1.1	10			HUG 245
Ixonanthaceae	S						2	1.2	10			IXO 248

TABLE 2. *Continued.*

Family	Types	PSP[1]	PDIA	N	PMA	PS	SSP	SDIA	SN	SO	SODI	Dahlgren
Lepidobotryaceae	S						1	1.2	10			LPB 250
Hypseocharitaceae	S						1	1.3	15			OXL 251
Oxalidaceae	S, Pc	8	0.8	2	0.5	4	1	0.8	3			OXL 251
Averrhoaceae	Pcfs	2	1.1	2	0.4	4						OXL 251
Humiriaceae	P5cs	4	1.2	12	0.3	9						HOU 246
Erythroxylaceae	P5c	4	1.2	10	0.6							ERX 249
Rhizophoraceae	P5c	13	1.4	20	0.4							RHZ 257
Celastraceae	S						14	1.3	7			CEL 256
Elaeocarpaceae	S						5	1.4	7			ELC 258
Cyrillaceae	P5cf	2	1.6	9	0.8							CYR 297

[1] PSP = number of P-type species; PDIA = average diameter of P-type plastids; N = average number of protein crystals; PS = average number of starch grains in P-type plastids; SSP = number of S-type species; SDIA = average diameter of S-type plastids; SN = average number of starch grains in S-type plastids; SO = number of form-So plastids; SODI = average diameter of form-So plastids; Dahlgren = family acronym and position of family in Dahlgren (in press).

10 globular starch grains, often surrounded by additional tiny granules. (See also Behnke, 1985.)

Baueraceae (BAU; Fig. 6: *Bauera*). *Bauera rubioides* as representative of the monogeneric family contains very small (diameter 0.8 μm) S-type plastids with up to five small irregular starch grains.

Brunelliaceae (BNL; Fig. 6: *Brunellia*). The three species of *Brunellia* investigated contain S-type plastids. Their globular starch grains (about 10 in the average) often seem to disintegrate into tiny pieces. The plastid diameter is 1.4 μm.

Davidsoniaceae (DVS; Fig. 6: *Davidsonia*). The monotypic *Davidsonia pruriens* contains S-type plastids with about 10 strictly globular starch grains. The plastid diameter is 1.4 μm.

Eucryphiaceae (ECR; Fig. 6: *Eucryphia*). Four of the five species of this monogeneric family and one hybrid were found to contain form-Pc sieve-element plastids with two protein crystals, one with a diameter of about 0.3 μm. The sieve-element plastids of *Eucryphia* are among the tiniest recorded within the dicotyledons (average diameter of 0.6 μm). (See also Behnke, 1985.)

Crossosomataceae (CRO; Fig. 8: *Crossosoma*). Three species in two genera investigated, all with S-type plastids. The two *Crossosoma* species are identical, both in respect to their plastid diameter (1.8 μm) and the starch content (about 10 globular grains). *Forsellesia* has smaller plastids (diameter 1.0 μm) and fewer starch grains.

Rosaceae (ROS; Fig. 7: *Duchesnea*). Sixteen species in 16 genera investigated; all species with S-type plastids, but nine of them without starch (with form-So plastids). The average diameter of the plastids is 1.0 μm, with an average of 0.9 μm for the So form and of 1.2 μm for those with starch grains. The average number of grains in the starch-containing species is six.

Neuradaceae (NRD; Fig. 8: *Neurada*). *Neurada procumbens* contains form-Pcs sieve-element plastids with one rectangular protein crystal (diameter 0.4 μm) and up to five large starch grains. The diameter of the plastids is 1.5 μm. With these characteristics, there is resemblance to the sieve-element plastids of *Gunnera*. (See Behnke, 1986b.)

Anisophylleaceae (ANS; Fig. 8: *Anisophyllea*, *Combretocarpus*, *Poga*, *Polygonanthus*). Five species in four genera investigated; all have S-type plastids. With diameters of about 1.2 μm and some ten globular starch grains, the sieve-element plas-

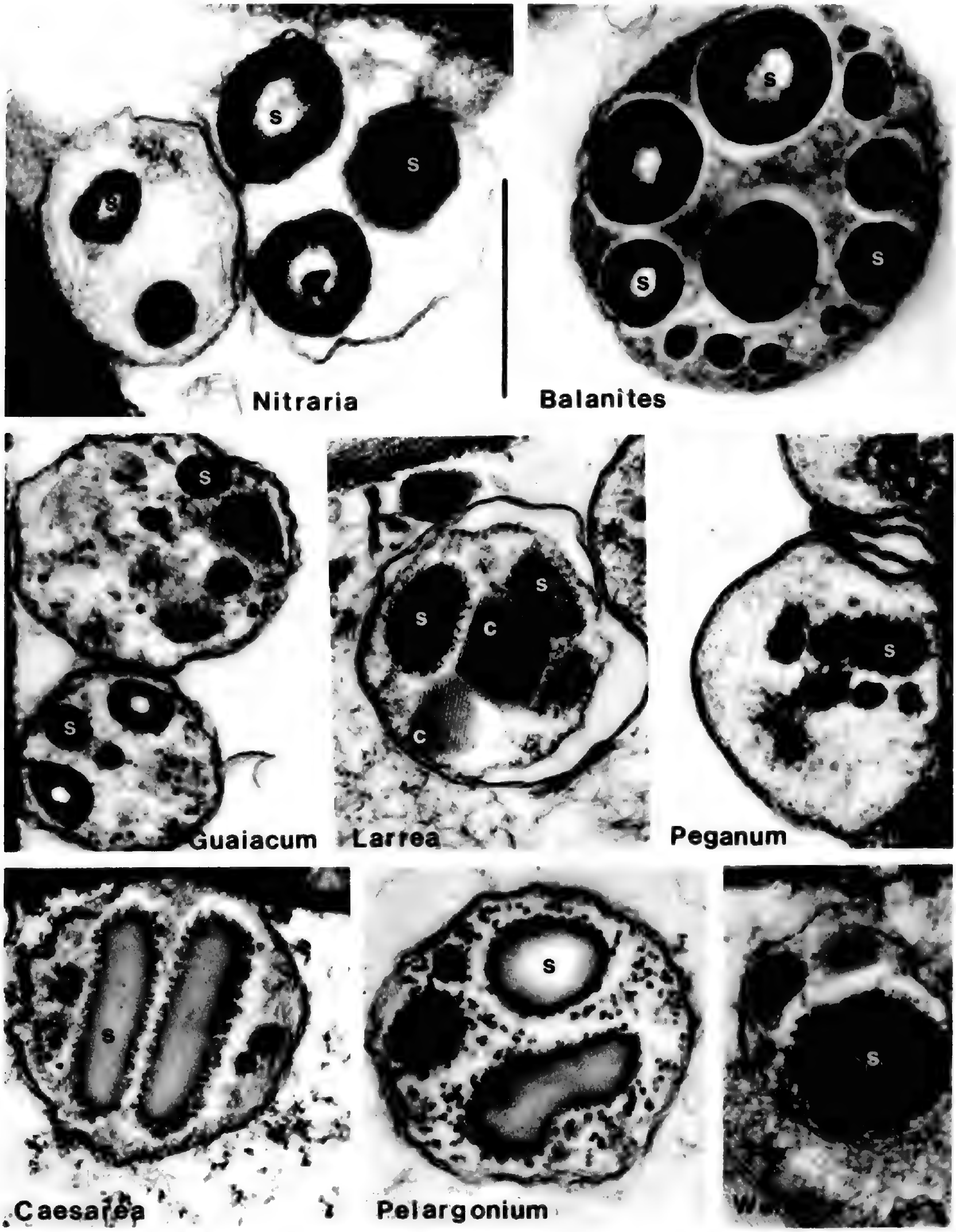


FIGURE 1. *S-type sieve-element plastids of* Nitraria retusa, Balanites aegyptiaca, Guaiacum coulteri, Peganum harmala, Caesarea albiflora, Pelargonium tetragonum, *and* Wendtia gracilis; *and P-type plastids of* Larrea divaricata. *All* ×*30,000. c = protein crystals, s = starch grains. Scale bar = 1 μm.*

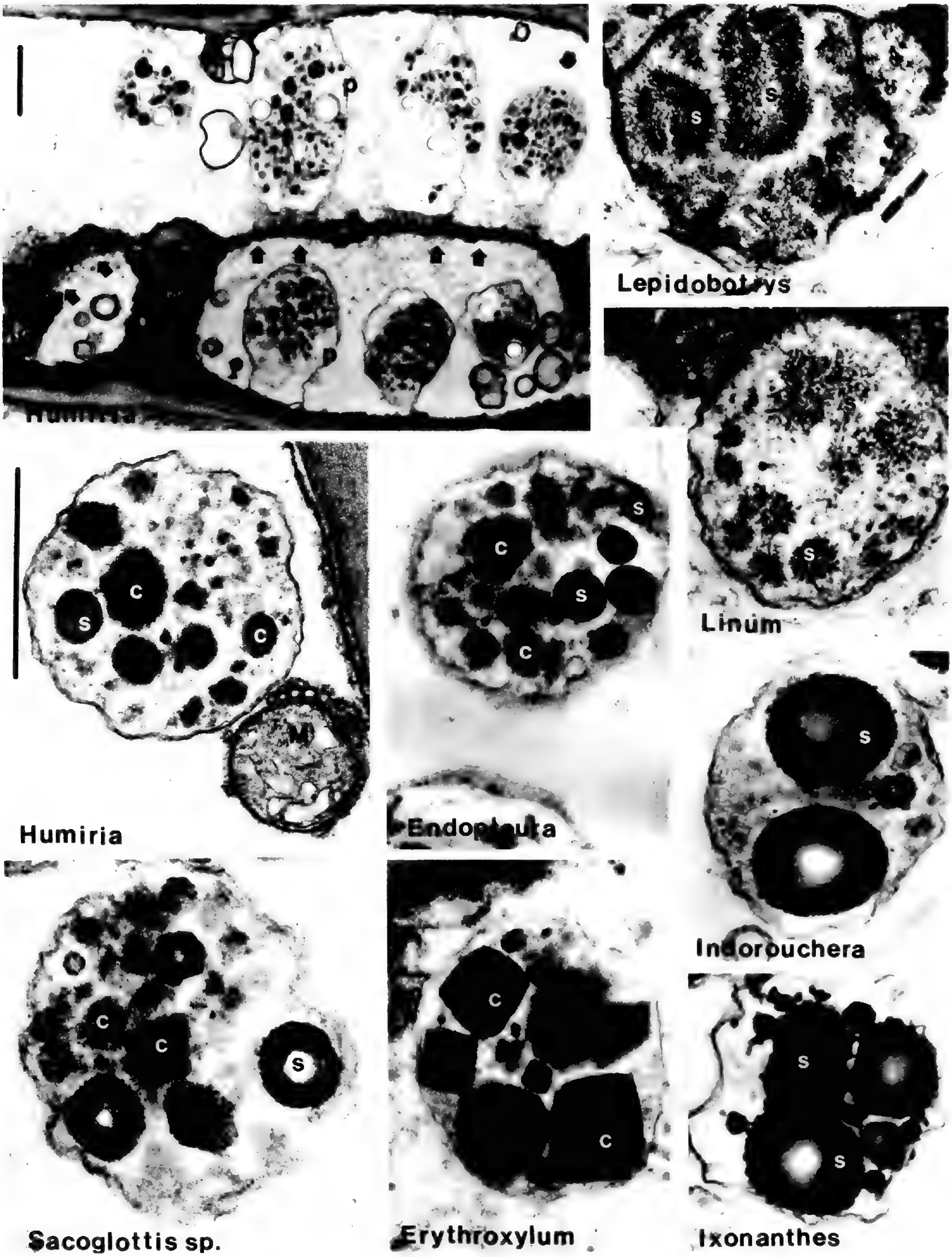


FIGURE 2. *Upper left: longitudinal section through sieve elements of* Humiria balsamifer *with compound sieve plate (arrows) and several P-type sieve-element plastids (p),* × *10,000. Other photographs: sieve-element plastids of* Lepidobotrys staudtii, Linum flavum, Indorouchera griffithiana, Ixonanthes grandiflora; *and P-type plastids of* Humiria balsamifer, Endopleura *sp.,* Sacoglottis *sp., and* Erythroxylum coca. *All* × *30,000. c = protein crystals, s = starch grains, M = mitochondrion. Scale bars = 1 μm.*

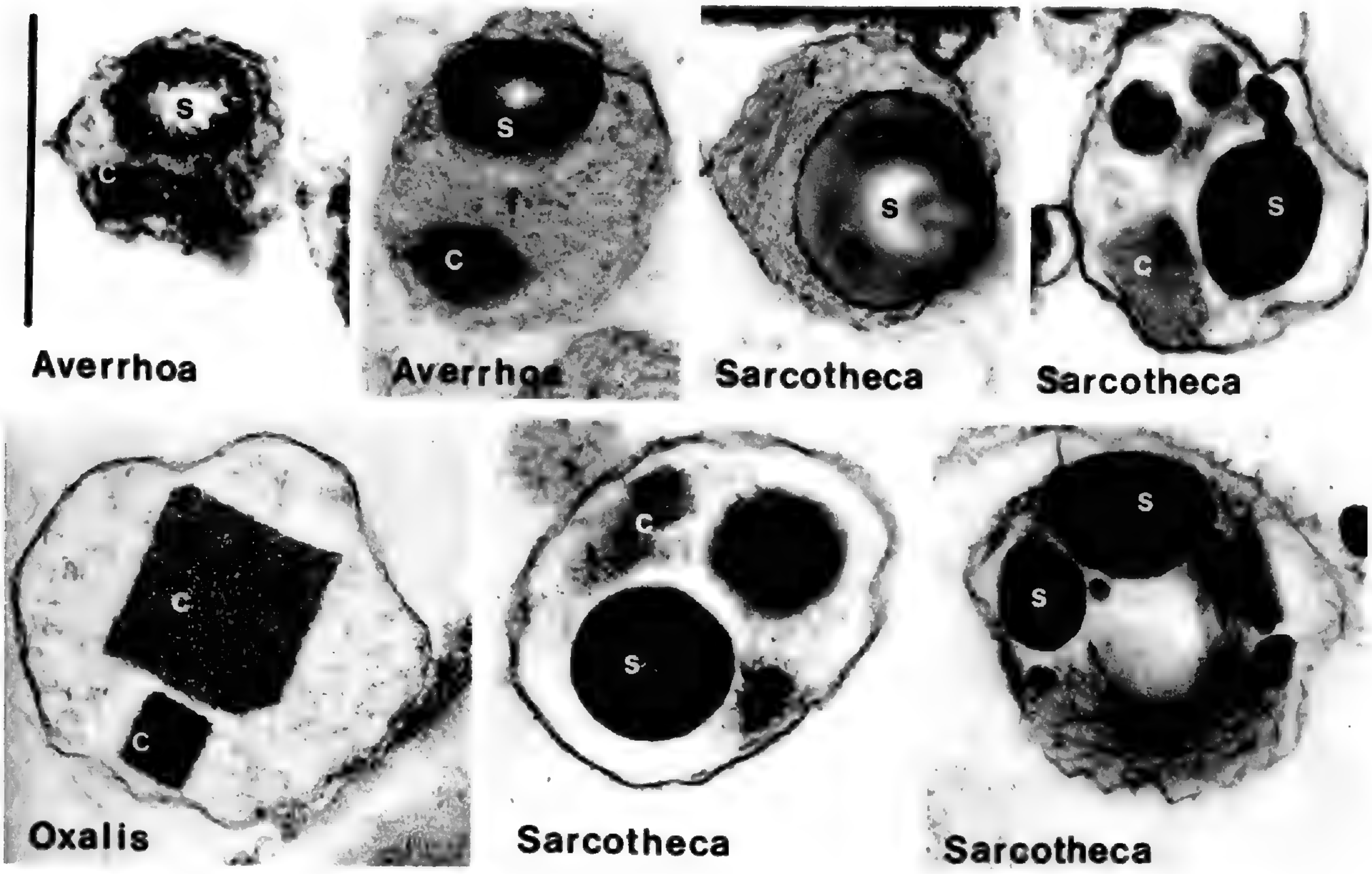


FIGURE 3. *P-type sieve-element plastids of* Averrhoa carambola, Sarcotheca diversifolia, *and* Oxalis deppei. *All ×30,000. c = protein crystals, f = protein filaments, s = starch grains. Scale bar = 1 μm.*

tids of the Anisophylleaceae are rather homogeneous and very distinct from those of the Rhizophoraceae. The difference in the plastid types supports elevation of the former tribe Anisophylleeae to family status. (See also Behnke, 1984.)

Malaceae (MAL; Fig. 7: *Amelanchier*). Thirteen species in 13 genera investigated; all have S-type plastids. The average diameter of the plastids is 1.2 μm, and the average number of starch grains eight. These data do not differ from those of the S-type Rosaceae. No form-So plastids are found in the Malaceae.

Amygdalaceae (AMY; Fig. 7: *Prunus*). Four species in two genera investigated, all with S-type plastids. The plastids in this family are smaller (average diameter 1.0 μm) than those in ROS and MAL, although their starch content is similar.

Rhabdodendraceae (RHB; Fig. 8: *Rhabdodendron*). The two species investigated of this monogeneric family contain form-Psc sieve-element plastids. Their single protein crystal is rectangular and about 0.2 μm in diameter. There are about five irregular starch grains. The average plastid diameter is 1.2 μm. (See also Behnke, 1976a.)

Saxifragaceae (SAX; Fig. 7: *Bergenia*). Six species in six genera investigated, all with S-type plastids. The average plastid diameter is 1.3 μm; there are about eight irregularly shaped starch grains in the plastids.

Penthoraceae (PTH; Fig. 7: *Penthorum*). *Penthorum sedoides* as representative of the monogeneric family contains S-type plastids with characters almost identical to those in SAX, i.e., with a diameter of 1.2 μm and containing about eight starch grains.

Vahliaceae (VHL; Fig. 7: *Vahlia*). The S-type plastids recorded for *Vahlia capensis* show the same pattern as found in SAX—diameter 1.2 μm and containing about ten starch grains.

Francoaceae (FCO; Fig. 7: *Francoa*). The investigated *Francoa sonchifolia* contains S-type plastids only slightly different from those in SAX; their diameter is 1.4 μm; the number of starch grains is about three.

Greyiaceae (GRY; Fig. 7: *Greyia*). *Greyia sutherlandii* contains S-type plastids with about five globular starch granis. The plastid diameter is 1.2 μm.

Brexiaceae (BRX; Fig. 7: *Brexia*). *Brexia madagascariensis* was shown to contain S-type plastids about 1.1 μm in diameter with about five starch grains.

Grossulariaceae (GRS; Fig. 7: *Ribes*). *Ribes* *bracteosum* contains S-type plastids with about ten globular starch grains and a diameter of 1.2 μm.

Iteaceae (ITE; Fig. 7: *Itea*). Two species in the two genera investigated; both contain S-type plastids with about five starch grains that disintegrate into tiny particles. The average plastid diameter is 1.5 μm.

Cephalotaceae (CPH; Fig. 7: *Cephalotus*). The monotypic *Cephalotus follicularis* contains S-type plastids with about five starch grains and a diameter of 1.1 μm. The starch grains are slightly disc-shaped and surrounded by tiny particles.

Crassulaceae (CRS; Fig. 7: *Cotyledon*). Three species in two genera shown to contain form-So sieve-element plastids. Their average diameter is 0.9 μm. Many more species were investigated, but although the fixation of the material was satisfactory, repeated screening failed to detect sieve-element plastids. Most likely, the So-plastids easily break down during the differentiation of the sieve elements. Similar conclusions were made from studies with *Cucurbita* species that also contain form-So plastids (Buvat, 1963; Esau & Cronshaw, 1968).

In Crassulaceae the form-So plastids sometimes contain small inclusions, which rarely show a crystalline composition. Since they are probably related to protein crystals, sieve-element plastids of CRS were also defined as Po/So. (See Behnke, 1981.)

Podostemaceae (PDS; Fig. 7: *Podostemum*). *Podostemum ceratophyllum* contains S-type plastids with about eight starch grains, often surrounded by tiny particles. The diameter of the plastids is 2.3 μm, by far the highest found among the taxa studied for this report.

DISCUSSION

The results from investigations of the sieve-element plastids reported here unambiguously support separation of the tribe Aniosphylleeae from the Rhizophoraceae and its elevation to the rank of a family. The very distinct and remarkable form-P5c sieve-element plastids of Rhizophoraceae s. str.—without any incorporation of even traces of starch—has no direct relationhip to the pure S-type (lacking any amount of protein) as found in the Anisophylleaceae. According to a model demonstrating the interrelationships between the different forms of sieve-element plastids (proposed by Behnke, 1988), at least two evolutionary steps would be necessary to change the S-type into a form-Pc sieve-element plastid. Without the presence of in-

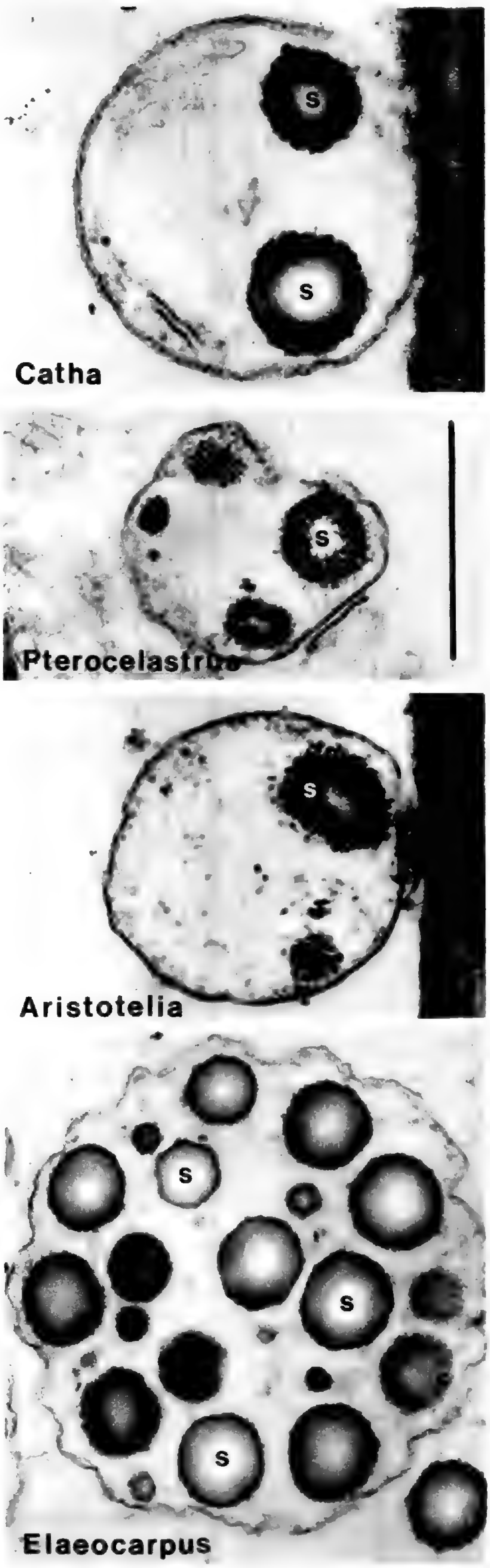


FIGURE 4. *S-type sieve-element plastids of* Catha edulis, Pterocelastrus tricuspidatus, Aristotelia chilensis, *and* Elaeocarpus ganitrus. *All ×30,000. s = starch grains. Scale bar = 1 μm.*

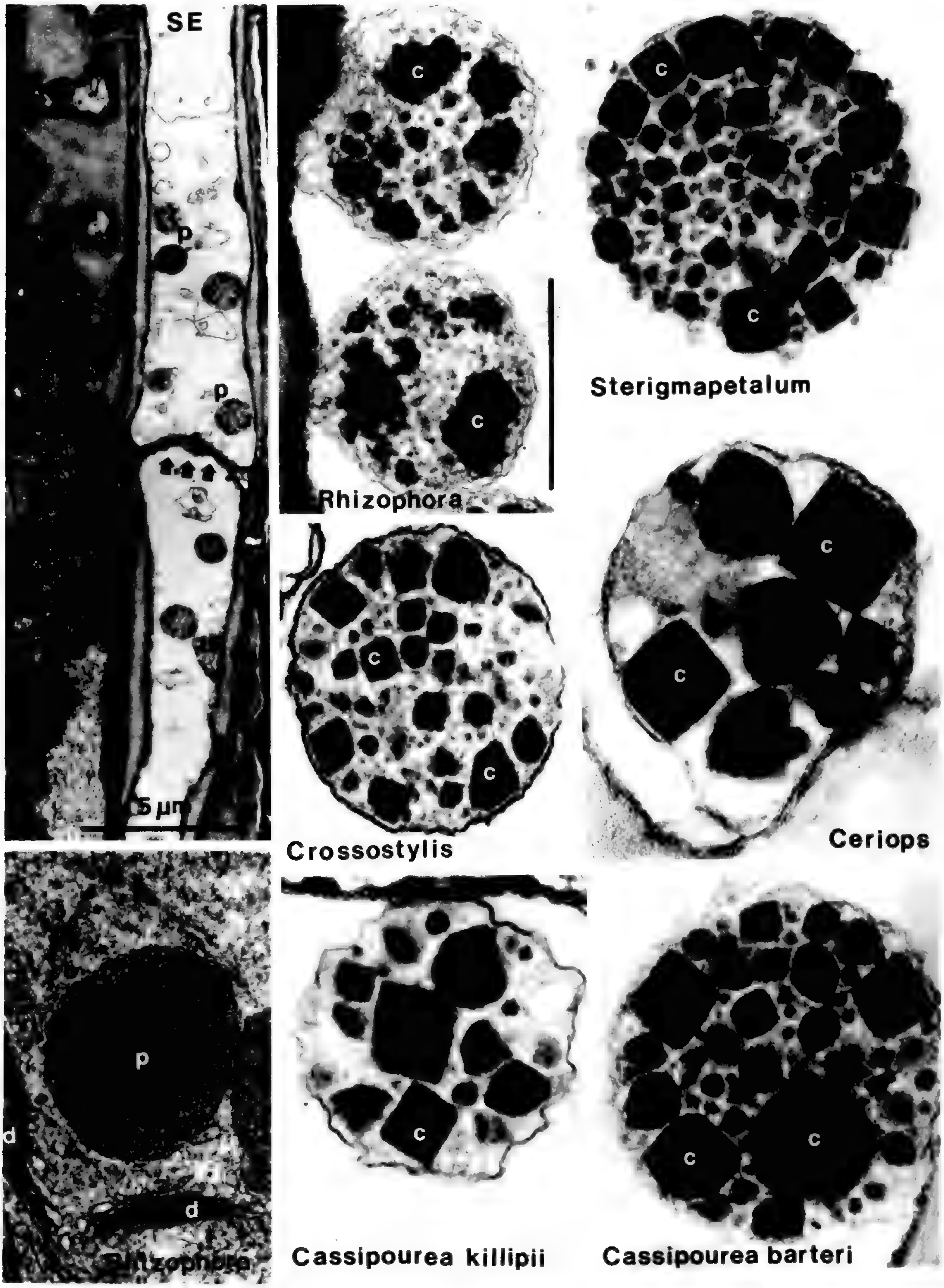


FIGURE 5. *P-type sieve-element plastids of the Rhizophoraceae. Upper left: longitudinal section through primary phloem of* Rhizophora mangle *showing two members of a sieve tube (SE) connected by a sieve plate (arrows) and containing several P-type plastids (p); ×5,000. Lower left: P-type plastids of a young sieve element of* R. mangle. *Plastid matrix filled with granular protein material (p), not yet differentiated into crystals; d = dictyosomes; ×30,000. Other photographs, from top to bottom: P-type plastids of* R. mangle, Sterigmapetalum heterodoxum, Crossostylis grandiflora, Ceriops tagal, Cassipourea killipii, *and* Cassipourea barteri. *All ×30,000. c = protein crystals. Scale bar = 1 µm.*

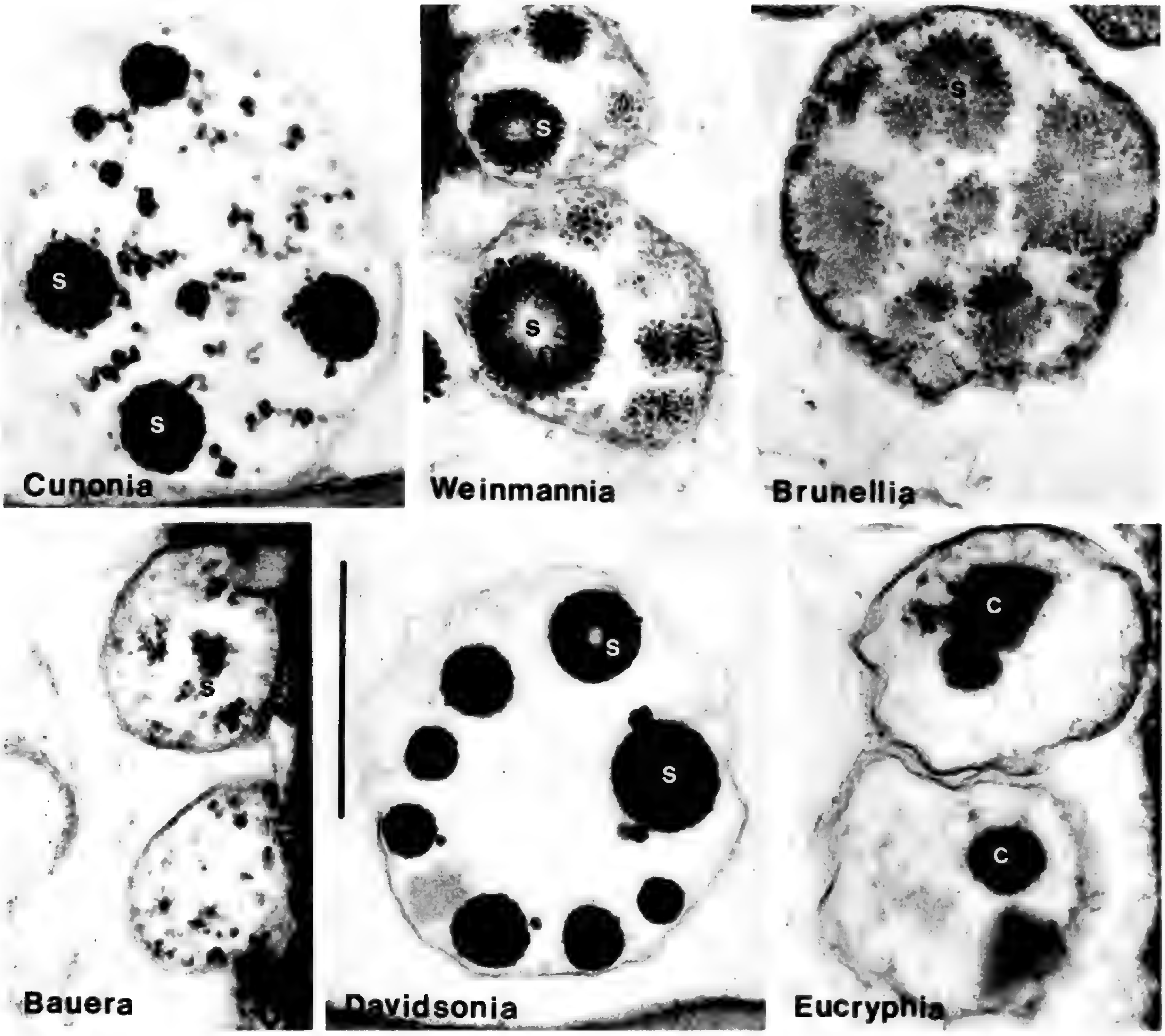


FIGURE 6. *S-type sieve-element plastids of* Cunonia capensis, Weinmannia trichosperma, Brunellia *sp.*, Bauera rubioides, Davidsonia pruriens, *and form-Pc sieve-element plastids of* Eucryphia billardieri. *All ×30,000. c = protein crystals, s = starch grains. Scale bar = 1 μm.*

termediates the coexistence of both types within one family is not very likely.

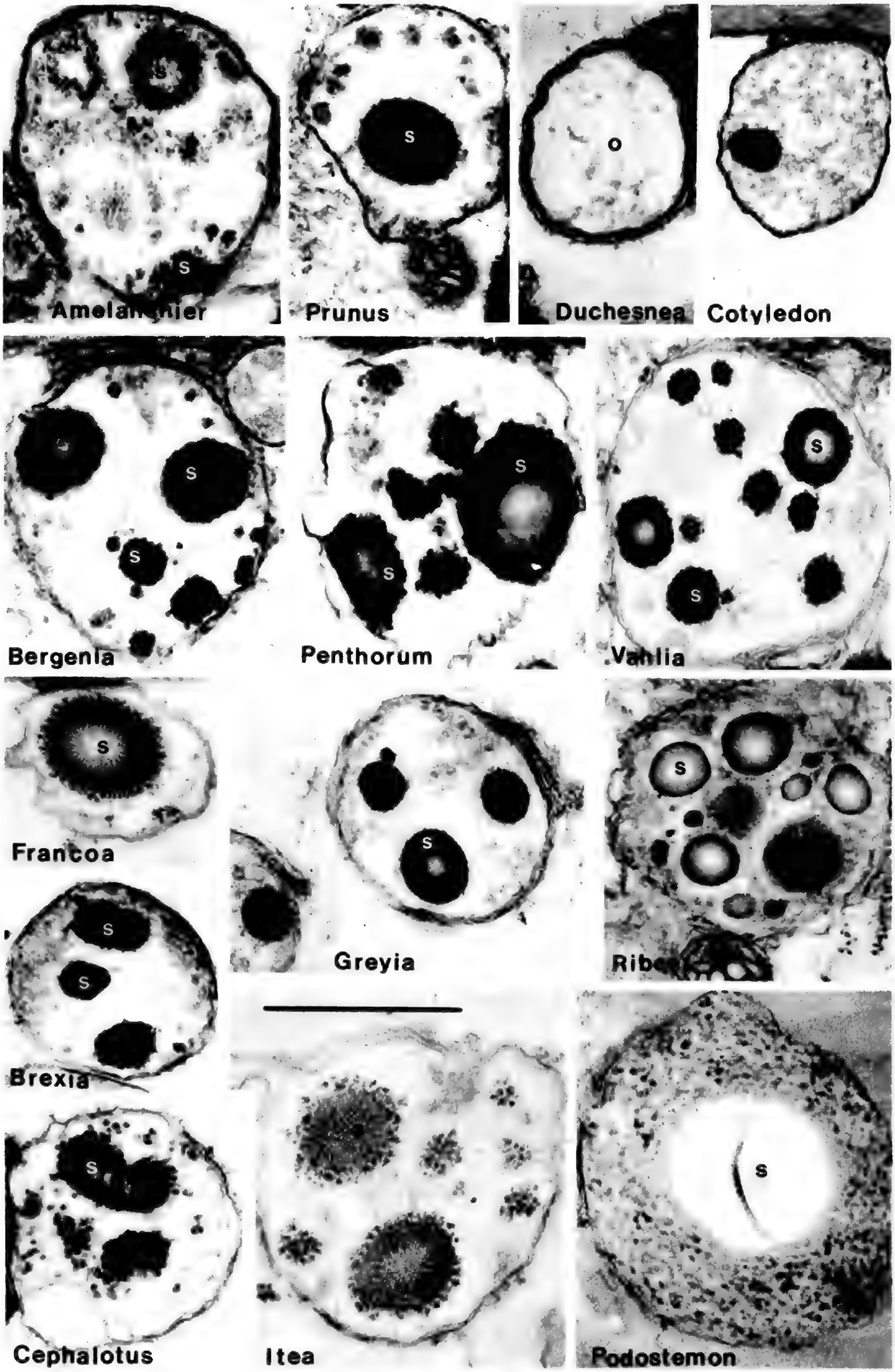
While sieve-element plastids help discriminate between Rhizophoraceae and Anisophylleaceae, determination of their affiliations to other taxa is possible only to a limited extent. Therefore, the position of the two families relative to the taxa proposed by Dahlgren (this volume) to constitute the ordinal periphery will now be discussed.

GERANIALES SENSU LATO

In his last version of the system of classification of dicotyledons, Dahlgren (in press) divided the Geraniales s.l. into two orders, the Geraniales s. str. and the Linales. The following discussion makes use of this separation.

1. (= Geraniales s. str.). Dahlgren (in press) listed Zygophyllaceae, Peganaceae, Nitrariaceae, Geraniaceae, Vivianiaceae, Ledocarpaceae, Biebersteiniaceae, Dirachmaceae, and Balanitaceae in this alliance. Among the families available for our studies (see Table 2) S-type sieve-element plastids are most common and P-type plastids are found only in *Larrea* (Zygophyllaceae). The diameter of the plastids is rather uniform, varying around 1.1 μm. Some families contain disc-shaped starch grains as a specific marker: Geraniaceae, Vivianiaceae, and Zygophyllaceae (in part).

The S-type plastids of Balanitaceae diverge more from the above pattern (see also Fig. 1). Both Cronquist (1981) and Thorne (1983) placed *Balanites* within Zygophyllaceae; Takhtajan (1987) transferred to Rutales the Zygophyllaceae and those families that, like Balanitaceae, Nitrariaceae, and Peganaceae, were split off earlier. Neither of these assignments is strongly supported by the plastid data.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Cephalotus
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2. (= Linales). Dahlgren (in press), included Linaceae, Hugoniaceae, Humiriaceae, Ctenolophonaceae, Ixonanthaceae, Erythroxylaceae, Lepidobotryaceae, and Oxalidaceae in the Linales. With four S-type families, two P-type families, and one family containing both S-type and two different forms of P-type sieve-element plastids, this suborder is very heterogeneous (fresh material from *Ctenolophon* was not available).

The S-type plastids (in Linaceae, Hugoniaceae, Ixonanthaceae, Lepidobotryaceae, Biebersteiniaceae, and Oxalidaceae) are rather small: their average diameter is about 1.1 μm. From five to ten starch grains, often disintegrating into small particles and sometimes including a very large one, are found within these plastids (see Figs. 2, 3; Behnke, 1982c); a few species differ slightly from this pattern, e.g., in *Reinwardtia* (Linaceae) (Table 1).

The two different forms of P-type plastids recorded within the Oxalidaceae are restricted to different genera: *Averrhoa* and *Sarcotheca* contain form-Pcfs, while *Oxalis* has highly specialized and very small form-Pc sieve-element plastids. Diameters and compositions of these two forms are so different (see Table 1) that it seems justified from the plastid data to support the separation of the families Averrhoaceae (see Hutchinson, 1959) and Hypseocharitaceae (see Takhtajan, 1987).

The two remaining P-type families, Humiriaceae and Erythroxylaceae, contain P-forms not directly related to those of the Oxalidaceae. The form-P5cs plastids found in Humiriaceae are similar to the P4cs plastids of Fabales (cf. Fig. 2 with Behnke & Pop, 1981, figs. 5–15) and can be regarded as transitional between S-type and form-P5c plastids of the Erythroxylaceae. The latter are extraordinarily distinct from all other sieve-element plastids, and the only other family reported to contain this form is the Rhizophoraceae.

Cronquist (1981), Thorne (1983), and Takhtajan (1987) incorporated the Oxalidaceae and Lepidobotryaceae in the Geraniales s. str. Their Geraniales (Geraniineae of Thorne, 1983) differ from each other only slightly. The patterns of the S-type plastids in the Linales and Geraniales are not sufficiently different to favor one or other treatment—and the plastids of *Lepidobotrys*, *Biophytum*, and *Hypseocharis* are intermediate.

Therefore, in the familial sequence given in Table 2, which is arranged according to the data obtained with the sieve-element plastids, the order Geraniales s.l. is maintained.

CELASTRALES

Celastraceae and Elaeocarpaceae contain S-type sieve-element plastids to some extent alike in pattern but not very specialized. The families are not very uniform in their sieve-element plastids (e.g., see Fig. 4: *Aristotelia* and *Elaeocarpus*).

Rhizophoraceae contain form-P5c plastids, a highly specialized pattern that is found throughout all genera investigated. In addition, variation in the diameter of the plastids is very small. There seem to be no common sieve-element plastid characters between the Rhizophoraceae and the other two families of this order; the closest similarities are with plastids of Erythroxylaceae.

Thorne (1983) placed Rhizophoraceae in his Cornales; Cronquist (1981) and Takhtajan (1987) regarded their order Rhizophorales as a close ally of the Myrtales. Dahlgren in his last version (in press) put Rhizophoraceae together with Elaeocarpaceae into his order Rhizophorales and gave it a position after Geraniales/Linales and his newly defined Celastrales (including S-type families only).

Sieve-element plastid data suggest a close association of Rhizophoraceae with Humiriaceae and Erythroxylaceae (see Table 2).

CUNONIALES

The S-type sieve-element plastids present in four of the five families of this order are heterogeneous. Plastid diameter and starch content range from large with ten grains to very small with little starch (see Table 1). The sequence given in Table 2 suggests an evolution from the large unspecialized to the small specialized plastid and enables a connection to the only P-type family (Eucryphiaceae).

Exactly the same five families constitute Takhtajan's (1987) Cunoniales. Thorne (1983) added Staphyleaceae and Corynocarpaceae to his suborder Cunoniinae, while Cronquist distributed them among his Rosales.

SAXIFRAGALES

All families within this order contain S-type sieve-element plastids, of which Crassulaceae is special-

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FIGURE 7. *S-type sieve-element plastids of* Amelanchier canadensis, Prunus padus, Duchesnea indica *(form-So)*, Cotyledon orbiculatum *(form-So)*, Bergenia purpurascens, Penthorum sedoides, Vahlia capensis, Francoa sonchifolia, Greyia sutherlandii, Ribes bracteosum, Brexia madagascariensis, Cephalotus follicularis, Itea ilicifolia, *and* Podostemum ceratophyllum. *All ×30,000. s = starch grains, o = form-So plastid. Scale bar = 1 μm.*

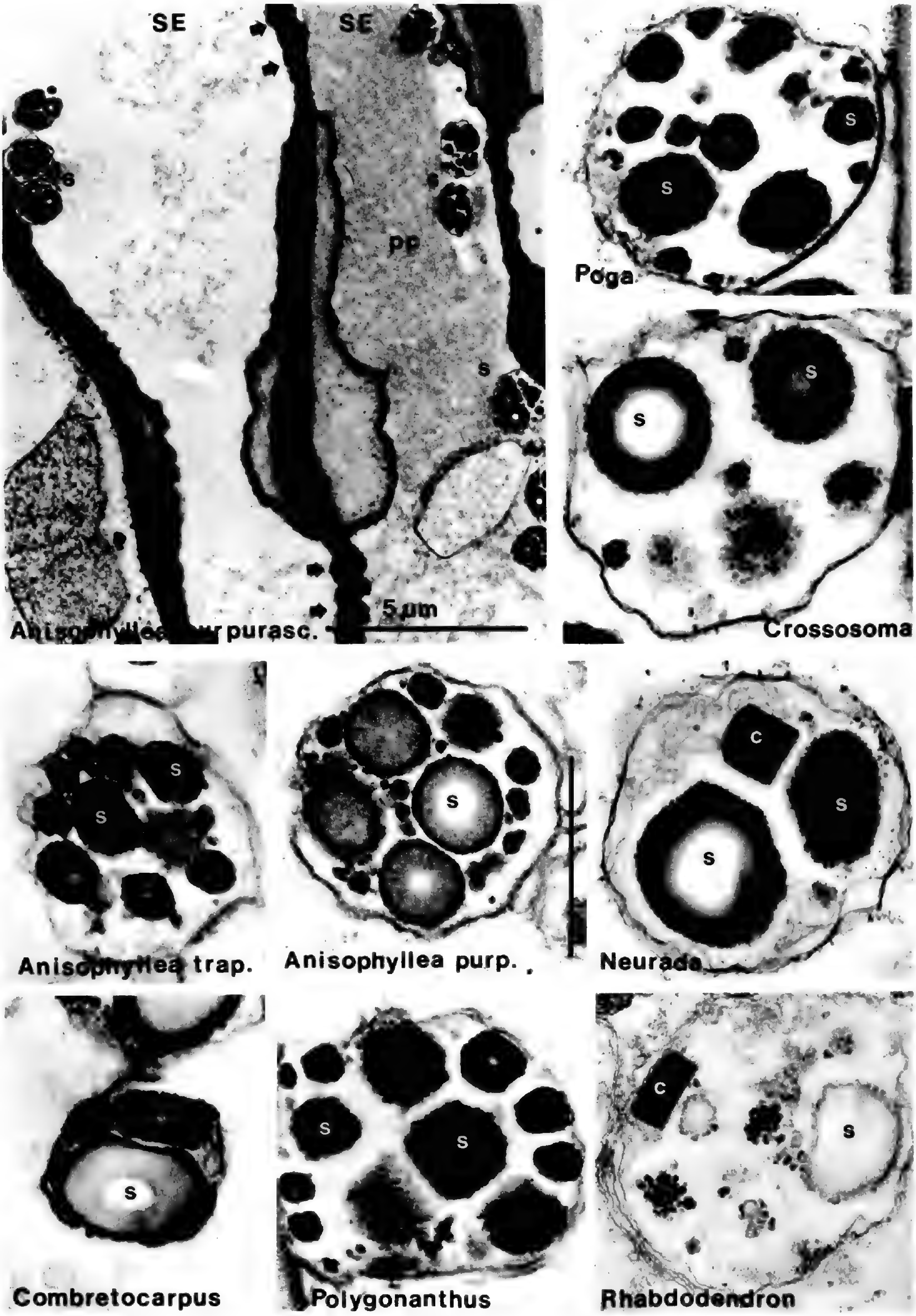

FIGURE 8. *Upper left: longitudinal section through sieve elements (SE) of* Anisophyllea purpurascens *connected by lateral sieve areas (arrows) and containing many S-type plastids (s); ×6,000; pp = phloem protein. Other*

ized by form-So plastids. Sizes and starch content of the S-type plastids are rather homogeneous. The only exception is *Podostemum*, which has very large plastids (Fig. 7, Table 1) and does not fit into this order, nor in the entire alliance. Cronquist (1981) and Takhtajan (1987) separated the Podostemaceae in its own order. Thorne (1983) placed this family within his Saxifragineae. Until further evidence from other characters emerges, we prefer the treatment as a separate order, somewhat peripheral to the Saxifragales/Rosales.

ROSALES

S-type sieve-element plastids are recorded except for the two families Neuradaceae and Rhabdodendraceae. The pattern of the S-type plastids (diameter and starch content) is similar to that of the Saxifragales. One family includes form-So plastids: the Rosaceae. The presence of these So plastids in at least some genera (see Table 1 for details, e.g., smaller diameter) makes the Rosaceae s. str. distinct from the Malaceae and Amygdalaceae. The plastid pattern of the latter family is not different from that of the S-type genera in the Rosaceae.

Sieve-element plastids of the four genera tested from the Anisophylleaceae display a rather uniform pattern: while their sizes conform with that of both Saxifragales and Rosales, the amount of starch within a plastid is much higher than in the other taxa (cf. Figs. 7, 8). Therefore, on account of the plastid data, an association of Anisophylleaceae with either Saxifragales or Rosales is not excluded, but a positive decision cannot be made.

The remaining two P-type families of Rosales both contain Psc sieve-element plastids, but of different pattern.

Rhabdodendraceae contain in their sieve-element plastids a tiny rectangular protein crystal and up to five irregular starch grains, a pattern repeatedly found within the Magnoliiflorae (see Behnke, 1988).

Neurada is more distinct because of its larger crystal (diameter 0.4 μm) and higher starch content. Its sieve-element plastids come very close to those of the Gunneraceae (see Behnke, 1986b).

CONCLUSIONS DRAWN FROM THE PLASTID DATA

Given the periphery of families and orders around the Rhizophoraceae—including a few additional ones discussed during the preparation of this Rhizophoraceae symposium—and the distribution of types and forms of sieve-element plastids, the following annotations to the relationships between the different taxa can be made.

The ordinal placement of the Aniosphylleaceae. This is still uncertain as far as sieve-element plastids are concerned. Pattern similarities exist to S-type plastids in the Saxifragales–Rosales groups (not to the Cunoniales), but affinities to other taxa are not ruled out.

If a closer relation to the Rhizophoraceae is still considered, the diameter of the plastids (average of 1.3 μm in both families) would be the only supporting plastid data; otherwise their contents, as discussed, differ by at least two evolutionary steps.

The ordinal placement of the Rhizophoraceae. The identical sieve-element plastids in Rhizophoraceae and Erythroxylaceae, together with the fact that within the dicotyledons the form-P5c is exclusive to these two families, strongly favors their close alliance (see also the ordinal restriction of the subtype-P3 sieve-element plastids, Behnke, 1976b). Related plastid forms are found in the Cyrillaceae (P5cf) and the Humiriaceae (P5cs).

Sieve-element plastids of the Cyrillaceae are distinguished from those of the Rhizophoraceae by the presence of protein filaments in addition to protein crystals (Behnke, 1982a) and a larger diameter (average of 1.6 μm). Nevertheless, their similarity is reason enough to propose at least distant relationships. Traditionally, Cyrillaceae have been placed into Celastrales, Theales, and (recently more often) Ericales (cf. Behnke, 1982a). In view of Dahlgren's (this volume) proposal to associate closely the Rhizophoraceae with the Celastraceae, the inclusion of the Cyrillaceae within the Celastrales (see e.g., Melchior, 1964) may be worth reconsidering.

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*photographs show S-type sieve-element plastids in the five investigated species of Anisophylleaceae (*A. trapezoidales, A. purpurascens, Combretocarpus motleyi, Polygonanthus amazonicus, Poga oleosa*) and of* Crossosoma bigelovii, *as well as form-Pc plastids of* Neurada procumbens *and* Rhabdodendron macrophyllum. *All ×30,000. c = protein crystals, s = starch grains. Scale bar = 1 μm.*

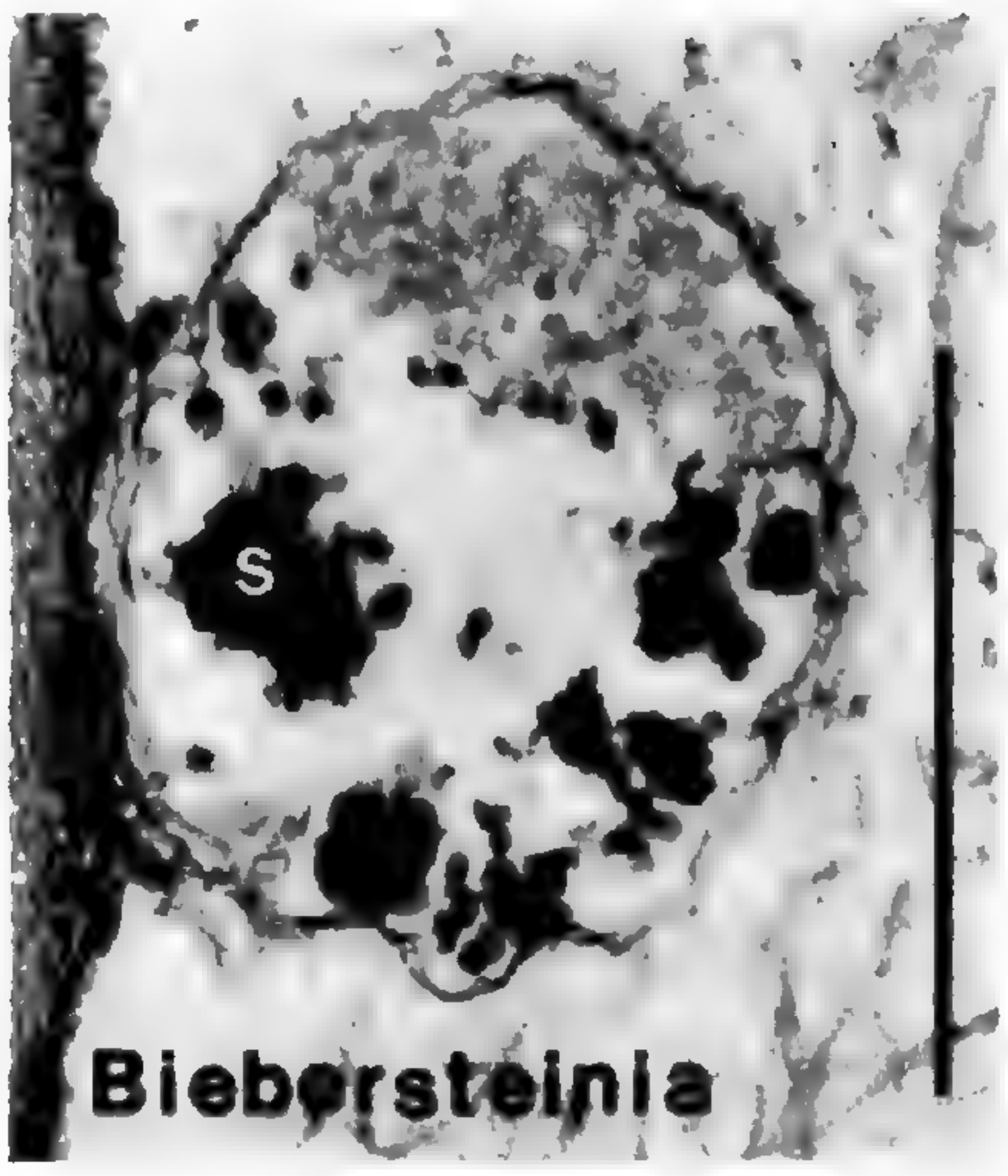

FIGURE 9. *S-type sieve-element plastid of* Biebersteinia multifida. *×30,000. s = starch grain. Scale bar = 1 μm.*

The first and only record for form-P5cs plastids in the Humiriaceae links the form-P5c plastids of the Rhizophoraceae and Erythroxylaceae to the S-type families in the Geraniales s.l. It has further potential in bridging the entire subtype-P5 to the subtype-P4 of the Fabales, thus making the subtype-P4/P5 a characteristic pattern of sieve-element plastids restricted to the Rutinae (sensu Dahlgren, this volume).

The form-P5cs plastids found in the Humiriaceae connect the form-P5c to the S-type plastids in the Geraniales: their number of protein crystals (more than ten on average) is the second highest recorded in the dicotyledons (after those in RHZ and ERY), their number of starch grains and average plastid diameter are compatible with the S-type plastids in the Geraniales. The shape of the protein crystals is not as distinctly rectangular as in the form-P5c plastids (cf. Figs. 2, 5), but even within *Rhizophora* the crystals have no sharp edges (Fig. 5).

The P5cs pattern is very close to that of the form-P4cs plastids present in the Fabales: both contain five or more irregular protein crystals in addition to a variable number of starch grains. It is suggested that from a common ancestor with the plastid inheritance several parallel lines lead to Fabales, Geraniales, Rhizophorales, and probably Celastrales.

However, data from sieve-element plastids do not contribute to the placement of Celastrales unless the inclusion of the Cyrillaceae (cf. Hutchinson, 1959; Melchior, 1964) is followed.

Dahlgren transferred Elaeocarpaceae from Malvales to either the newly defined Celastrales (Dahlgren, this volume: together with RHZ and CEL) or to his Rhizophorales (Dahlgren, in press: as the only other family of this order in addition to the RHZ). The data from sieve-element plastids support neither of the two arrangements. However, another phloem character corroborates the exclusion of Elaeocarpaceae from the Malvales: Bombacaceae, Malvaceae, Sterculiaceae, and Tiliaceae have within their sieve elements so-called persistent, crystalline p-protein bodies, which are absent from the Elaeocarpaceae. The persistent p-protein bodies are a typical character of the Malvanae/Violanae and a few other taxa (see Behnke, 1981).

In summary, data from sieve-element plastids suggest the following parallel sequences of families (those not yet investigated are in parentheses; cf. Table 2):

1. Balanitaceae, Zygophyllaceae, Nitrariaceae, Peganaceae, Geraniaceae, Vivianiaceae, Ledocarpaceae, (Biebersteiniaceae), (Dirachmaceae)
2. Linaceae, Hugoniaceae, (Ctenolophonaceae), Ixonanthaceae
   2.1 Lepidobotryaceae, Hypseocharitaceae, Oxalidaceae, Averrhoaceae
   2.2 Humiriaceae, Erythroxylaceae
      2.2.1 Rhizophoraceae
3. Celastraceae, Elaeocarpaceae
4. Cyrillaceae

Families excluded. On the basis of the sieve-element characters two families discussed during the preparation for this symposium as putative allies are to be definitely excluded: the Flacourtiaceae and Podostemaceae.

The Flacourtiaceae contain S-type sieve-element plastids, but their persistent p-protein bodies (cf. Behnke, 1981) place them in the Violales.

Podostemaceae differ from the discussed orders by their large S-type plastids and the pattern of starch grains.

NOTE ADDED IN PROOF

Fresh rhizomes of *Biebersteinia multifida* DC. kindly have been made available by E. Gabrielian (Erevan, USSR). The following paragraph should be read after Ledocarpaceae (on page 1389):

Biebersteiniaceae (BBS; Fig. 9) *Biebersteinia multifida* contains S-type plastids with one or few globular starch grains, often disintegrated into tiny particles. The plastid diameter is 1.2 μm.

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EMBRYOLOGY OF TRIBE GYNOTROCHEAE (RHIZOPHORACEAE) AND ITS DEVELOPMENTAL AND SYSTEMATIC IMPLICATIONS[1]

Adrian M. Juncosa[2] *and Hiroshi Tobe*[3]

ABSTRACT

*A complete embryological description of the four genera traditionally circumscribed as tribe Gynotrocheae (*Carallia, Crossostylis, Gynotroches, *and* Pellacalyx*) is presented. Most of the character states are consistent with those known for other genera of the family that have been studied, but several are not. In* Crossostylis, Gynotroches, *and* Pellacalyx, *microsporogenesis occurs by both simultaneous and successive meiotic cytokinesis, even in a single flower. This is apparently previously unreported in any angiosperm and suggests that meiosis in the anther may be under tapetal, not sporocytic, control. Dioecy in* Gynotroches *results from late-developmental phenomena: in female flowers sporopollenin pollen walls fail to form, and in male flowers late ovule development and megagametogenesis are abnormal. Embryological and other morphological data indicate that Gynotrocheae are paraphyletic and could be narrowed to only* Gynotroches *and* Pellacalyx, *which are distinct from all other Rhizophoraceae in having tenuinucellate ovules and outer integuments that remain biseriate throughout ovule and seed development.* Crossostylis *is intermediate between these two genera and the ancestral tribe Macarisieae, and* Carallia *is probably intermediate between all other inland genera and the mangrove tribe (Rhizophoreae).*

The family Rhizophoraceae is generally accepted as comprising three tribes: Macarisieae (six or seven inland genera), Gynotrocheae (four inland genera), and Rhizophoreae (four mangrove genera). The four genera previously included as tribe Anisophylleeae or as a subfamily are now segregated as an unrelated family, a disposition originally suggested by Ridley (1922) and now supported by many lines of evidence (Behnke, 1982; Tobe & Raven, 1987a; Juncosa & Tomlinson, 1987, this volume).

Embryological evidence (Tobe & Raven, 1987a) and some aspects of vegetative anatomy (Juncosa & Tomlinson, this volume) suggest that the Anisophylleaceae may be related to Myrtales, but the infrafamilial systematics and extrafamilial phylogenetic relationships of the Rhizophoraceae remain uncertain. Much of this uncertainty results from the great variability in many systematic characters in this family and the paucity of information about certain key genera. While many later-developmental and sporophytic characters exhibit considerable adaptive radiation, embryological characters are usually more conservative. Furthermore, because embryological characters are inherently developmental, homologies are more reliable and the polarity of the characters can often be determined, lending additional weight to a phylogenetic hypothesis.

The Gynotrocheae are of pivotal systematic importance within the context of the family for several reasons. There is greater variability in conventional taxonomic characters within this tribe than in the other two: phyllotaxy, wood, flowers, fruits, and seeds all afford good examples (Schimper, 1893; van Vliet, 1976; Juncosa & Tomlinson, this volume). It has even been suggested that *Pellacalyx* could be excluded from the family (Marco, 1935; Dahlgren, pers. comm.). In another direction, the floral morphology of the Rhizophoreae is very sim-

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TABLE 1. *Collection localities and voucher information for species studied.*

Species	Locality	Collection Number	Location of Voucher
Carallia borneensis Oliver	Andulau Forest Reserve, Brunei	*Juncosa 464*	(lost)
Crossostylis grandiflora Brongn. & Gris.	Mt. Panie, New Caledonia	*Juncosa 388*	NOUM, DUKE
	Yate, New Caledonia	*Juncosa 413*	NOUM, DUKE
	New Caledonia	*G. McPherson 1617*	MO
Gynotroches axillaris Blume[1]	Padawan, Sarawak, Malaysia	*Juncosa 481, 482*	SAR, DUKE
	Kuching vicinity, Sarawak, Malaysia	*Juncosa 440, 442*	SAR, DUKE
	Maxwell Hill, Perak, Malaysia	*B. C. Stone 15397*	KLU
Pellacalyx cristatus Hemsl.	Kampong Tepoi vicinity, Sarawak	*Juncosa 488*	SAR, DUKE
P. lobbii (Hook. f.) Schimp.	Andulau Forest Reserve, Brunei	*Juncosa 465*	(lost)
P. cf. *saccardianus* Scort.	Maxwell Hill, Perak, Malaysia	*B. C. Stone 15396*	KLU
P. symphiodiscus Stapf	Kuching vicinity, Sarawak, Malaysia	*Juncosa 486*	SAR, DUKE

[1] Material from the two Sarawak localities represented two distinct species (see text for details).

ilar to that of *Carallia* (Juncosa & Tomlinson, 1987; Juncosa, pers. obs.); so clues to the evolution of vivipary might be found indirectly among the embryological characteristics of this and other genera of the Gynotrocheae. Although data are not yet available for all genera of Macarisieae, they comprise a relatively homogeneous tribe in other respects (Schimper, 1893; Hutchinson & Dalziel, 1954; Floret, 1976; van Vliet, 1976; Juncosa & Tomlinson, this volume), and comprehensive embryological data for *Cassipourea* and *Sterigmapetalum* are available (Juncosa, 1984a; Tobe & Raven, 1987b). Fragmentary data are available for two genera of Gynotrocheae (Mauritzon, 1939), and seed coat anatomy of all four genera is now well known (Corner, 1976; Tobe & Raven, this volume).

MATERIALS AND METHODS

Species studied and collection data are listed in Table 1. Identification and nomenclature follow Ding Hou (1958). In this treatment, *Gynotroches* is considered to consist of one rather variable species, but material used for this study appeared to represent two very distinct ecotypes or species; differences are noted below. Adequate embryological material was available for only one species in each of the genera *Carallia* (eight species) and *Crossostylis* (six species). Only four of the nine species of *Pellacalyx* were examined, and although complete series of all developmental stages were not available for all four, the data obtained suggest that the genus is probably embryologically uniform.

Material was generally fixed in the field in formalin-acetic acid-60% ethanol (10:5:85 or 5:5:90), but some Brunei collections were fixed in whiskey and formalin (about 10:1). Most material was dehydrated in a tertiary butanol/ethanol series and embedded in paraffin, then sectioned at 8–10 μm and stained with either Heidenhain's iron hematoxylin or safranin followed by fast green (Johansen, 1940). Other material was dehydrated in ethanol, embedded in Polysciences JB-4 resin, sectioned with glass knives at 4–6 μm, and stained with iron hematoxylin.

OBSERVATIONS

Embryological character states are summarized in Tables 2 and 3. Detailed descriptions follow, including notes of occasional variations in character states and some features not always included in embryological summaries.

Carallia borneensis Oliver

Anthers of this species are medifixed, and the connective and the tips of the two halves of the anther are slightly prolonged. The anther consists of four microsporangia. The sporangial wall development is of the "basic" type, that is, having two middle layers, one sharing a common origin with the endothecium; the other, with the tapetum (Fig. 1). Neither the epidermis nor the middle layers persist to anthesis. The endothecial cell walls have very few thick bars of secondary wall (so-called "fibrous" thickenings; Fig. 2). The tapetum is glandular; its cells have two nuclei. Cytokinesis in microspore mother cells is simultaneous, producing tetrahedral tetrads. Anther dehiscence is introrse and occurs by longitudinal slits.

TABLE 2. *Anther and pollen characteristics of tribe Gynotrocheae.*

	Carallia	*Crossostylis*	*Gynotroches*	*Pellacalyx*
Number of microsporangia	4	4	4	4
Anther wall development	basic	basic	monocotyledonous	basic
Epidermis at anthesis	degenerate	persistent	degenerate	persistent, collapsed
Middle layers	degenerate	degenerate	degenerate	degenerate
Endothecial wall thickenings	present	present	present	present
Tapetum	glandular	glandular	glandular	glandular
Tapetal cell nuclei	2	2	2	2
Meiotic cytokinesis	simultaneous	simultaneous or successive	simultaneous or successive	simultaneous or successive
Pollen tetrads	tetrahedral	tetrahedral or decussate	tetrahedral or decussate	tetrahedral or decussate
Pollen nuclei	2	2	2	2

Ovules of *C. borneensis* are bitegmic, and even at early stages of development each integument consists of more than two cell layers (Fig. 3). Early cell divisions in the integuments are irregularly oriented, as would be expected in a multiseriate, parenchymatous structure; by contrast, the anticlinal divisions in the biseriate integuments of other inland Rhizophoraceae are usually uniformly perpendicular to the surface, as would be expected in a structure consisting of two protodermal layers. The outer integument of *C. borneensis* thickens to 7–15 cell layers by the time of anthesis; the inner integument, to about 10 cell layers (Fig. 4). Both integuments contribute to forming the micropyle, and the endostome and exostome are not aligned. The outer integument is vascularized, but the inner integument is not (Fig. 5). The outer epidermis of the inner integument, which forms the prominent exotegmen in other genera, is distinctly differentiated, and a pronounced endothelium is formed as megagametogenesis begins; its cells are densely staining and palisadelike by the two-celled stage of gametogenesis (Fig. 4). At anthesis, the endothelium becomes tanninized and thick-walled.

The archesporial cell divides once periclinally, and the parietal derivative usually divides once anticlinally (Fig. 6). The ovule is thus crassinucellate. A cell wall is formed after meiosis I, and a linear, T-shaped, or irregular tetrad of megaspores is formed. The gametophyte develops from the chalazal megaspore. The observation of two-, four-, and eight-nucleate stages confirmed that gametogenesis occurs according to the *Polygonum*-type pattern. Three antipodal cells are formed, but their nuclei appear condensed or degenerate at anthesis. The mature synergids are pyriform and stain very densely. The polar nuclei are closely appressed but do not fuse to form a secondary nucleus before fertilization. Most of the nucellus, particularly its micropylar half, degenerates during megagametogenesis (Fig. 4).

Fertilization is porogamous, and endosperm formation is initially free-nuclear. Endosperm development and expansion of the fertilized ovule both proceed for some time before embryogenesis begins. The first division of the zygote was roughly transverse in all specimens studied (over 100 seeds in early developmental stages). However, the orientation of the second division was variable. In most cases it was parallel to the axis of the proembryos ("vertical" or longitudinal, although the axis of the proembryo was not usually parallel to the long axis of the ovule), but in many other specimens it was oblique (Figs. 7, 8). Although the basal cell subsequently divides transversely and these derivatives divide both transversely and longitudinally, none of the resultant cells contribute to the embryo proper. Thus, allowing for a slight relaxation of the definition of onagrad-type embryogenesis to accommodate the variability in orientation of the plane of division of the terminal cell, embryogenesis in *C. borneensis* can be described as being fundamentally of this type. During the early globular stage (proembryo consisting of up to about 20 cells in median longitudinal section), both the basal cell of the suspensor and the cells closest to the embryo proper divide longitudinally, producing a mostly multiseriate suspensor, sometimes with a uniseriate section in the middle (Fig. 8).

The mature embryo consists of two laminar cotyledons and a straight hypocotyl, this making up about two-thirds of the length of the embryo. The axial vascular cylinder is medullated throughout its length. The embryo is green and enveloped by abundant endosperm. The seed coat is mostly testal and 20–50 cell layers thick; its surface is bullate

TABLE 3. *Ovule and seed characteristics of tribe Gynotrocheae. See text for additional details.*

	Carallia	*Crossostylis*	*Gynotroches*	*Pellacalyx*
Inner integument cell layers at inception/anthesis	2–3/many[1]	2/20	2/5–6	2/8–10
Outer integument cell layers at inception/anthesis	3 or more/many[1]	2–3/4–5[2]	2/2	2/2
Integument vascularization	outer only[3]	none	none	none
Micropyle	diplostomic	diplostomic	diplostomic	diplostomic
Endothelium	present	present	present	present
Archesporial cell(s)	several	several	1	1
Megasporangium	crassinucellate	crassinucellate	tenuinucellate	tenuinucellate
Megaspore tetrad	T-shaped or linear	linear	T-shaped	linear
Megagametogenesis	chalazal-monosporic	chalazal-monosporic	chalazal-monosporic	chalazal-monosporic
Antipodals at anthesis	condensed	condensed	persistent	persistent
Synergid shape	pyriform	pyriform	pyriform	pyriform
Secondary nucleus	not formed	not formed	not formed	not formed
Endosperm development	free-nuclear	—	free-nuclear	free-nuclear
Endosperm transfer cells	absent	—	absent	absent
Embryogenesis	variable	—	variable	variable
Exotegmen	unsclerified	—	sclerified	sclerified
Cotyledons	2, foliaceous	—	2, foliaceous	2, foliaceous

[1] Integuments of species other than *C. borneensis* are thinner at maturity and possibly also at inception.
[2] Strictly biseriate outer integument was never observed, possibly because periclinal divisions begin very early.
[3] Presently known only in *C. borneensis*; not found in *C. brachiata* or *C. eugenioidea*.

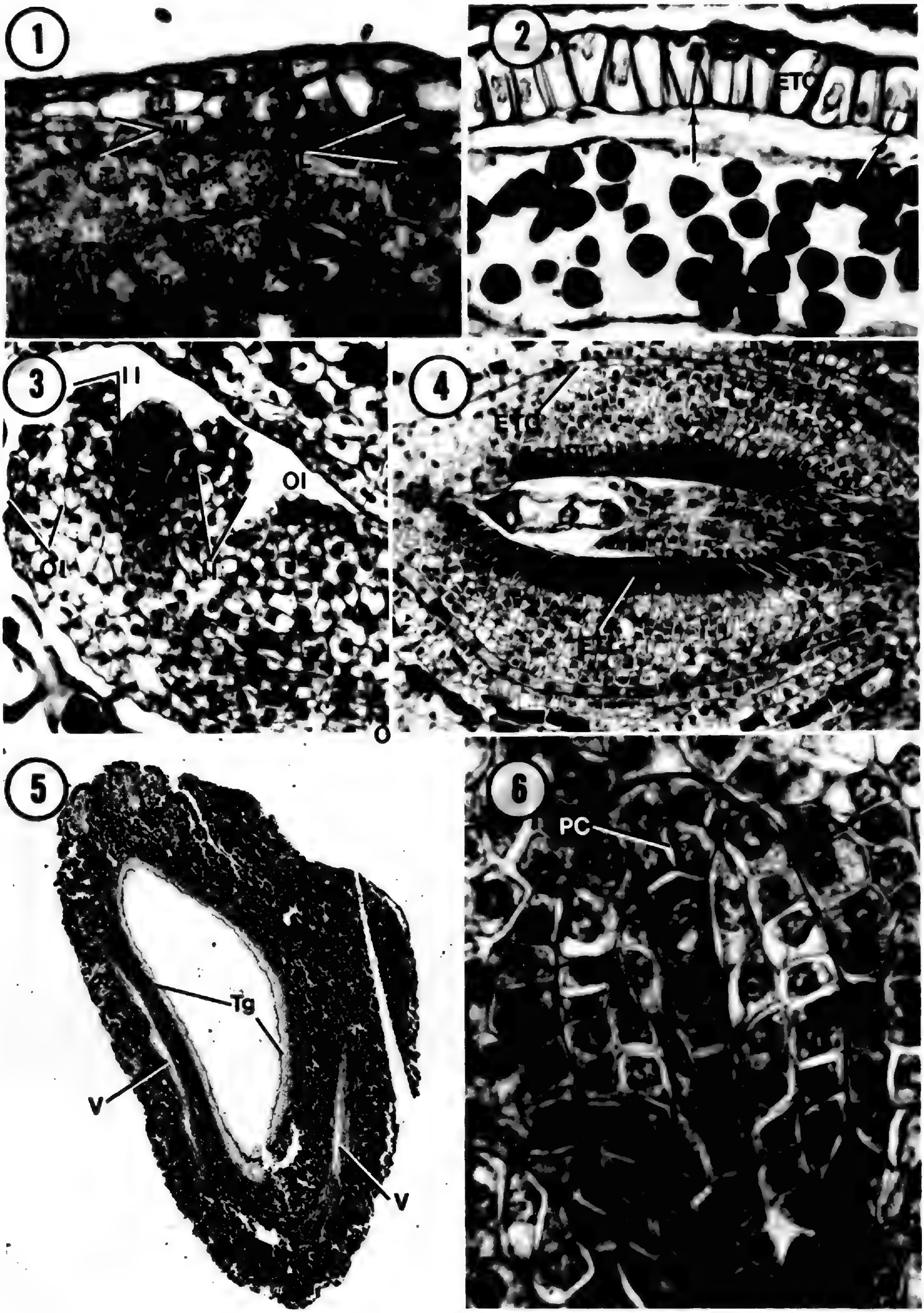
due to localized growth of hypodermal parenchyma and expansion of the overlying epidermis (Fig. 9). Although the exotegmen is a distinctive cell layer in the unfertilized ovule, it does not persist to form a prominent sclerified layer in the mature seed, as in other inland genera of Rhizophoraceae; instead, the tegmen gradually degenerates and/or is crushed during later seed development.

Crossostylis grandiflora Brongn. & Gris.

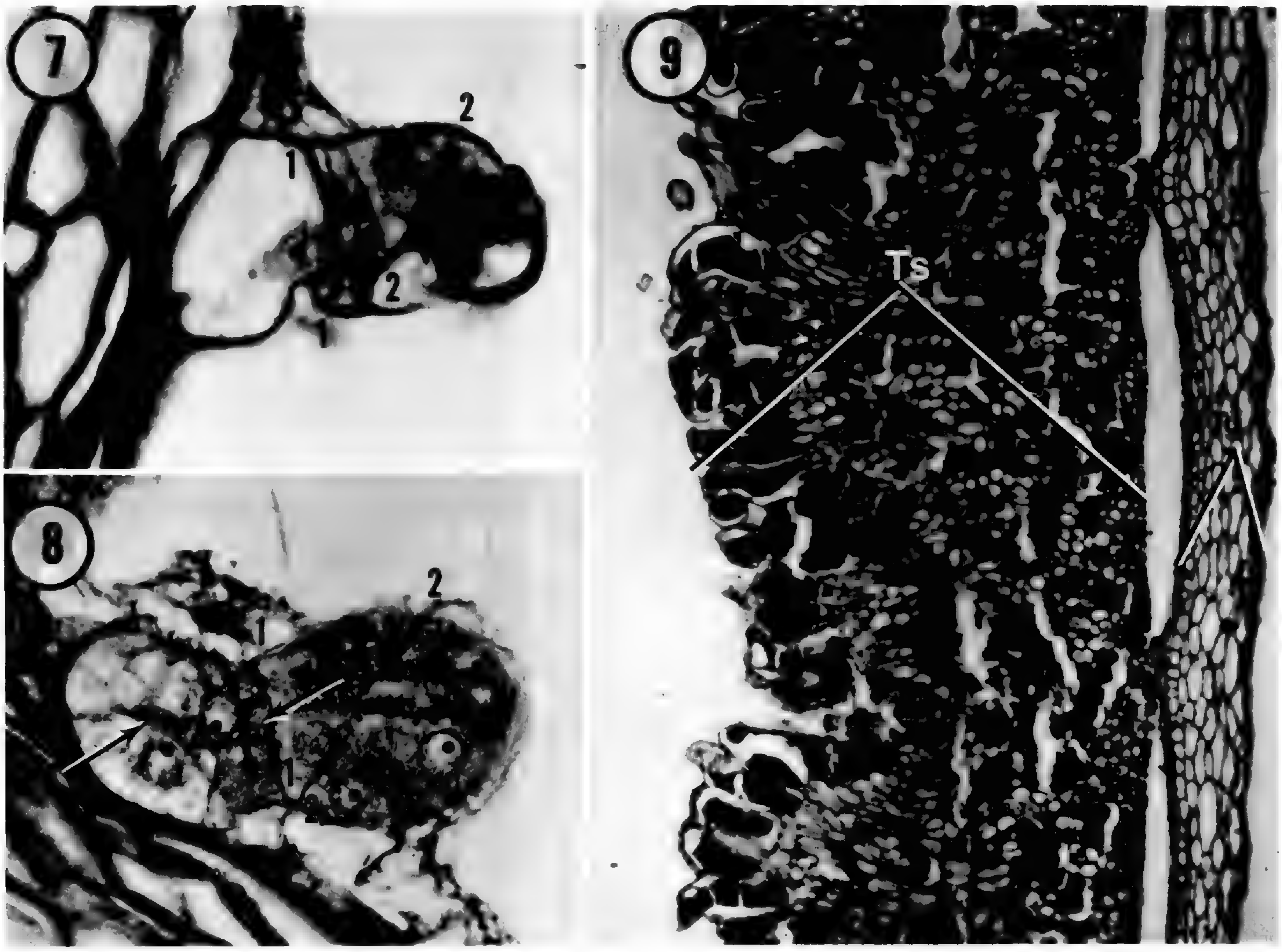
The anther consists of four microsporangia. Periclinal divisions in the outer parietal cell layer produce the endothecium and a primary middle layer, which in turn divides to form two cell layers. Later, the inner parietal cells divide, producing the tapetum and a third middle layer (Fig. 10). Thus, anther wall development follows the basic type. The middle layers degenerate during microsporogenesis. The epidermis persists to anthesis, although tannins are deposited in its cells. A few thick bars of secondary wall are formed by the endothecial cells (Fig. 11). As in other Rhizophoraceae, the tapetum is glandular, and its cells are binucleate. However, unlike other genera, the tapetal cytoplasm in *C. grandiflora* stains more densely with hematoxylin and may include several to many unstained globules of uncertain composition.

Microsporogenesis occurs by both simultaneous and successive cytokinesis, but most cytokineses in a single microsporangium occur by only one pattern (Figs. 12, 13). Although any one cell in which simultaneous nuclear division (but not wall formation) has occurred may resemble a cell at the end of the nuclear division of meiosis I, careful examination at various focal levels of hundreds of meiotic figures in many serial sections of several different flowers revealed virtually no cells with tetrahedrally arranged nuclei in "successive" thecae, such as the one shown in Figure 13, and revealed virtually no binucleate cells or portions of cells in "simultaneous" thecae, such as that shown in Figure 12. The very large number of observations makes us confident that this conclusion is not due to orientation of the cells relative to the plane of sectioning, but rather reflects actual variability in the meiotic division pattern. In successively dividing cells, wall formation occurs after meiosis I but is not documented here for this genus (see also Fig. 25, *Pellacalyx*). Pollen tetrads of *C. grandiflora* are either tetrahedral or decussate. The mature anthers are strongly reniform, even semicircular, and dehisce introrsely by longitudinal slits.

The ovule is bitegmic. At inception and during early development, the inner integument is biseriate (Fig. 15). Later, numerous peripheral divi-



FIGURES 1–6. Carallia borneensis. *1. Basic-type anther wall development. ML, middle layers; Sp, sporogenous cells; T, tapetum.* ×*1,140.—2. Anther just before anthesis; of the wall layers, only the endothecium (ETC) persists. Longitudinal radial walls have at most one wall thickening (arrows).* ×*455.—3. Ovule, early devel-*



FIGURES 7–9. Carallia borneensis, *proembryo and seed coat.—7. Proembryo showing transverse first division (1) and oblique second division (2).* ×*635.—8. Later proembryo showing longitudinal divisions in suspensor cells (arrows).* ×*650.—9. Developing seed coat. Bumps on its surface are formed by growth of both epidermis and hypodermis of testa (Ts). Some of tegmen (Tg) persists at this stage but degenerates later; its outer epidermis does not sclerify.* ×*120.*

sions occur, and it becomes about 20 cells thick by the time of anthesis (Fig. 16). The exotegmen and endothelium are sharply differentiated throughout megagametogenesis. The outer integument is probably biseriate at its inception, although this stage was not observed. In the premeiotic stages that we studied in which the outer integument (or at least its abaxial portion) was present, its basal half was triseriate and the distal portion was biseriate. During the remainder of ovule development very few periclinal divisions occur in the outer integument, and at anthesis it is only about four cell layers thick. Its outer epidermal cells expand considerably and are filled with tannin.

Gynotroches axillaris Blume

Collections used for this study came from two sites in southern Sarawak. Study of plants from these and a number of other sites suggests that at least two ecotypes, probably constituting distinct species, are found in this region. This lends strong support to the suggestion by Ding Hou (1958) that, with further study, this highly variable and widely

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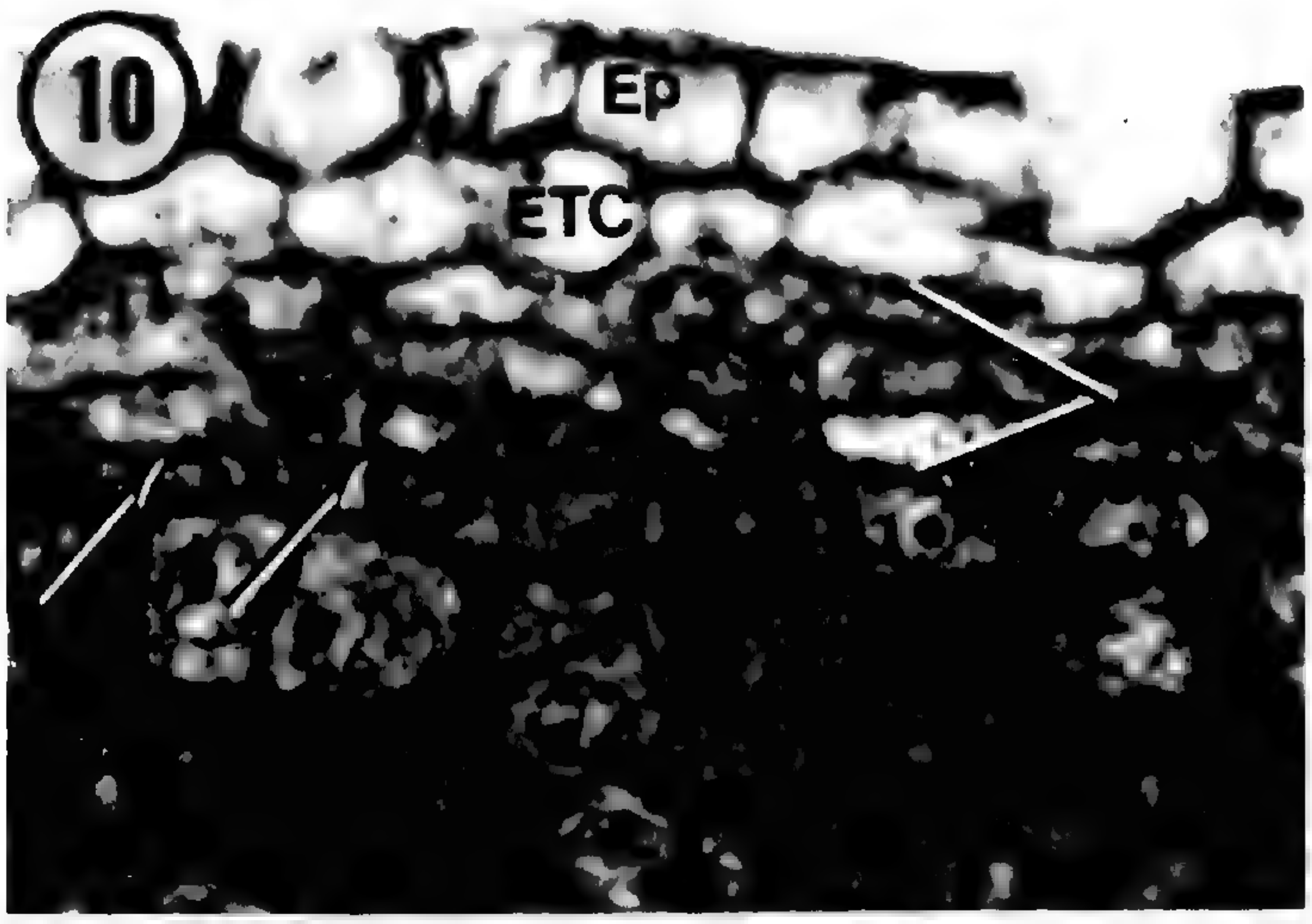
opmental stage. Adaxial portion of inner integument (II at center) is three cell layers thick; abaxial portion (II above left) is partly biseriate. Outer integument is not yet developed adaxially (OI at right indicates the primordium), but its abaxial portion (OI at left) is multiseriate. ×*445.—4. Ovule shortly before anthesis. Megagametophyte had eight nuclei, some in adjacent section; note also degeneration of nucellus and presence of endothelium (ETL) and differentiated outer epidermis (ETG) in inner integument.* ×*285.—5. Developing seed, showing vascularization of outer integument (V). In this very immature seed, some inner integument or tegmen persists (Tg), but this degenerates as the seed develops.* ×*20.—6. Nucellus with megaspore mother cell (MMC) separated from epidermis by two parietal cells (PC).* ×*1,140.*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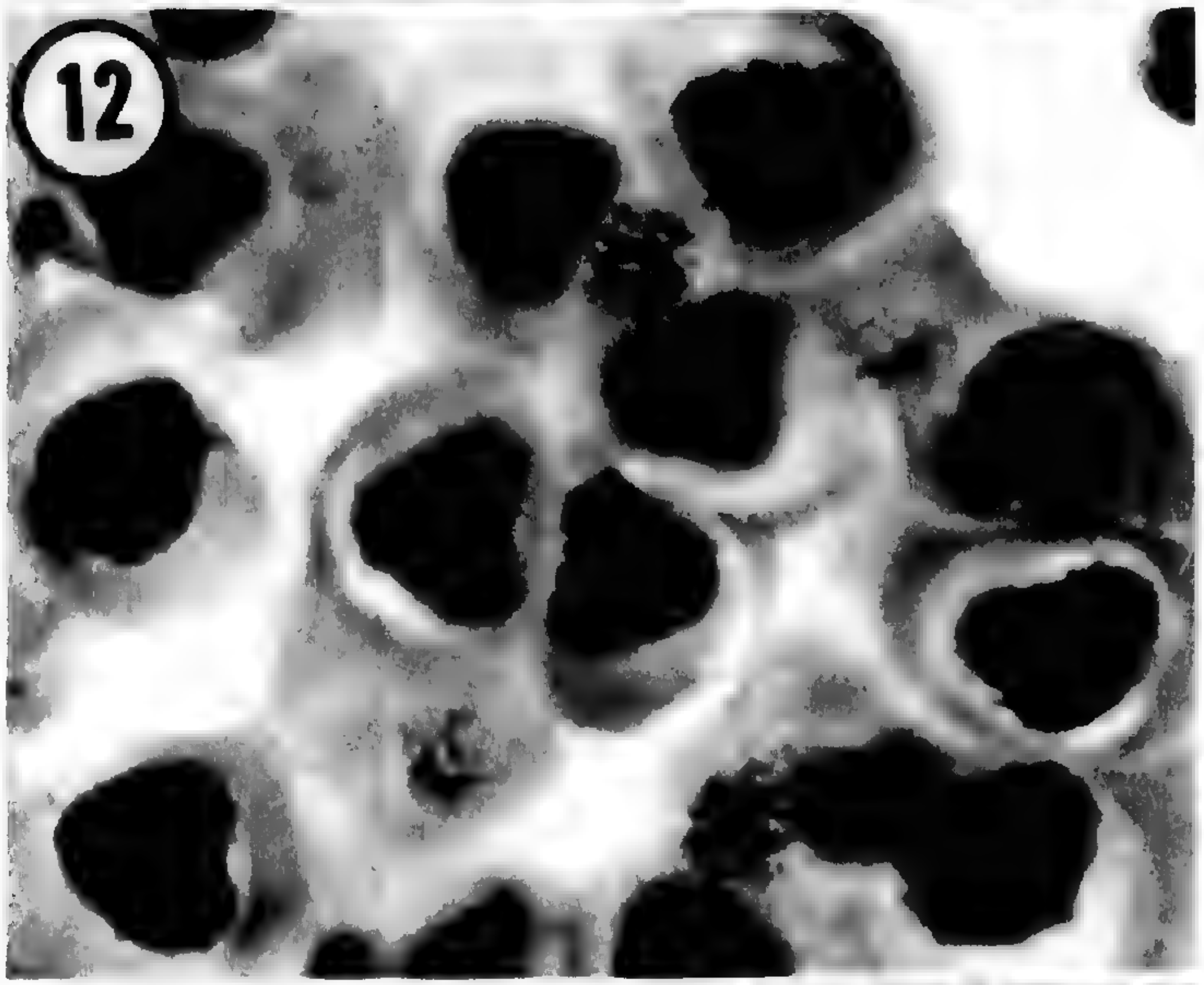
11
Ep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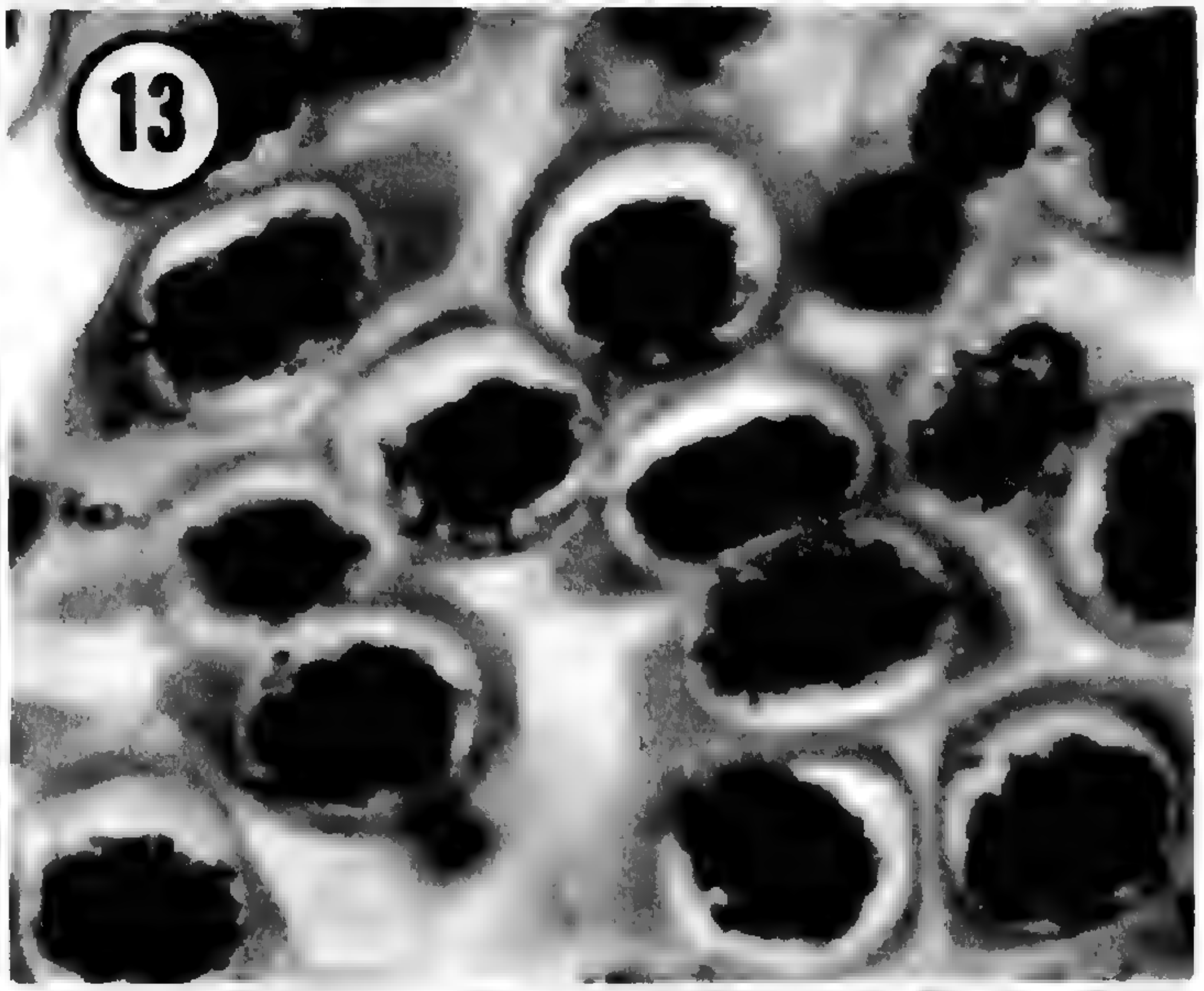
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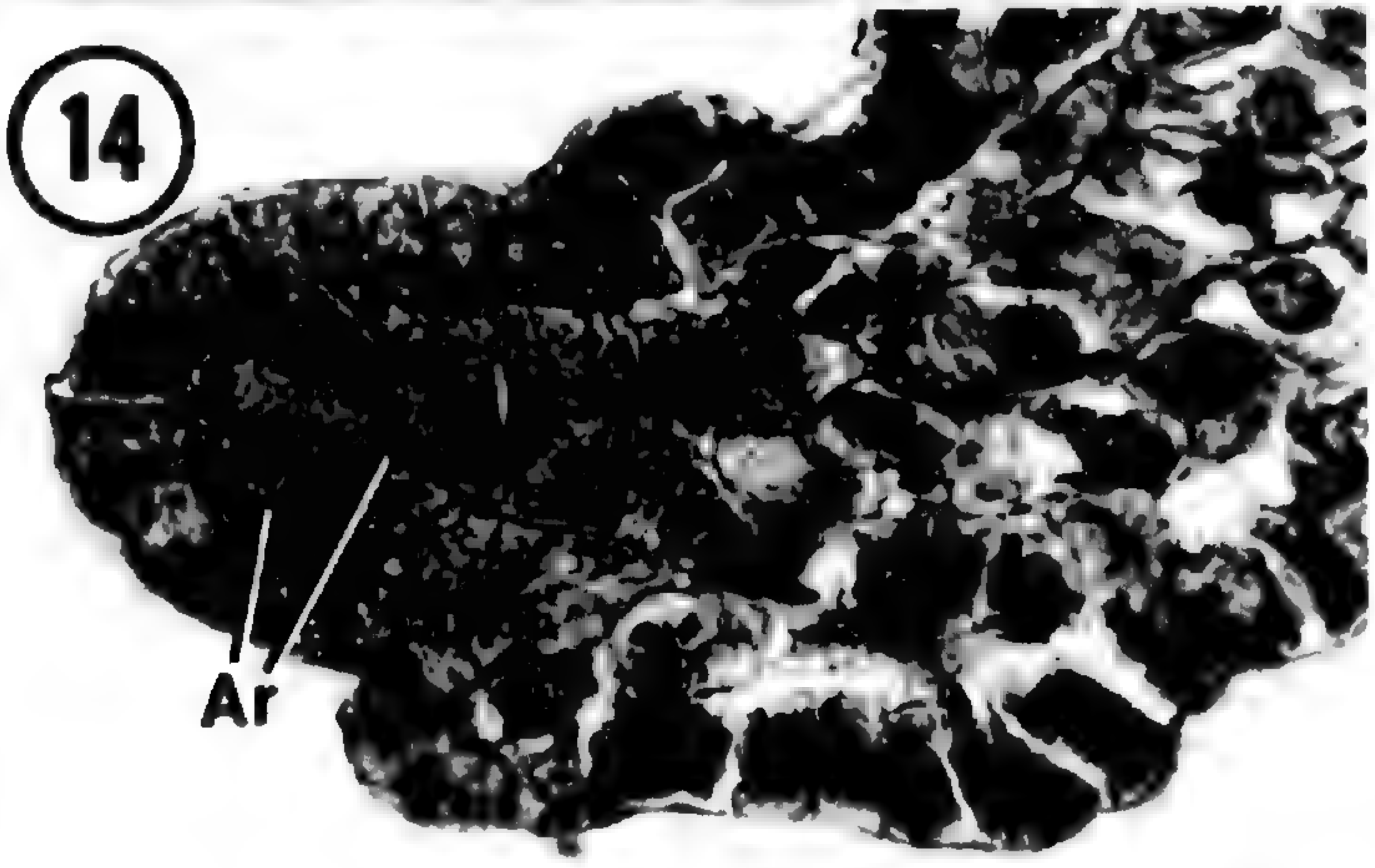
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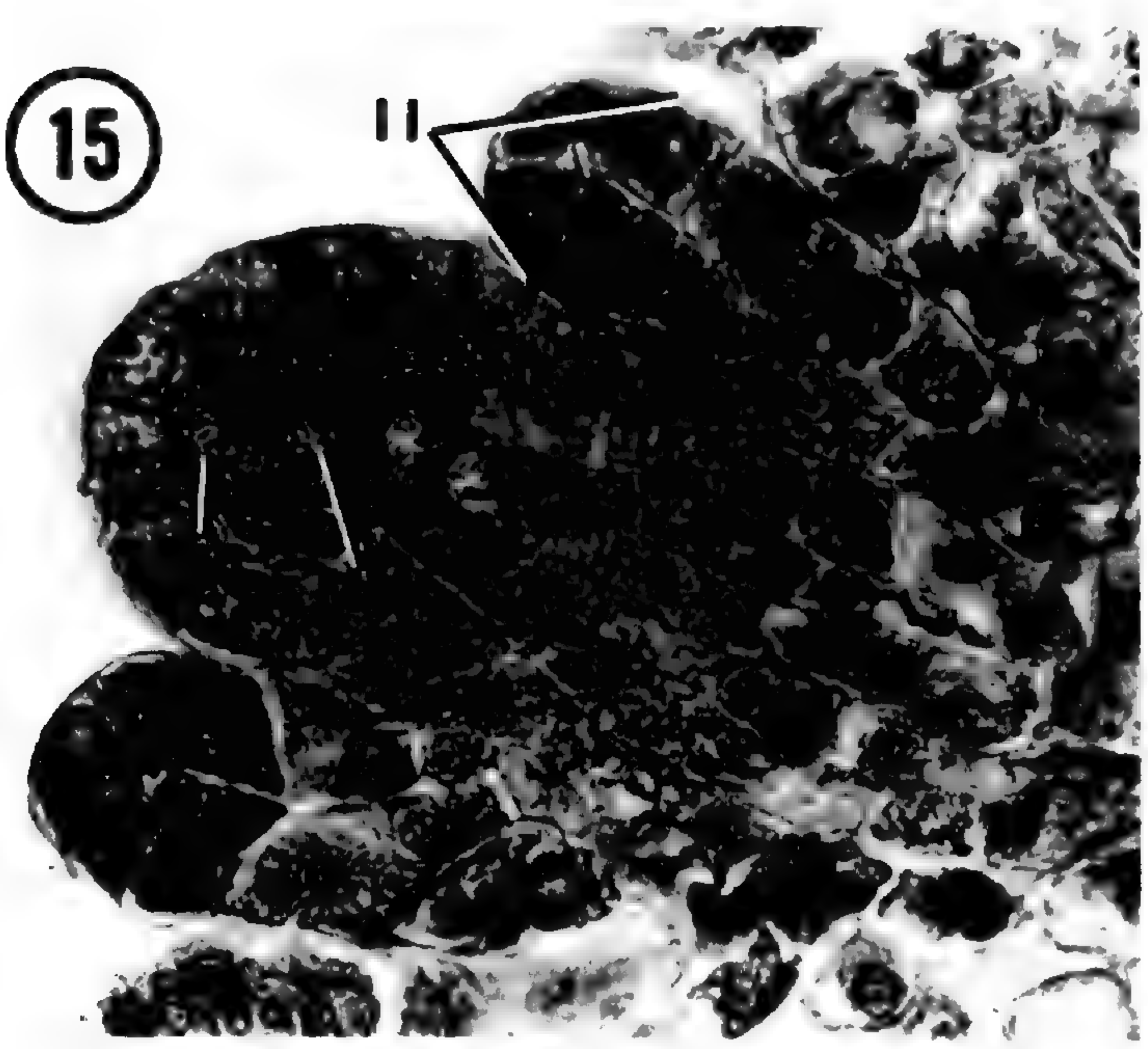
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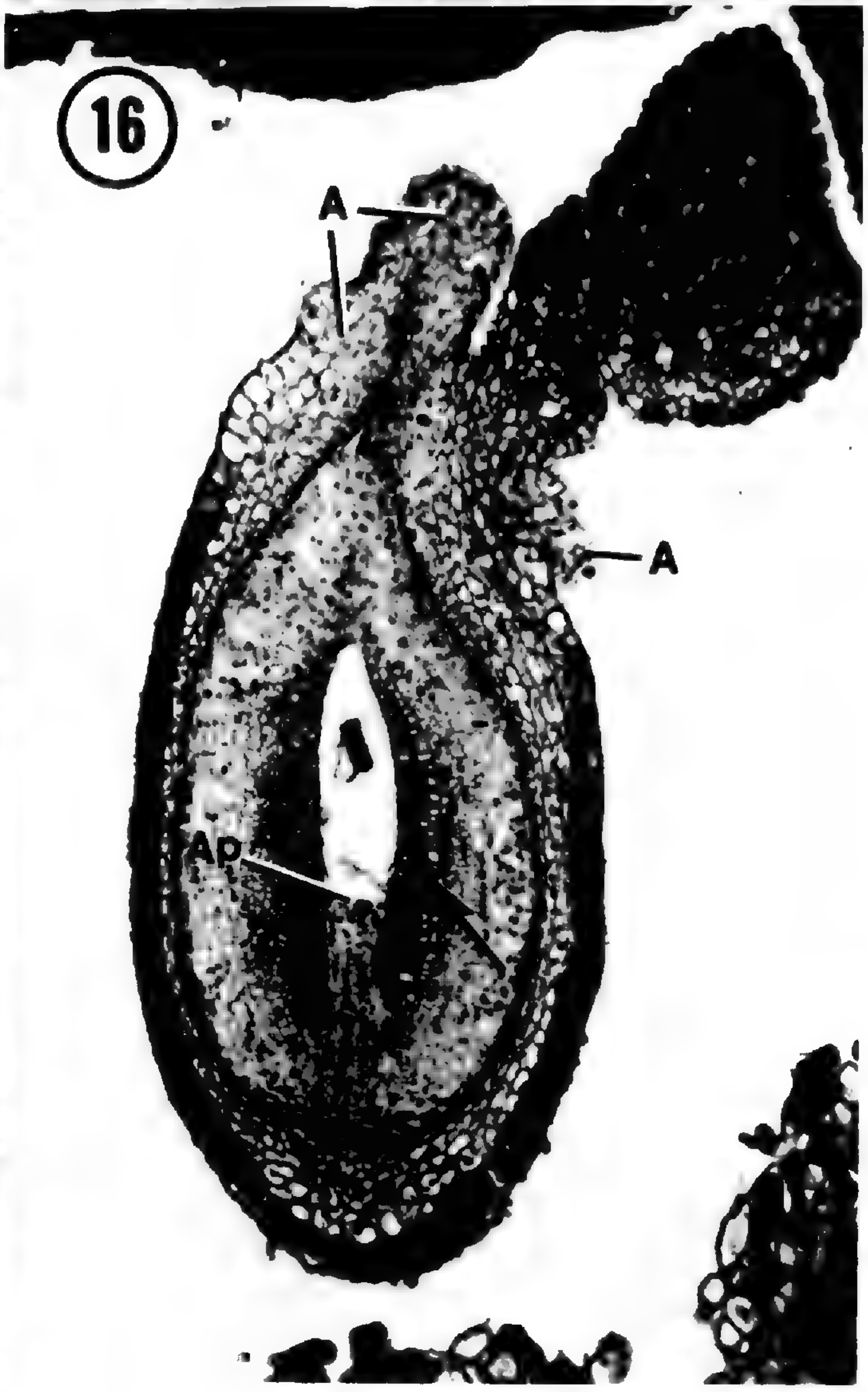
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distributed genus will be amenable to subdivision into several distinct species. Accordingly, brief descriptions of the taxa collected are given so that future readers will be able to ascertain to which species the embryological data pertain. Trees found in secondary vegetation on low altitude kerangas sites or peat swamps had smooth leaves about 6–9 cm long and reddish fruits about 4 mm in diameter at maturity, usually largely covered by a cracked periderm. Trees found along the banks of small streams in hill forest at 50–200 m elevation had bullate leaves 20–25 cm long and yellow, noncorky fruits at least 5–6 mm in diameter at maturity. In addition to these nonoverlapping color and size differences, the trees had very different habits and leaf colors. Both species produce aerial stilt roots, which are more numerous on trees growing in very swampy sites. Both taxa observed appeared to be dioecious. Absence of developing or mature fruits on trees bearing male flowers suggests that the apparent dioecy did not result merely from a temporal separation of the two types of flowers. Almost all of the embryological data reported herein were derived from study of specimens collected in the hill forest.

The anther of *Gynotroches* consists of four microsporangia. Only one middle layer is present between the endothecium and tapetum; because this layer shares its origin with the tapetum, anther wall development is of the "monocotyledonous" type (Fig. 17). The tapetum is glandular; its cells have two nuclei. In some microsporangia, meiotic cytokinesis was successive, producing isobilateral or decussate tetrads (Fig. 18), but in others, even within the same stamen, simultaneous cytokinesis occurred, producing tetrahedral tetrads (Fig. 19). As with *Crossostylis* (see above), numerous meiotic figures were examined to insure that we were not misled by an artifact of the plane of sectioning, although only a few cells are shown in the figures. Mature pollen grains in male flowers are binucleate. In female flowers, the anther as a whole develops more or less normally, having at least a partially functional tapetum and an endothecium with secondary wall thickenings (Fig. 20). Meiosis also occurs, forming numerous microspores, but the normal sporopollenin wall does not form around them (Fig. 20).

Functional ovules of *Gynotroches* are bitegmic and anatropous. Early in development, both integuments are two cell layers thick (Fig. 21). The inner integument thickens to 5–6 cell layers by the time of anthesis, but the outer integument remains only two cell layers thick in most places, except for its expanded micropylar portion (Fig. 22). A funicular (raphe) vascular bundle extends along the adaxial side of the outer integument, but neither integument proper is vascularized. An endothelium is formed early in megagametogenesis (Fig. 22). The micropylar half of the nucellus degenerates before gametogenesis is complete. The micropyle is quite short and is formed by both integuments. Occasionally, however, extension of the inner integument makes the micropyle endostomic. The single archesporial cell functions directly as the megaspore mother cell; thus, the ovule is tenuinucellate (Fig. 21). A cell wall forms after meiosis I, and the megaspore tetrad is usually T-shaped. The chalazal megaspore forms a normal 8-nucleate megagametophyte via *Polygonum*-type development. The synergids are large and pyriform, and the polar nuclei do not fuse to form a secondary nucleus. Antipodals are formed and persist to anthesis (Fig. 22).

In male flowers, early ovule development is more or less similar to that in female flowers, although the nonfunctional ovules are somewhat smaller and irregularly shaped compared with the fertile ones of female flowers, primarily due to irregularities in integument development (Fig. 23). A normal micropyle can rarely be seen. No obvious irregularities in megasporogensis were noted in the nonfunctional ovules, and megagametogenesis may either proceed normally through at least the four-nucleate stage (Fig. 23) or may be somewhat disordered. Gynoecial development is also modified in

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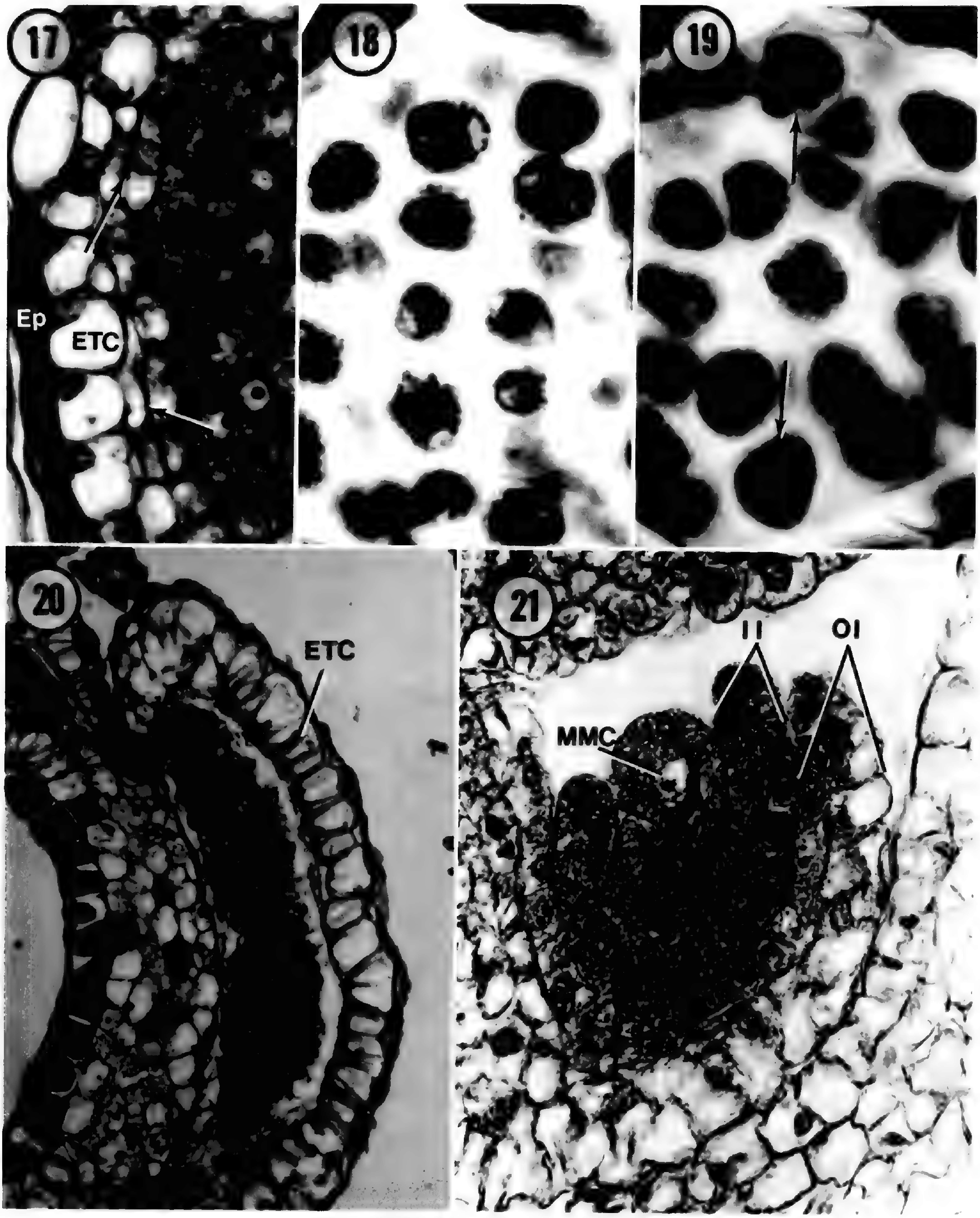
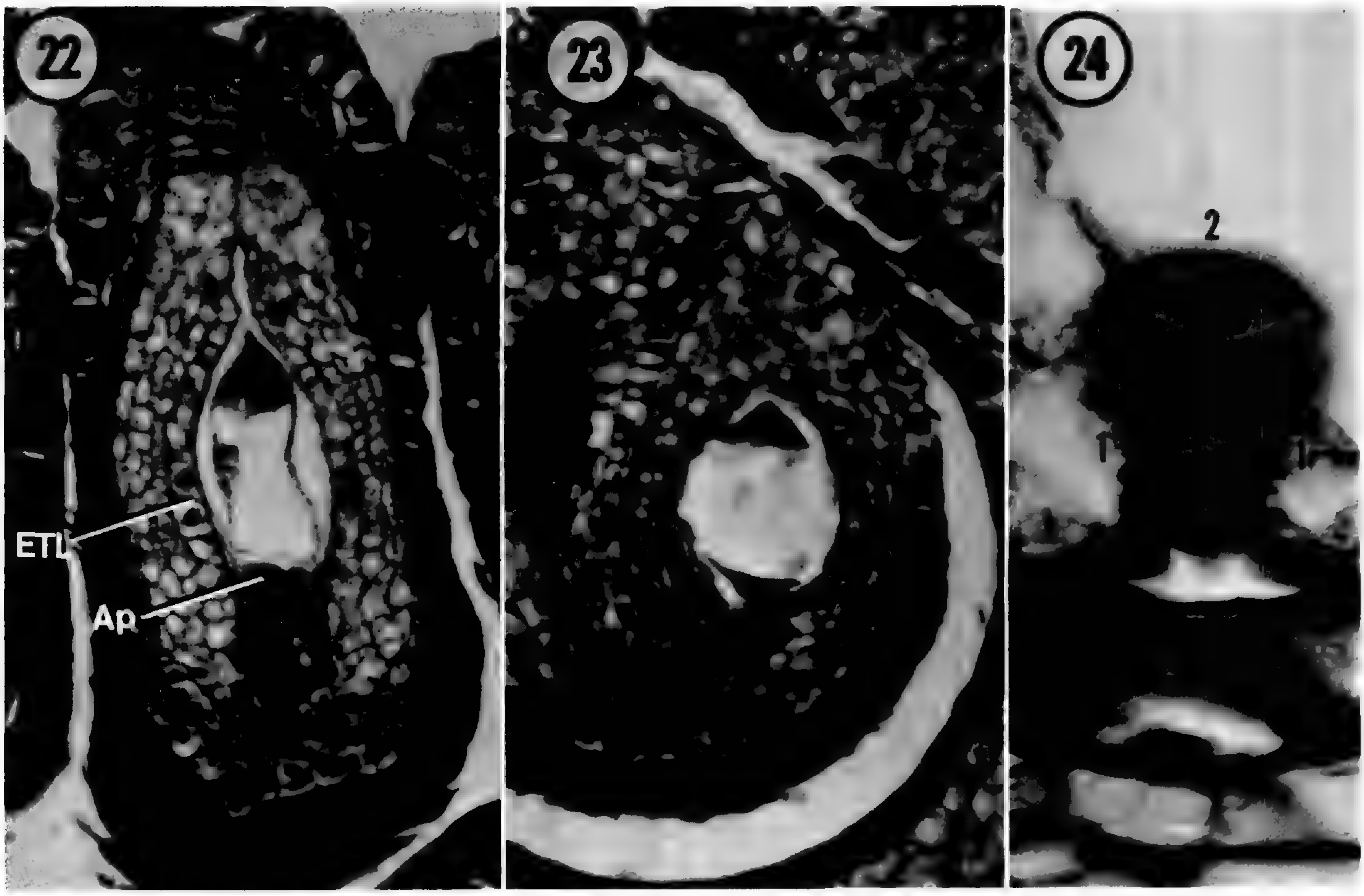
FIGURES 10–16. Crossostylis grandiflora.—*10. Developing anther wall. Typically, at least three middle layers form (ML); periclinal divisions of inner parietal cells are seen here (arrows). Ep, epidermis; ETC, endothecium. ×1,140.—11. Mature anther wall. Epidermis (Ep) persists, and radial walls of endothecial cells have one or two secondary wall thickenings (arrows). ×265.—12. Microsporogenesis in a theca where most meiotic divisions were simultaneous. ×1,140—13. Meiosis I in a theca where most divisions were successive. ×1,140.—14. Early ovule with at least two archesporial cells (Ar). ×800.—15. Later ovule, in which the archesporial cell has divided periclinally to form a megaspore mother cell (MMC) and a parietal cell (PC). ×800.—16. Ovule at anthesis. Inner integument has thickened considerably; outer integument, only slightly, to about four cell layers. Endothelium is prominent (arrow), and aril primordium (A) has begun to develop. Ap, condensed antipodals. ×100.*



FIGURES 17–21. Gynotroches axillaris, *anther and early ovule.*—*17. Monocotyledonous-type development of anther wall; arrows indicate divisions forming the tapetum and single middle layer.* ×*1,060. Ep, epidermis; ETC, endothecium.*—*18. Meiosis I in a microsporangium where most divisions were successive.* ×*1,500.*—*19. Microsporogenesis in a theca where most meiotic cytokineses were simultaneous. Arrows indicate cells with tetrahedrally arranged nuclei, just prior to wall formation.* ×*1,500.*—*20. Anther of female flower at anthesis. Normal endothecium is formed, but pollen development is arrested before deposition of sporopollenin wall, which would stain darkly in safranin (used here).* ×*310.*—*21. Developing tenuinucellate ovule; archesporial cell functions as megaspore mother cell (MMC) without first dividing periclinally. Both inner (II) and outer integuments (OI) consist of two cell layers.* ×*900.*



FIGURES 22–24. Gynotroches axillaris, *mature ovule and proembryo.—22. Functional ovule from female flower at anthesis. Most of nucellus has degenerated; endothelium (ETL) is only slightly differentiated. Antipodals persist (Ap).* ×*425.—23. Sterile ovule from male flower at anthesis. Megagametogenesis has proceeded to the four-celled stage, but ovule morphology is abnormal; micropyle was not evident in this or adjacent sections.* ×*425.—24. Proembryo formed by classic onagrad-type embryogenesis, which predominates in this genus. 1, first division; 2, second division.* ×*1,060.*

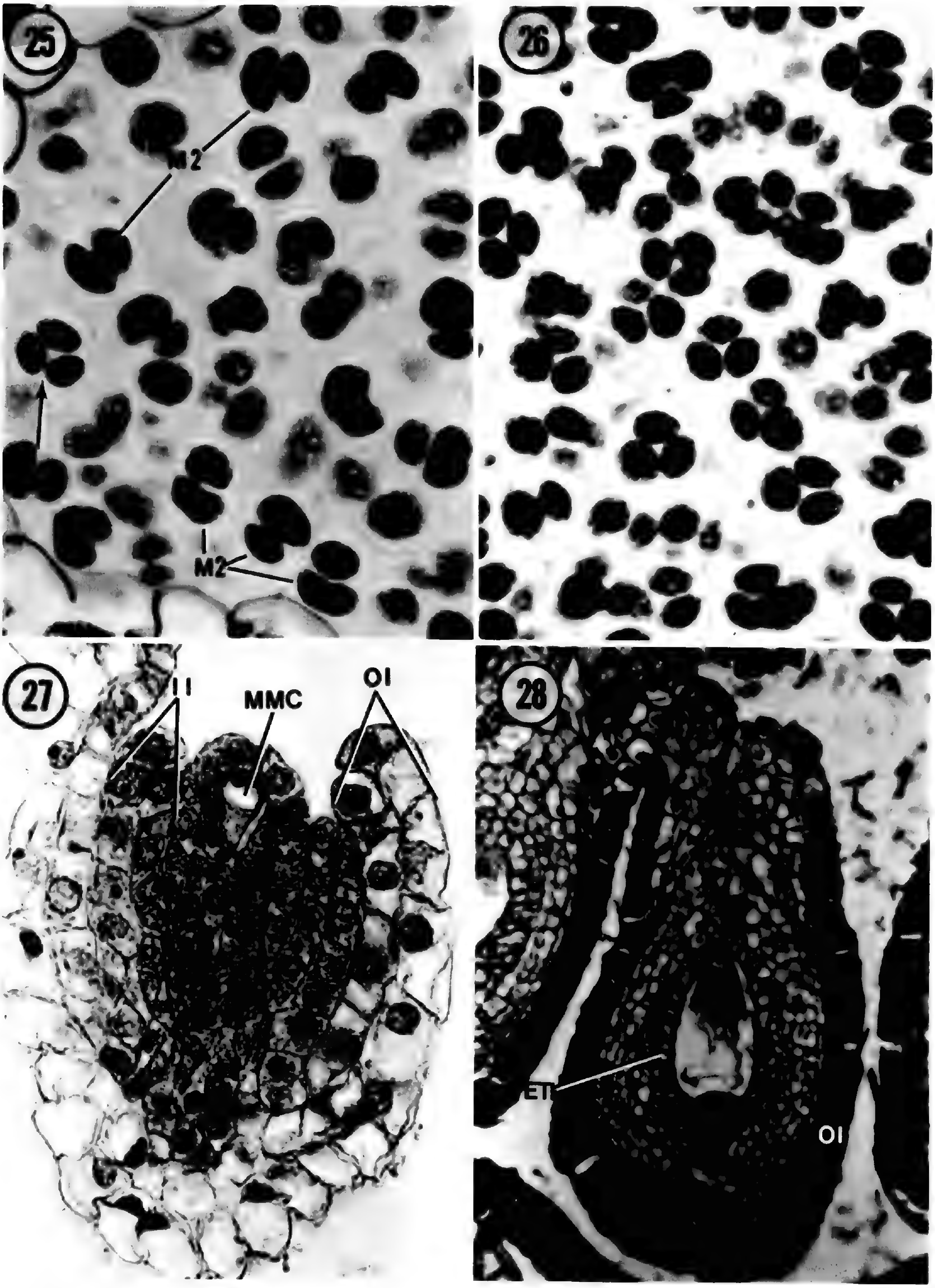
male flowers. In particular, the style may become necrotic or may elongate abnormally, with the stigmatic lobes remaining inserted at its base (Juncosa, pers. obs.). Further details of floral development will appear separately.

In fertilized ovules of female flowers, both cell layers of the outer integument persist and form a distinctive testa, in which the outer epidermal cells are very large and tanniniferous, and the inner epidermal cells are small and compact, with prominent nuclei and dense cytoplasm. This latter layer of cells may play an important role in controlling the process of imbibition. The exotegmen is very prominent and sclerified; radial elongation of some of its cells makes its outline undulate. Several internal cell layers of the inner integument also persist but remain unspecialized. Mature endosperm cells contain many large inclusions of undetermined composition. These inclusions stain weakly with safranin and are not birefringent. As in other Rhizophoraceae, the embryogenetic cell division pattern in *Gynotroches* is variable. However, in this genus, the overwhelming majority of proembryos observed had developed according to the typical onagrad-type pattern (Fig. 24), and only a few exhibited an oblique division of the terminal cell. The mature embryo is straight, and both the hypocotyl and cotyledons are well developed; they are of roughly equal length. The provascular cylinder in the radicle is not medullated.

Pellacalyx species

Complete prefertilization embryological data were determined from studies of *P. cristatus* Hemsl. Using the scanty available material of *P. symphiodiscus* Stapf, we confirmed that in anther wall, pollen tetrad, and ovule integument characters, it agreed exactly with *P. cristatus*. Ovules of *P.* cf. *saccardianus* Scort. were examined, and seeds of *P. cristatus* and *P. lobbii* (Hook. f.) Schimp. were studied.

The anther in species of *Pellacalyx* has four microsporangia, the exterior walls of which develop according to the basic-type pattern. The two middle layers degenerate before pollen develops, but the



FIGURES 25–28. Pellacalyx *species.—25.* P. cristatus, *microsporogenesis by predominantly successive meiotic division (M2); some simultaneous divisions are also seen (arrow).* ×485.*—26.* P. cristatus, *microsporogenesis by almost exclusively simultaneous cytokinesis.* ×485.*—27.* P. *cf.* saccardianus, *early ovule. Both integuments initially consist of only two cell layers. Archesporial cell functions directly as megaspore mother cell (MMC); thus, ovule is tenuinucellate.* ×900.*—28. Ovule at anthesis. Except for proliferation of micropylar region, outer integument (OI) remains biseriate, but inner integument (II) has thickened. Nucellus has degenerated; endothelium (ETL) is indicated.* ×315.

epidermis persists to anthesis, although its cells are somewhat collapsed by that time. Secondary wall thickenings are found in the endothecial cells. The tapetum is glandular and composed of binucleate cells. Both successive and simultaneous meiotic cytokineses occur (Figs. 25, 26), producing decussate and tetrahedral pollen tetrads, respectively. Generally, only one type of cytokinesis occurred in any one microsporangium, but incongruent divisions were observed (Fig. 25). Pollen grains are binucleate when dispersed. Anther dehiscence is introrse, occurring by longitudinal slits.

Both integuments of the ovule of *P. cristatus* and *P. saccardianus* are initially two cell layers thick (Fig. 27), but divisions in the inner layer of the inner integument soon form three, then eight to ten cell layers (Fig. 28). The outer integument remains biseriate. Neither integument is vascularized, and both contribute to forming the micropyle. A prominent endothelium is formed during megagametogenesis. The single archesporial cell functions directly as the megaspore mother cell (Fig. 27); thus, the ovule is tenuinucellate. A cell wall is formed after meiosis I, and the megaspore tetrad is usually linear. The chalazal megaspore forms a normal megagametophyte via *Polygonum*-type megagametogenesis. Antipodals are formed but become condensed by the time of anthesis. The polar nuclei remain separate until fertilization. The synergids are pyriform, with prominent chalazal vacuoles.

DISCUSSION

Although this study was limited to one of the two inland tribes of the familiar but poorly understood family Rhizophoraceae, some of the characteristics observed are strongly discordant with embryological dogma and may have significant implications in the study of the control of critical stages of plant development. These features are discussed separately at the end of this section.

SYSTEMATIC SIGNIFICANCE

The data reported here combined with information from other sources (Karsten, 1891; Mauritzon, 1939; Tobe & Raven, 1987a, b, this volume; Juncosa, 1982b, 1984a, b) permit a relatively complete embryological characterization of the family Rhizophoraceae. Reports for African genera of tribe Macarisieae are not yet available, but data from *Cassipourea* and *Sterigmapetalum* (Tobe & Raven, 1987b) are taken as representative of that tribe.

Despite the occurrence of certain derived character states in some genera, the family is remarkably homogeneous embryologically. This contrasts somewhat with the wide range of variation in wood anatomy, mature floral morphology, and chromosome number (Juncosa & Tomlinson, this volume). Allowing for some exceptions, a generalized embryological summary is as follows:

Anthers tetrasporangiate, wall development basic-type (monocotyledonous-type in *Gynotroches*), endothecium with few secondary wall thickenings (more numerous in Macarisieae), middle layers degenerate, tapetum glandular, its cells binucleate; microspore cytokinesis simultaneous (or also successive, in most Gynotrocheae); pollen tetrads tetrahedral or decussate, pollen binucleate. Ovules anatropous, bitegmic, crassinucellate (tenuinucellate in *Gynotroches* and *Pellacalyx*), integuments two cell layers thick at inception (multiseriate in *Carallia* and Rhizophoreae), usually thickening subsequently, endothelium present, micropyle diplostomic, nucellus ephemeral; megagametogenesis chalazal-monosporic (*Polygonum*-type), synergids pyriform with large chalazal vacuoles, antipodals usually degenerate (persistent in *Gynotroches* and *Pellacalyx*). Fertilization porogamous, endosperm initially free-nuclear, embryogenesis variable within species. Mature seeds usually with sclerified exotegmen and abundant nonstarchy endosperm; embryo chlorophyllous, straight, with prominent cotyledons and hypocotyl; radicular vascular cylinder usually medullated; germination epigeal or *Durian*-type.

For most of these characters, the states given above are merely the most common ones among dicotyledons and are regarded as plesiomorphic and therefore not phylogenetically diagnostic. However, the presence of an endothelium is relatively rare in bitegmic ovules (Kapil & Tiwari, 1978). Also, variable orientation of the first and second embryogenetic cell divisions has almost never been reported in families other than Rhizophoraceae, although it may be common in woody plants with large proembryos (Nast, 1941; Souèges et al., 1967). Among temperate herbs, it is apparently common only in Dipsacaceae (Souèges, 1957). Nucellar degeneration, which occurs in all Rhizophoraceae yet studied, is of some diagnostic value. Sclerified exotegmen is not common (Corner, 1976).

The new data reported here support the contention that Rhizophoraceae and Anisophylleaceae are not related (Juncosa, 1982a; Juncosa & Tomlinson, 1987, this volume; Tobe & Raven, 1987a). This latter family differs sharply from the former in all of the apomorphic character states just enumerated (endothelium, degenerate nucellus, exotegmen) as well as in others that are of more general occurrence in dicotyledons. Also, as previously pointed out (Tobe & Raven, 1983), Rhizophoraceae are embryologically out of place in either Myrtales or Cornales, two orders in which the family has often been placed by phylogeneticists (Cronquist, 1968; Thorne, 1976; Takhtajan, 1980). Assignment of the Rhizophoraceae to their own order (Cronquist, 1981; Dahlgren, 1983) merely raises the question of the proper placement of that order. As suggested and discussed by Dahlgren (this volume), the alignment of the Rhizophoraceae with the Celastraceae, Elaeocarpaceae, Erythroxylaceae, and possibly other families is well supported by the embryological data.

These data also have clear implications for intrafamilial systematics. Among the ten genera of Rhizophoraceae so far investigated, only *Gynotroches* and *Pellacalyx* have tenuinucellate ovules and an outer integument that remains two-layered throughout development; the histology of the seed coats in these two genera is similar and differs from that of all other genera in the family (see also Tobe & Raven, this volume). These embryological synapomorphies also correlate with distinctive characteristics of the inflorescence and floral anatomy that are unique to these two genera, such as fasciculate monochasial inflorescences, multiovulate carpels, and idioblastic laticifers (Juncosa & Tomlinson, this volume). Therefore, we conclude that *Gynotroches* and *Pellacalyx* are sister genera, despite the pronounced differences in mature floral morphology that have led some to question even the inclusion of the latter in the family.

As judged by embryological criteria, the systematic position of *Crossostylis* is likely to be intermediate between the Macarisieae and the *Gynotroches/Pellacalyx* clade. The outer integument of the mature ovules of *Crossostylis* is about four cell layers thick, as in *Cassipourea* and *Sterigmapetalum* (Juncosa, 1984a; Tobe & Raven, 1987b). Further, seeds of *Crossostylis* are arillate (Fig. 16; Corner, 1976; Smith, 1981; Tobe & Raven, this volume); seeds of Macarisieae are invariably winged or arillate. This suggests the possibility of merely reassigning *Crossostylis* to the Macarisieae. However, the number of secondary wall thickenings of endothecial cells of *Crossostylis* and other Gynotrocheae is quite low (one to three), whereas five or more such bars are found in *Cassipourea* (Juncosa, pers. obs.). Also, microsporogenesis in *Crossostylis grandiflora* occurs by both simultaneous and successive cytokinesis, a circumstance reported here for *Gynotroches* and *Pellacalyx* but otherwise unknown in the family. Furthermore, there are many important vegetative and floral morphological characters common to *Crossostylis* and other Gynotrocheae that do not occur in Macarisieae (Juncosa & Tomlinson, this volume). Therefore, a reassignment of *Crossostylis* based solely upon the outer integument and aril seems incorrect, despite the importance traditionally ascribed to this character.

Carallia seems also to be phylogenetically intermediate, standing between the *Gynotroches/Pellacalyx* clade and the mangrove tribe (Rhizophoreae). Within the Gynotrocheae, only *Carallia* has a prolonged anther connective and acute sterile tips on the two halves of the anther, characters also found in some Rhizophoreae (Juncosa & Tomlinson, 1987). Nonappendaged seeds and baccate fruits are found throughout the "higher" Gynotrocheae (that is, excepting *Crossostylis*) and Rhizophoreae and thus do not help clarify relationships among these seven genera. Seed coat anatomy of *C. eugenioidea* resembles that of other Gynotrocheae (Tobe & Raven, this volume), but that of *C. borneensis* is vascularized and quite thick, like those of the Rhizophoreae. The seed coat of *C. brachiata* is intermediate between these two in at least some respects (Tobe & Raven, this volume). The seed coat apomorphies of *C. brachiata* (degenerate tegmen) and especially *C. borneensis* may be homoplastic with those of the Rhizophoreae, but it is also possible that the genus *Carallia* is paraphyletic. Embryological data do not resolve this question, but *Carallia* and the Rhizophoreae do share several floral synapomorphies (Juncosa & Tomlinson, this volume and unpubl. obs.), and only one putative autapomorphy distinguishes the genus *Carallia* (stalked extrastipular glands). This character is known to occur only in *C. longipes* (Ding Hou, 1960) and *C. borneensis* (Juncosa & Tomlinson, this volume), but other species have yet to be examined critically; if these glands prove not to be ubiquitous in the genus, its monophyly will be questionable. With the possible exception of the vascularized integument of *C. borneensis*, we observed no embryological peculiarities in *Carallia* that could be construed as any kind of preadaptation to vivipary, which therefore appears to have arisen entirely within the mangrove tribe.

DEVELOPMENTAL IMPLICATIONS

It is generally believed that nearly all fundamental embryological characters are invariant for a given species (Davis, 1966). For example, the extensive literature on angiosperm embryogenesis is based upon this supposition (Schnarf, 1929; Johansen, 1950). However, variability in cell division pattern has been reported in two genera with relatively large embryos (*Juglans*: Nast, 1941; *Laurus*: Souèges et al., 1967) and is characteristic of all Rhizophoraceae yet studied (Juncosa, 1982b, 1984a, b). Interestingly, among Rhizophoraceae, the genus that most consistently exhibits the familiar onagrad-type pattern (as traditionally described) is *Gynotroches*, which has quite small embryos in comparison with those of other genera. This suggests a correlation between small embryo size at cotyledonary initiation and consistency in orientation of cell divisions that has not previously been recognized. Unfortunately, most of the embryogenetic literature pertains to temperate, herbaceous species with small seeds and embryos, so it is not clear from this limited example whether this correlation is generally true or not.

Another embryological characteristic that may have developmental implications is variability in meiotic cytokinesis in the anthers of all Gynotrocheae except *Carallia*. This has not previously been reported in any angiosperm, although the variation in pollen tetrad configuration that has occasionally been noted (Davis, 1966) suggests that variable cytokinesis may occur widely. However, it is not merely the occurrence of this variation in Gynotrocheae, but especially the pattern of variation that is developmentally significant: nearly all meioses in a single microsporangium occur by only one cytokinetic pattern, yet adjacent sporangia in a single stamen may exhibit different patterns (Figs. 12, 13, 18, 19, 25, 26). This suggests strongly that the pattern of cytokinesis is controlled by tapetal secretions, not by the individual microspore mother cells. Further investigation of this system is certain to yield significant new insights into the process of meiosis in angiosperms.

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ADDITIONAL NOTES ON THE EMBRYOLOGY OF *POLYGONANTHUS* (ANISOPHYLLEACEAE) AND RELATIONSHIPS OF THE FAMILY[1]

Hiroshi Tobe[2] *and Peter H. Raven*[3]

ABSTRACT

Polygonanthus *is reported here to have a* Polygonum*-type embryo sac, like* Anisophyllea *but unlike* Combretocarpus *(with an Allium-type embryo sac). This, together with the results of comparisons of other embyrological character states reported earlier, indicates an isolated position for* Combretocarpus *within the family Anisophylleaceae. On the basis of the available embryological data, we suggest that Anisophylleaceae appear to be distinct from both Rosales sensu stricto and Saxifragales. The family shares many embryological features with Myrtales and may be regarded, at least for the time being, as constituting a distinct order in that phylogenetic lineage.*

In the course of our earlier study of the embryology of Anisophylleaceae (comprising *Anisophyllea, Combretocarpus, Poga,* and *Polygonanthus*), we were unable to determine several important characters for *Polygonanthus* (Tobe & Raven, 1987a). The collection of an additional sample of *Polygonanthus amazonicus* has made it possible for us to report supplemental embryological results here.

Although we have already discussed the embryology and the floral morphology and anatomy of Anisophylleaceae (Tobe & Raven, 1987a, 1988a), our new results, together with the analysis of wood anatomical characters made by Dr. Elisabeth A. Wheeler on the basis of computerized databases and the suggestion by Dahlgren (this volume) that the family belongs in his narrowly defined order Rosales, necessitate further analysis. We have, therefore, returned to the question of the relationships of Anisophylleaceae in the present paper.

The fixed female flower buds of *Polygonanthus amazonicus* Ducke used in this study were collected by Bruce W. Nelson at Maue, Amazonas, Brazil (voucher *J. L. Zarucchi 3138,* MO) and fixed in FAA. Microtome sections for observations were made following the standard methods discussed in the previous paper (Tobe & Raven, 1987a).

EMBRYO SAC FORMATION IN *POLYGONANTHUS*

As previously reported, the ovule is anatropous and crassinucellate. At least one parietal cell is observed above a megaspore mother cell, and the occurrence of periclinal cell division in the nucellar apical epidermis is also confirmed (Fig. 1). The megaspore mother cell divides into two cells, with the upper micropylar cell much smaller than the lower chalazal cell (Fig. 2). Subsequent division occurs only in the chalazal cell, giving rise to a triad of megaspores (Fig. 3). Only the chalazal megaspore functions, developing into a monosporic eight-nucleate embryo sac; therefore, embryo sac formation of *Polygonanthus* conforms to the *Polygonum*-type, in agreement with that of *Anisophyllea* but not with that of *Combretocarpus,* which has a bisporic *Allium*-type embryo sac (Tobe & Raven, 1987a).

With respect to other embryological characters,

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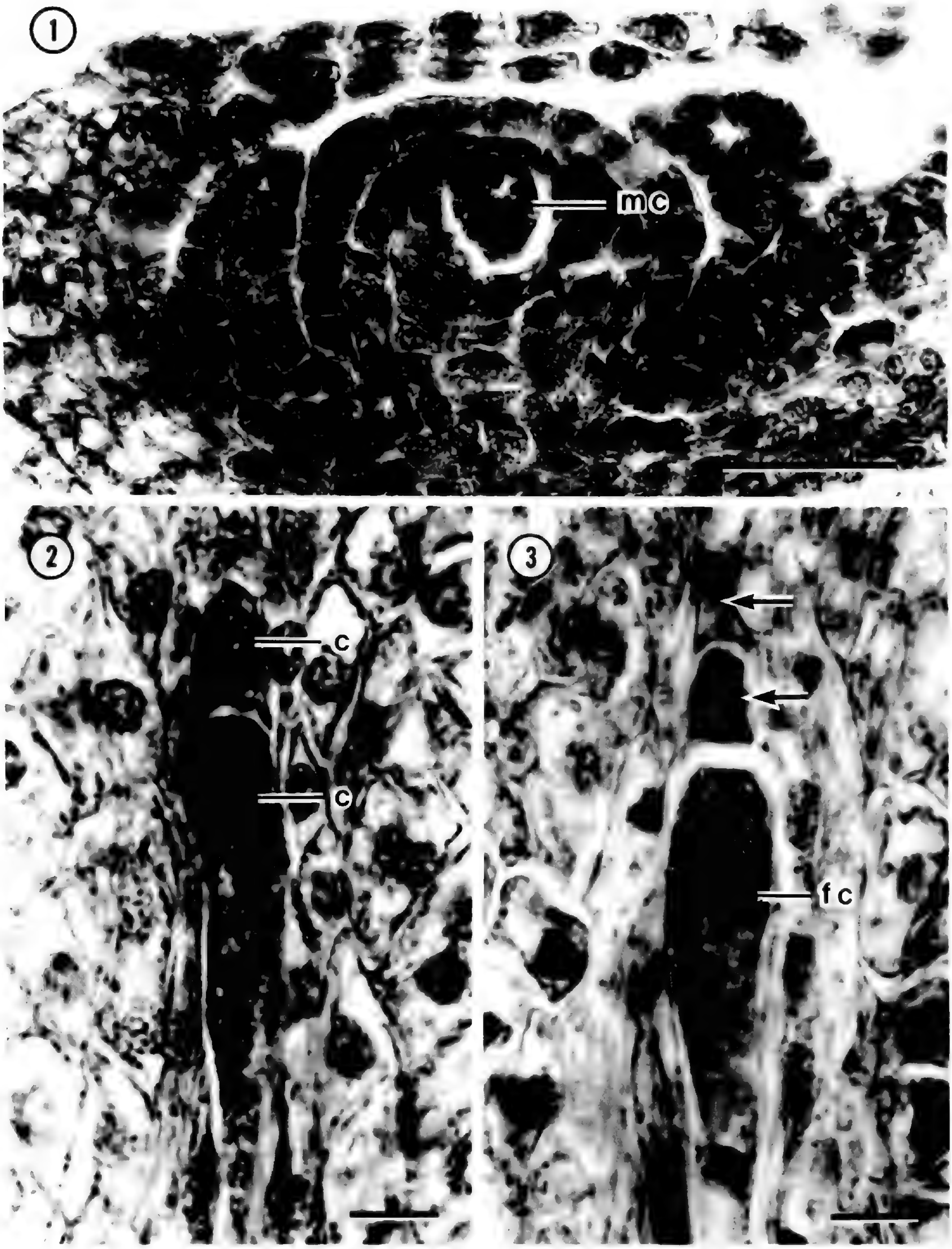

FIGURES 1-3. *Longitudinal sections of young ovules of* Polygonanthus *showing megasporogenesis.—1. Megaspore mother cell stage.—2. Dyad of megaspores.—3. Triad of megaspores. Abbreviations:* mc, *megaspore mother cell;* c, *megaspore;* fc, *functioning megaspore. Arrows in Figure 3 indicate degenerating megaspores. Scale bars equal 50 μm, 10 μm, and 10 μm, respectively.*

Polygonanthus and *Poga* share many plesiomorphies, most of which are common even to *Anisophyllea* (see cladogram in Tobe & Raven, 1987a, fig. 71). In view of these features, the occurrence of *Polygonum*-type embryo sac formation in *Polygonanthus* (also in *Anisophyllea*) indicates an isolated position for *Combretocarpus* within the family. *Combretocarpus* is characterized by many apomorphies, including *Allium*-type embryo sac formation. *Polygonanthus*, like *Poga*, seems to be a relictual genus whose embryological features were mostly inherited from ancestral Anisophylleaceae (Tobe & Raven, 1987a).

RELATIONSHIPS OF ANISOPHYLLEACEAE

We discussed the relationships of Anisophylleaceae (and Rhizophoraceae) earlier (Tobe & Raven, 1987a, b, 1988a), as have other authors in this symposium (e.g., Juncosa & Tomlinson, this volume). Historical views on these relationships are reviewed in these papers, and it seems unnecessary to repeat them here. Instead, we shall use recent suggestions (Tobe & Raven, 1987a, 1988a; Baas, pers. comm.; Dahlgren, this volume) as our point of departure.

Anisophylleaceae have traditionally been assigned to Rhizophoraceae as a subfamily or a tribe. The close resemblance with Rhizophoraceae (particularly with *Carallia*) has been strongly supported by evidence from wood anatomy (van Vliet, 1976; Baas, pers. comm.). Additionally, the result of the computer search by Dr. Wheeler, which incorporated wood anatomical data of about 5,000 dicotyledonous species representing all major and many minor woody genera, confirms that Anisophylleaceae agree completely with *Carallia* and largely with *Crossostylis* and *Gynotroches*; all three of these genera are Rhizophoraceae sensu stricto. In terms of wood anatomy, therefore, Rhizophoraceae undoubtedly agree most closely with Anisophylleaceae, and Baas (pers. comm.) suggested that this evidence rules out many other families as close relatives. Nonetheless, overall evidence from many other lines of investigation, including embryology, makes it absolutely clear that Rhizophoraceae and Anisophylleaceae belong to different evolutionary lines (Tobe & Raven, 1987a, 1988a; Dahlgren, this volume).

What then are their relatives? Dahlgren (this volume) proposed that Rhizophoraceae be placed in Celastrales along with Celastraceae and Elaeocarpaceae, and we agreed with this suggestion on the basis of embryological evidence (Tobe & Raven, this volume). It seems, therefore, to be the best available hypothesis. Concerning the affinities of Anisophylleaceae, we proposed Myrtales on the basis of embryological evidence (Tobe & Raven, 1987a); in contrast, Dahlgren (this volume) suggested that they belonged in Rosales sensu stricto. On the basis of our analysis (Tobe & Raven, 1988a), Dahlgren concluded that the floral structure of Anisophylleaceae agreed completely with that of Rosales sensu stricto.

Rosales sensu Dahlgren (= Rosales sensu stricto in the following discussion), for comparison with Anisophylleaceae, comprise Crossosomataceae, Rosaceae, Malaceae, Neuradaceae, and Amygdalaceae (Dahlgren, 1983, this volume). Crossosomataceae have often been placed in Dilleniales (e.g., Melchior, 1964; Takhtajan, 1980). On the basis of embryological evidence, Kapil (1970) supported this traditional treatment and rejected the inclusion of Crossosomataceae in Rosales. Despite this, we are not aware of any essential difference in embryological features between Crossosomataceae and Rosaceae, and therefore disagree with Kapil's view. Except for Crossosomataceae, these families are closely related; they are often grouped into a broadly defined family Rosaceae (e.g., Thorne, 1983). Among them, Crossosomataceae, Rosaceae, and Malaceae are relatively well known embryologically, but Neuradaceae and Amygdalaceae are poorly known. The embryological features of Rosales sensu stricto, on the basis of available data, are surveyed in our paper on the embryology of Rhabdodendraceae (Tobe & Raven, 1988b), which is also assigned by Dahlgren (1983) to Rosales sensu stricto. If we compare the embryological features of Anisophylleaceae (see Tobe & Raven, 1987a, for data) with those of Rosales sensu stricto (see Tobe & Raven, 1988b, for data), we find that although Anisophylleaceae share many embryological features with Rosales sensu stricto, the family is distinguished from Rosales sensu stricto in having vascularized integuments, no hypostase, no persistent nucellar tissue in the mature seed, a two-cell-layered thin inner integument (mostly thicker in Rosales sensu stricto), no obturator, and no endosperm in the mature seed. These embryological features suggest strongly that Anisophylleaceae, even though there are some points of similarity to Rosales sensu stricto, do not belong in that order.

We have searched for combinations of embryological features similar to that found in Anisophylleaceae among groups related to Rosales sensu stricto such as Saxifragales sensu Dahlgren. This order comprises 11 families, including several families of "Glossulariineae," a group to which Cronquist (1981, 1983) considered Anisophylleaceae to belong. We also considered Cunoniales sensu Dahlgren (five families) as possible relatives. We found that Anisophylleaceae are clearly distinct from Saxifragales in lacking the Cellular- or Helobial-type endosperm formation and a persistent endosperm in the mature seed, characteristic features of Saxifragales. As regards Cunoniales, the five constituent families (Cunoniaceae, Baueraceae, Brunelliaceae, Davidsoniaceae, and Eucryphiaceae) are so poorly known embryologically that an adequate comparison with Anisophylleaceae on this basis is not possible at present.

As discussed above, Anisophylleaceae differ strongly from Rosales sensu stricto and Saxifragales in their very different combinations of embryological features. Once more, we emphasize that Anisophylleaceae, on the basis of their embryological features, most closely resemble Myrtales (see Tobe & Raven, 1987a), although Anisophylleaceae do not share the characteristic wood anatomical features of Myrtales (i.e., intraxylary phloem and vestured pitting; see van Vliet & Baas, 1984). Myrtales are generally considered to be allied to Rosales(–Saxifragales–Cunoniales) (e.g., Takhtajan, 1980; Cronquist, 1981; Dahlgren & Thorne, 1984). Compared with Rosales sensu stricto and with Saxifragales, Anisophylleaceae and Myrtales apparently share at least one apomorphy, namely, the lack of endosperm in mature seeds. In contrast, Rosales sensu stricto and Saxifragales are apparently more specialized than Anisophylleaceae and Myrtales in other embryological characteristics. For example, in Rosales sensu stricto the inner integument is thicker than the outer one, a feature found only in derived families (Boesewinkel, 1981); and Saxifragales have a Cellular- or Helobial-type endosperm formation, which predominantly occurs in sympetalous groups with a tenuinucellate ovule (Dahlgren, 1975). Therefore, even though the floral morphology of Anisophylleaceae closely resembles that of Rosales sensu stricto(–Saxifragales) (Dahlgren, this volume; see also Cronquist, 1981, 1983), Anisophylleaceae seem, on the basis of their embryological features, to represent a different evolutionary line.

In conclusion, we need further information on the embryology of Rosales sensu stricto and particularly of Cunoniales for more critical comparison. Meanwhile, however, considering evidence of various kinds, it seems appropriate to conclude that Anisophylleaceae, like Myrtales, are one of the derivatives from the common ancestor of Rosales–Saxifragales–Cunoniales. Anisophylleaceae may or may not be directly related to Myrtales, but they do appear to be at approximately the same evolutionary level as that order, at least with respect to embryological features. It might be most appropriate, at least for the time being, to regard Anisophylleaceae as constituting a distinct order in this general phylogenetic lineage.

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NEW SPECIES AND A NEW COMBINATION FOR PLANTS FROM TRANS-ANDEAN SOUTH AMERICA[1]

Alwyn H. Gentry[2]

ABSTRACT

Eight new species from the trans-Andean parts of Colombia, Ecuador, and Peru are described, each in a different family. The new species are: Bonamia leonii *(Convolvulaceae)*, Prockia pentamera *(Flacourtiaceae)*, Marila parviflora *(Guttiferae)*, Lozania glabrata *(Lacistemataceae)*, Rouchera monsalveae *(Linaceae)*, Carapa megistocarpa *(Meliaceae)*, Desmoncus cirrhifera *(Palmae)*, *and* Allophylus dodsonii *(Sapindaceae). In addition, a new combination for* Albizia paucipinnata—Pithecellobium paucipinnatum—*is proposed.*

In the course of preparing local florulas in western Colombia (*A Checklist of Plants of Chocó Department, Colombia* (Forero & Gentry, in press), *Flora de Bajo Calima* (Gentry & Monsalve, in prep.), and Ecuador (*Flora of Capeira* (Dodson & Gentry, in press), *Flora of the Río Palenque Science Center*, Revised edition (Dodson & Gentry, in prep.)) we have encountered the following eight novelties, each in a different family. In addition, a new combination is needed for one of the species included in the Capeira florula.

CONVOLVULACEAE

Bonamia leonii A. Gentry & Austin, sp. nov. TYPE. Colombia. Chocó: Municipio de Riosucio, Parque Natural Nacional "Los Katyos," Camino Tilupo Alto via Sautatá, desviando por el camino a Tilupo Salto parte baja, 250–100 m, bejuco, flor lila, 25 Feb. 1976, *H. León 525* (holotype, COL; isotype, MO).

Frutex scandens, ramulis tomentosis. Folia ovata, acuminata, dense tomentosa. Cyma densa, axillaris, pedunculo 1–3 cm longo. Sepala 6–7 mm longa, extima elliptica, obtusa, puberula; corolla infundibuliformis, ca. 1.5 cm longa, extra pilosa. Fructus ignotus.

Liana, the stems densely tannish-tomentose, becoming partially glabrescent. Leaves ovate, sharply acuminate, rounded at base, 8–15 cm long, 3–6.5 cm wide; densely tomentose with golden tannish trichomes, these forming a slightly thickened base, erect with curving tips, appearing macroscopically ± sericeous; petiole 0.3–2 cm long, tomentose. Inflorescence a compound axillary cyme, rather dense, ca. 3 cm across, the peduncle 1–3 cm long; bracts and bracteoles narrowly oblanceolate, tannish tomentose, to ca. 8 mm long. Flowers with the sepals 6–7 mm long, subequal (outermost somewhat longer), the outermost elliptic with obtuse tips, the inner sepals ovate with ± acute tips, appressed puberulous; corolla (only 1 seen) infundibuliform, lilac, ca. 1.5 cm long, pilose outside, slightly lobed, the lobes ca. 2 mm long; stamens 5, the anthers 2–2.5 mm long, on slender glabrous 3–4 mm long filaments; styles 2, free to near base, glabrous, the stigmas biglobose. Fruit not seen.

Known only from Parque Natural Nacional "Los Katyos" in northern Chocó Department of Colombia.

This plant was originally identified tentatively as *Tetralocularia pennellii* O'Donell; however, it does

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ANN. MISSOURI BOT. GARD. 75: 1429–1439. 1988.

not closely resemble that monotypic genus and clearly belongs to *Bonamia*. In Myint & Ward's key to *Bonamia* (Phytologia 17: 121–239. 1968) this new species will key out with three species that they recognize from Southeastern Brazil—*B. agrostopolis* (Vell.) Hall. f., *B. burchellii* (Choisy) Hall. f., and *B. tomentosa* Hassler. All of these have the upper leaf surface densely pubescent and belong to sect. *Trichantha*. Recently, Austin & Staples (unpubl.) examined the types of these Brazilian names and concluded that they represent a single variable species that should be known as *B. agrostopolis*. This Brazilian species differs from *B. leonii* in having slightly smaller leaves; scalelike, linear, caducous bracts only 2–3 mm long rather than oblanceolate, persistent bracts ca. 8 mm long; corolla 2–3 cm long vs. 1.5 cm long; villous lower filaments; and a reniform to sub-bilobed rather than biglobose stigma.

Bonamia leonii appears to be most closely related to *B. trichantha* H. Hallier of northwestern South America and Mesoamerica and to *B. apurensis* Austin of Amazonian Venezuela. Although *B. trichantha* and *B. leonii* overlap geographically, they appear to be ecologically separated, with *B. trichantha* usually found in drier, more seasonal habitats. *Bonamia trichantha* differs further in having white flowers, more glabrescent leaves with glabrous or very sparsely puberulous upper surfaces, and densely glandular pubescent rather than glabrous filament bases.

Allopatric *B. apurensis* is the only *Bonamia* described (*Flora de Venezuela* 8(3): 40. 1982) since Myint & Ward's monograph. That species differs from *B. leonii* in the more broadly ovate leaf shape, cordate base, obtuse apex, more glabrescent upper leaf surface, simple capitate stigma, and especially the larger, more openly corymbose inflorescence with elongate peduncles (12–14 cm long in the MO isotype vs. 1–3 cm long in *B. leonii*).

It is a pleasure to dedicate this distinctive species to its collector, Henry Léon, who made extensive collections in the Katíos Park area of northern Chocó Department, where it is apparently endemic.

FLACOURTIACEAE

Prockia pentamera A. Gentry, sp. nov. TYPE. Peru. Tumbes: Prov. Contralmirante Villar, Huasimo, Quebrada Ucumares, 550 m, 12 Feb. 1976, *T. Plowman 5443* (holotype, USM; isotype, GH, photocopy MO).

Arbor parva. Folia late ovata, acuta vel breviter acuminata, ad basim truncata vel cordata. Flores 2–2.8 cm diametro, sepalis 5, ovatis, ca. 10 mm longis, petalis 5, dense tomentosis, stigmate 5-lobato.

Small tree 5–6 m tall, the bark rough, dark brown, the branchlets appressed puberulous when very young, soon glabrescent except at nodes, lenticellate, the stipules tiny and apparently (only one seen) very early caducous, linear, less than 1 mm long, with a pair of thick yellow glands in lower half. Leaves ovate to broadly ovate, acute to short-acuminate, the base truncate to broadly and shallowly cordate, with 2–4 basal glands at petiole insertion above, membranaceous, glabrous above except for small appressed trichomes on midvein, below rather sparsely hirtellous to glabrous over surface, persistently pubescent at least in and above axils of lateral nerves, serrate, 2.5–15 cm long, 1.3–12 cm wide, 5-nerved from base; petiole 0.5–3.5 cm long, pubescent with appressed or erect trichomes. Inflorescence of 2–3 flowers at end of lateral branches, the slender peduncle ca. 5 cm long, the pedicels 0.5–1 cm long, puberulous with mostly subappressed trichomes. Flowers green when fresh, the sepals five, densely grayish tomentose, ca. 10 mm long, 3–8 mm wide; the petals 5, narrowly oblong, acute, rather densely tomentose, about as long as sepals; stamens inserted on receptacle, the filaments glabrous; ovary subglobose, glabrous, the style ca. 4 mm long, the stigma distinctly 5-lobed. Fruit not seen.

Endemic to the now mostly destroyed dry forest of southwestern Ecuador and extreme northwestern Peru.

Additional specimens examined. ECUADOR: GUAYAS: Capeira, km 21, Guayaquil to Daule, 20–200 m, tropical dry forest, 17 Feb. 1982 (st), *Dodson & Gentry 12588* (GUA, MO, SEL). PERU. TUMBES: Cerros de Amotape 15–25 km SE of Cherrelique, 600–800m, premontane moist forest along Quebrada Los Conejos, 4°9'S, 80°37'W, 9 June 1987 (st), *Gentry & Díaz 58225* (MO, USM); Cerros de Amotape, Quebrada Los Conejos ca. 25 km SE of Cherrelique, 820 m, premontane moist forest, 4°9'S, 80°37'W, 9 June 1987 (st), *Gentry & Díaz 58245* (MO, USM).

Prockia pentamera, only the third species of *Prockia*, is very distinct from its closest relative, *P. crucis* L. *Prockia crucis* (fide Sleumer, 1980) is extremely polymorphic but always has smaller flowers (8–14 mm in diameter, with sepals and petals 4–7 mm long) with 3 (rarely 4) sepals, 3 petals (sometimes none by abortion), and a 3-lobed stigma, whereas all these parts are in 5s in *P. pentamera*. *Prockia pentamera* is the only pentamerous species of *Prockia*, necessitating changes in Sleumer's (1980) generic circumscription. Further, the leaves of *P. pentamera* are generally larger than in *P. crucis*, although only the largest exceed the largest extremes (to 10(–15) × 5(–10) cm) of the latter species. In *P. crucis*, the stipule is rather foliaceous, 5–8(–17) mm long, and persistent, unlike the minute (less than 1 mm long), early caducous stipule of *P. pentamera*.

This species was first collected as a sterile transect voucher at Capeira, near Guayaquil. During fieldwork for the *Florula of Capeira* (Dodson & Gentry, in press), we were unable to discover it in fertile condition despite repeated visits to the single tree. I tried comparing this sterile material in several herbaria with *Prockia* and related genera of Flacourtiaceae (as well as with *Morus* to which it has a superficial resemblance), but was unable to match it and decided that it must be undescribed.

When first found, there were numerous seedlings under the single capeira tree, but in 1985 both tree and seedlings were burned in one of the fires that devastate the remnants of dry forest in coastal Ecuador during the dry season. It seemed possible that an undescribed species had gone extinct. However, in the Universidad de San Marcos herbarium (USM) in Lima, I came across the fertile Plowman collection, which is here designated the type of *P. pentamera*.

Subsequent fieldwork in Tumbes, Peru, shows that *P. pentamera* can be locally very common in dry forest remnants. Indeed, it turns out to be the tenth-commonest species in a study site in the Cerros de Amotape, where there were eight individual plants of this species at least 2.5 cm dbh in a 0.1-ha sample; the largest tree measured 17 cm dbh (Díaz & Gentry, in prep.).

GUTTIFERAE

Marila parviflora A. Gentry, sp. nov. TYPE. Colombia. Valle: Bajo Calima, ca. 10 km N of Buenaventura, Cartón de Colombia concession, transition between tropical wet and pluvial forest, ca. 50 m, 3°56′N, 77°08′W, *H. Mazuero 47* (holotype, CUVC; isotype, MO, fragment and photocopy, IBE). Figure 1.

Arbor. Folia oblongo-ovata, acuta vel breviter acuminata. Inflorescentia spicato-racemosa, 9–13 cm longa, pedicellis 1–2(–3) mm longis. Flores 2 mm longi, petalis 2 mm longis, caducis, staminibus numerosis, ovario glabro.

Tree. Leaves simple, opposite, rigid-coriaceous, oblong-ovate, acute to short-acuminate at apex, obtuse at base, 14–19 cm long, 6–10 cm wide, drying dark gray-brown above, tan below, densely appressed-puberulous below on main veins, sparsely and ± glabrescently so over surface, the secondary nerves almost at right angle to midvein, 23–25 on a side, 4–8 mm apart, anastomosing with a strong submarginal collection vein; petiole 1.5–2.5 cm long. Inflorescences spicate-racemose, usually 3 per axil, the slender rachis 9–13 cm long, ca. 1 mm diam., puberulous with suberect trichomes, the pedicels 1–2(–3) mm long. Flowers tiny for the genus, 2 mm long, the sepals subappressed puberulous, 2 mm long; petals caducous, thinly membranaceous, strap-shaped, 2 mm long; stamens many, free, about as long as sepals, the minute anthers subglobose with the connective thick and patelliform-glandular; pistil ca. 2.5 cm long, the ovary ovoid, glabrous, the style linear, the stigma truncate, subcapitate.

Known only from the type locality, which appears to be in an area of high species richness for the genus. Cuatrecasas (1949) described five new species and a new variety of *Marila* from the central Pacific coastal region of Colombia. Two of these, *M. micrantha* and *M. geminata*, are closely related to *M. parviflora* by their very small flowers; indeed, *M. parviflora* and *M. micrantha* have the smallest flowers in the genus. Unique among described species of *Marila* is the almost spicate inflorescence of *M. parviflora*. *Marila parviflora* differs from *M. micrantha*, presumably its closest relative, by having shorter pedicels (1–2 mm vs. 3–6 mm long) and consequently spiciform inflorescence, inflorescences several per node (rather than solitary), larger, obtuse-based leaves with over twice as many straight (rather than arcuate-ascending) lateral veins, and subcapitate stigma. The other close relative of *M. parviflora* is *M. geminata*, which has similar multiple inflorescences at each node but distinctly larger flowers (sepals 3.5–4 mm long) and longer pedicels (4–7 mm long). The leaves of *M. geminata* differ in being larger and having acute bases and longer petioles and especially in the lateral nerves averaging almost twice as far (8–10 mm) apart.

An undescribed species of *Marila* from Amazonian Peru has a similarly spicate inflorescence but is amply distinct from *M. parviflora* (McDaniel, pers. comm.).

LACISTEMATACEAE

Lozania glabrata A. Gentry, sp. nov. TYPE. Colombia. Chocó: north ridge of Alto de Buey above Dos Bocas del Río Mutatá, tributary of

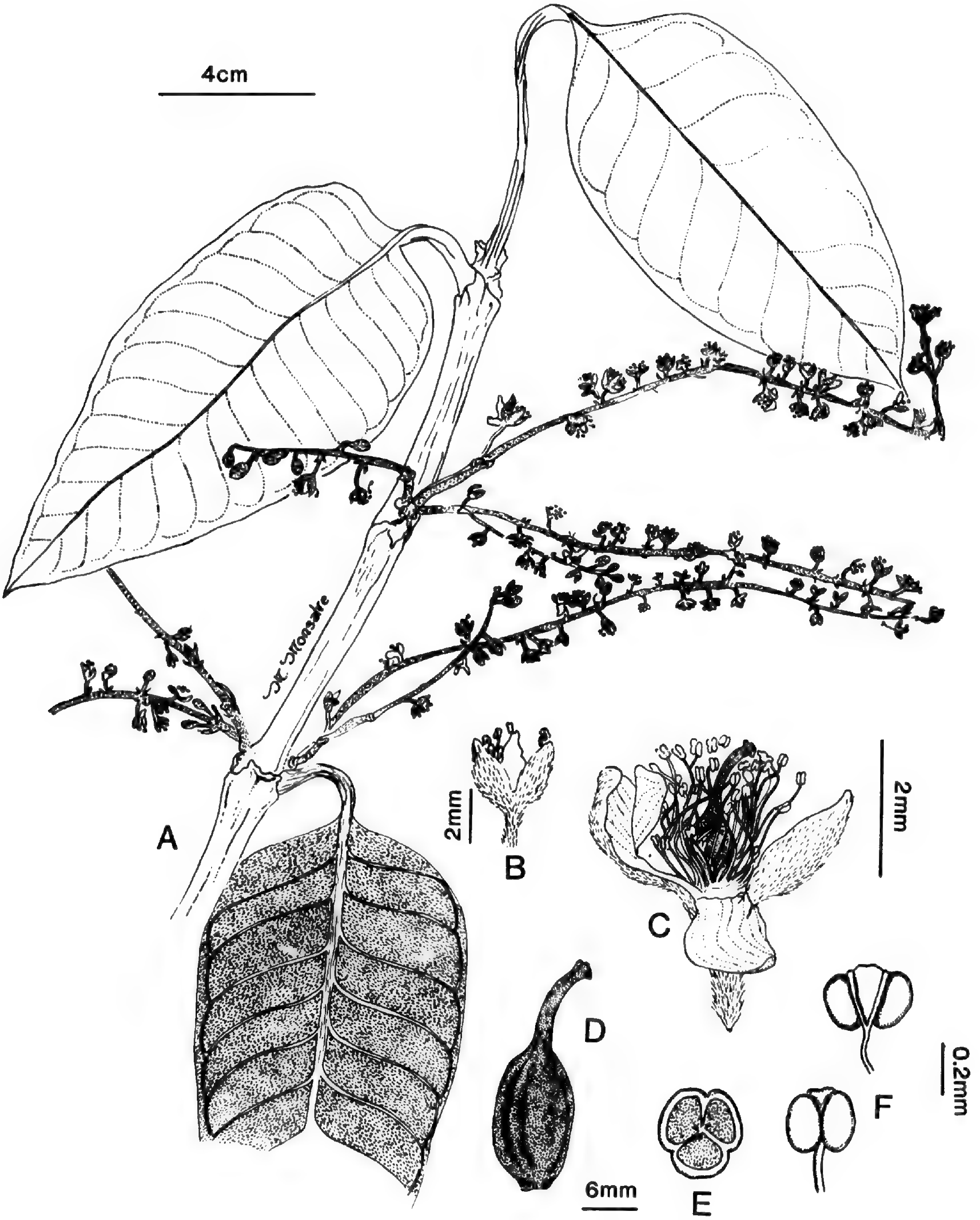

FIGURE 1. Marila parviflora (Mazuero 47).—*A. Habit.—B. Post-anthesis flower with petals fallen.—C. Open flower.—D. Pistil.—E. Ovary, cross section.—F. Anthers.*

Río El Valle, ESE of El Valle, 200–500 m, tropical and premontane wet forest, 8 Aug. 1976, *Gentry & Fallen 17425* (holotype, COL; isotype, F, MO, NY, U, UTD).

Arbor, ramuli glabri. Folia oblongo-elliptica, acuminata, glabra, subintegra. Inflorescentia axillaris, peranguste racemosa, 6–10 cm longa. Flores marronini, sepalis 4, ovatis, filo singulari furcato. Fructus ellipsoideo-trigonus, dehiscens, semine singulari.

Tree 6 m tall. Branchlets glabrous. Leaves oblong-elliptic, acuminate, cuneate at base, membranaceous, completely glabrous above and below, subentire to very inconspicuously serrulate, 9–16 cm long, 3.5–5 cm wide, the tertiary veins perpendicular to the midvein and ± parallel (but not as strikingly so as in other *Lozania* species); petiole 0.7–1.2 cm long, grooved above, glabrous or very inconspicuously puberulous with a few minute scattered trichomes. Inflorescence a long, slender, subspicate, axillary raceme, mostly in fascicles of several per node, 6–10 cm long, sparsely puberulous, the adjacent flowers separated by ca. 5 mm, the pedicels glabrous, ca. 1 mm long, subtended by a bilobed cupule formed by two 0.3-mm-long, sessile, basal bracteoles. Flowers with the sepals 4, ovate, spreading, ca. 1 mm long, maroon when fresh, drying dark brown with a brown-flecked cartilaginous apex and margin; petals absent; stamen 1, the short thick filament ca. 0.3 mm long, deeply forked apically, each side with a subglobose anther ca. 0.3 mm long, the ovary broadly ovoid, ca. 0.5 mm long, glabrous, the blunt apex with 3 slender, reflexed style branches ca. 0.2 mm long; ovary and stamen surrounded by a thick extra-staminal ± 4-lobed disk 1 mm across. Fruit irregularly ellipsoid-trigonous, 6–7 mm long and 4–6 mm wide, splitting incompletely at apex into 3 valves, with a single round orangish 5-mm-long and 4–5-mm-wide seed.

This is easily the most distinctive species of *Lozania*, a small genus traditionally assigned to Lacistemataceae but placed by Sleumer (1980) in Flacourtiaceae. It is closest to *L. mutisiana* J. A. Schultes on account of its very short filament and glabrous pedicels and sepals, although the relatively large fruit is closer to that of Amazonian *L. klugii* (Mansfeld) Mansfeld. *Lozania glabrata* is the only species of *Lozania* with glabrous leaves; the subentire leaf margin is also unusual, being approached only by occasional variants of *L. klugii*. The longest inflorescences are the longest in the genus, although shorter inflorescences are equalled by those of the type specimen of *L. bipinnata* L. B. Smith (a species merged into *L. mutisiana* by Sleumer but perhaps better maintained as distinct). *Lozania glabrata* is unique in the genus in the deeply split filament apex, which gives the illusion of two stamens.

LINACEAE

Rouchera monsalveae A. Gentry, sp. nov. TYPE: Colombia. Valle: Bajo Calima, Pulpapel concession, 100 m, bosque pluvial tropical, 3°55′N, 77°W, 14 Dec. 1984, *M. Monsalve 631* (holotype, CUVC; isotypes, MO, and to be distributed).

Arbor. Folia obovata, obtuse cuspidata vel acuminata, ad basim cuneata, margine subtiliter crenulata. Inflorescentia axillaris, fasciculata vel perbreviter racemosa. Flores lutei, petalis glabris, filis 10, ad basim connatis. Fructus ignotus.

Tree 6(–30?) m tall, mostly glabrous, inconspicuously puberulous on young branches, elenticellate, the stipules tiny, 1 mm long, caducous. Leaves alternate, obovate, oblanceolate when young, 2–8 cm long (–15 cm in juvenile state), 1–3.5 cm wide, obtusely cuspidate to acuminate at apex, the base cuneate, the margin finely and conspicuously crenulate, chartaceous to subcoriaceous, drying dark gray or olive gray above, tannish olive below, the secondary and intersecondary veins indistinguishable, close together, finely parallel, with an inconspicuous collecting vein ca. 0.5 mm from the margin, minutely glandular-punctate below, also with somewhat larger scattered disk-shaped glands, subsessile, the poorly defined petiole 1–3 mm long. Inflorescence a sessile or subsessile axillary fascicle of few flowers, sometimes extended as a contracted raceme or spike to 10 mm long with 2–3(–5)-mm-long peduncle, the flowers subtended by bracteoles 1–2 mm long, these glabrous except the ± ciliate margin. Flowers yellow; sepals 5, oblong, 2–3 mm long, glabrous except for the ± ciliate margin; petals narrowly obovate, contracted at base, to 5 mm long, completely glabrous; stamens 10, the filaments ca. 3 mm long, fused into a ca. 0.5-mm-long basal tube, the anthers flattened-globose, ca. 0.6 mm long; pistil glabrous, the ovary ovoid, ca. 1 mm long, the 3 styles separate, each with a discoid stigma. Fruits unknown.

Known only from Bajo Calima.

Additional specimen examined. COLOMBIA. VALLE: Bajo Calima, ca. 10 km N of Buenaventura, ca. 50 m, 3°56′N, 77°08′W, 13 Dec. 1981, *Gentry 35624* (CUVC, MO).

Common name. Juana se va.

The genus *Rouchera* has been used in a broad sense to include Asian and African lianas with hooked processes for climbing and in a narrow sense to exclude *Hebepetalum*, which differs in having hairy petals with a clawed base. *Rouchera* sensu stricto and *Hebepetalum* (now mostly included in *Rouchera*) are South American. This new species is most closely related to *R. calophylla* Planch., the type of the genus, and to *R. parviflora* (Ducke) Ducke. These are the only other species with reduced inflorescences and sessile or subsessile axillary flowers. *Rouchera calophylla*, which occurs in central and eastern Amazonia, differs in having more membranaceous narrower, narrowly oblong-elliptic leaves with less conspicuously crenate margins, better-defined petioles, and much longer (to 1 cm) petals. *Rouchera parviflora,* which occurs near Manaus in central Amazonian Brazil, has leaves similar to *R. calophylla* but smaller. According to the original description, it differs from *R. monsalveae* by its suborbicular, distinctly gland-margined sepals, completely glabrous young branches, and apparently larger flowers ("floribus dimidio brevioribus" compared with *R. calophyllum*). Although I have seen no material of *R. parvifolia* and the description is incomplete, its habitat (wet forest on sand) and distribution strongly argue against conspecificity with the coastal Colombian plant.

Only two other species of *Rouchera* are known from coastal Colombia. One is the very different *R. humiriifolia* (sometimes segregated as *Hebepetalum*), which has terminal paniculate inflorescences and white flowers with hairy petals. In view of the controversy over generic limits, it is interesting that at Bajo Calima *R. humiriifolia* bears the same common name as *R. monsalveae.* The second coastal Colombian species, *R. colombiana* Hall., differs according to the original description by its chartaceous leaves, petioles 6–8 mm long, collecting vein 2 mm from the leaf margin, flowers in a lax short-pedunculate axillary cyme, and especially by the conspicuous persistent stipule 5 mm long.

MELIACEAE

Carapa megistocarpa A. Gentry & Dodson, sp. nov. TYPE. Ecuador. Pichincha: Centinela, km 12 carretera Patricia Pilar–24 de Mayo, cima de las Montañas de Ila, 650 m, 26 July 1984 (fl, fr), *Dodson, Gentry, Palacios & Zaruma 14492* (holotype, MO; isotypes, MO, QCNE). Figure 2.

Arbor 15–20 m. Folia foliolis 7–multi-jugatis, oblongis, apiculatis vel acuminatis, ad basim rotundatis. Inflorescentia cauliflora, 27–50 cm longa, anguste paniculata. Flores calyce 4-lobato, staminorum tubo cylindrico. Fructus permagnus, ellipsoideus, apiculatus, 17–29 cm longus.

Slender unbranched or few-branched tree 15–20 m tall, to 20 cm diam., the branch apices conspicuously bracteate. Leaves with 7 or more leaflet pairs, the petiole and rachis woody, glabrous, finely longitudinally ridged, the leaflets oblong, apiculate to abruptly acuminate at apex, rounded at base, 17–55 cm long, 8–16 cm wide, coriaceous, completely glabrous. Inflorescence cauliflorous, borne usually several together from short shoots on main trunk, 27–50 cm long, irregularly scaly, otherwise glabrous, very narrowly paniculate, the longest (basal) side branches occasionally to 8 cm long. Flowers slender-pedicellate, white with greenish petals and yellowish nectary, functionally unisexual, the calyx 4-lobed to base, the lobes less than 1 mm long, the petals 4, broadly ovate, 4–5 mm long, glabrous, not ciliate, the staminal tube broadly cylindric, not urceolate, 4–5 mm long, apically split into 8 narrowly triangular acute or acutish lobes, the sessile anthers (or antherodes) alternating with lobes of staminal column, the pistil (or pistillode in male flowers) with a conspicuously discoid style-head, the nectary annular-pulvinate, yellowish when fresh. Fruit very large, ellipsoid, not at all tetragonal nor angled and lacking verrucose ridges, 17–29(–30?) cm long without the 1–3 cm-long apiculus, 13–16 cm diam., the surface uniformly brownish, even when young, covered with dense scalelike papillae.

Additional specimens examined. ECUADOR: LOS RIOS: km 12 road from Patricia Pilar to 24 de Mayo, 540 m, 7 Oct. 1976 (fl), *Dodson & Gentry 6593* (MO, SEL). PICHINCHA: type locality, 30 Jul 1984 (fl), *Dodson, Gentry, Palacios, Zaruma 14676* (MO, QCNE).

Only two species were recognized in *Carapa* in the recent *Flora Neotropica Monograph* of Meliaceae (Pennington & Styles, 1981). One of these, *C. procera* DC., occurs in the Guianas and Central Amazonia, and in Africa; the other, very heterogeneous *C. guianensis* Aubl., is widespread in the Neotropics. One collection of the new species (*Dodson & Gentry 6593*) was cited under *C. guianensis,* although the description of *C. guianensis* disagrees with the plant described above in numerous characters.

Typical *C. guianensis* and *C. megistocarpa* grow sympatrically in our study area in western Ecuador, and we are convinced that they cannot possibly be conspecific. At least in our study area, *Carapa guianensis* is large, freely branching, ramiflorous (never cauliflorous), and lacks conspicuous bracts at the branch apices. Its flowers (Fig. 2) have a subtle but characteristically different, distinctively more urceolate shape, with the apices of the otherwise fused filaments bent inward and more truncate and more closely appressed than in *C. megistocarpa.* The staminal tube of our population of *C. guianensis* has orange suture lines and the nectary is orange, whereas in *C. megistocarpa* the staminal tube is uniformly white and the nectary is yellowish. Moreover, the fruits of the two species are consistently and dramatically different, as indicated in Table 1. This whole suite of consistent differentiating characters (Table 1, Fig. 2) in two

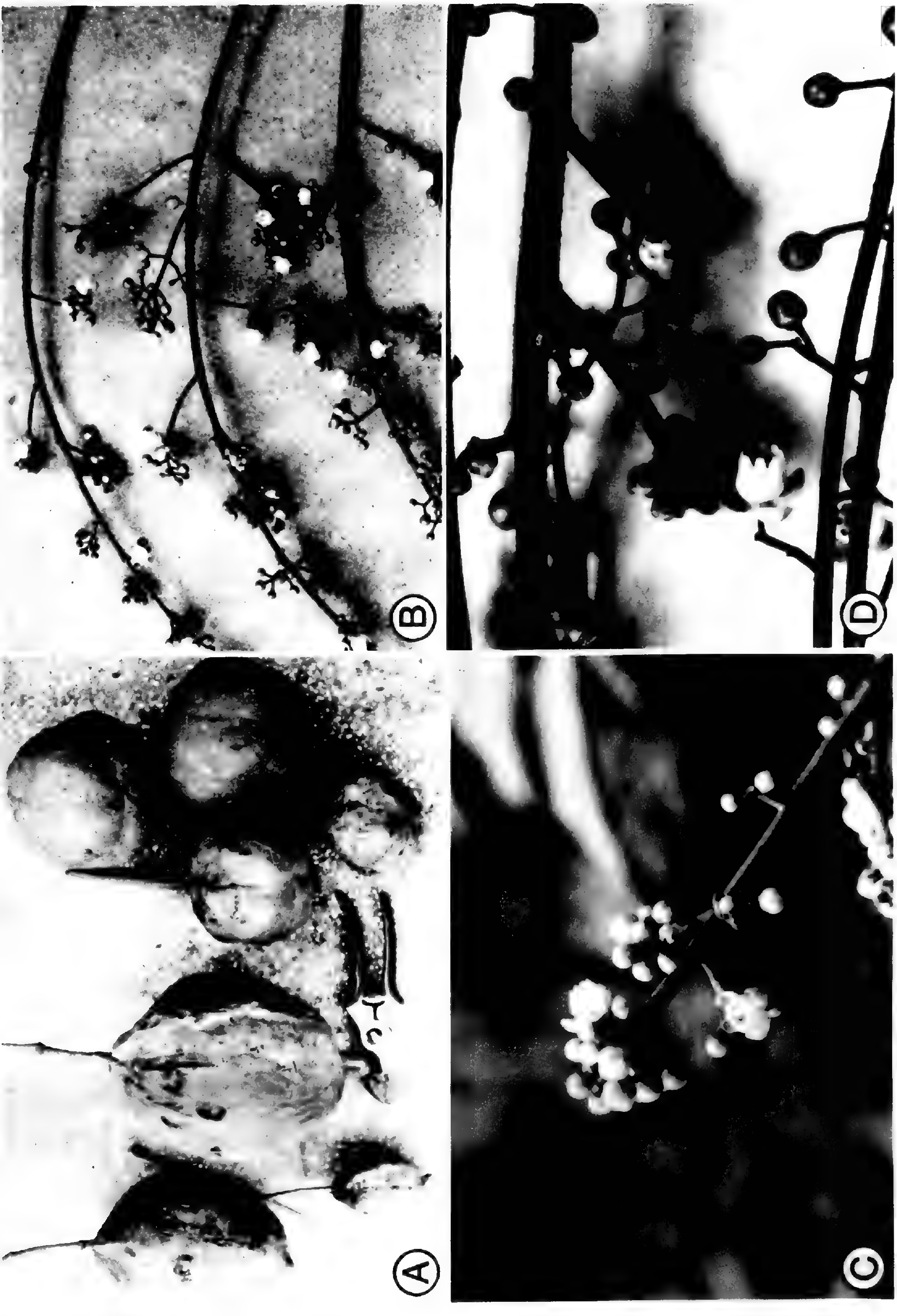

FIGURE 2. Carapa megistocarpa (Dodson et al. 14492) *and* C. guianensis (Dodson et al. 14675).—*A. Fruits (*C. megistocarpa *on left,* C. guianensis *on right; the shears are 20 cm long).—**B. Flowering inflorescences** of* C. megistocarpa.—*C. Flowering inflorescence of* C. guianensis.—*D. Closeup comparison of flowers of* C. guianensis *(top) and* C. megistophylla *(bottom).*

TABLE 1. *Features differentiating* Carapa megistocarpa *from* C. guianensis *at the Centinela study site.*

	C. guianensis	*C. megistocarpa*
Height	mostly 20–40 m	15–20 m
Habit	freely branching	unbranched or few-branched
Bracts at branch apices	lacking or inconspicuous	conspicuous
Inflorescence	ramiflorous on small branchlets	cauliflorous
Corolla	strongly urceolate	urceolate-tubular
Filament apices	truncate, bent strongly inward and closely appressed to adjacent apices	narrow, bent slightly inward and barely or not at all touching
Staminal tube	orange suture lines	uniformly white
Nectary	orange	yellowish
Fruit shape	subglobose to depressed-globose and slightly tetragonal	ellipsoid, not at all tetragonal
Fruit surface	greenish with numerous brown lenticels when young, each valve usually with a verrucose medial ridge	uniformly brownish, even when young, the valves unridged
Fruit size	11–14 cm long and wide[1]	17–30 cm long, 13–16 cm diameter
Fruit apex	truncate or depressed	apiculate (apicule 1–3 cm long)

[1] 5–10(–12) × 6–8(–10) cm fide Styles (in Pennington & Styles, 1981).

sympatric populations clearly mandates specific recognition. Although B. Styles (pers. comm.) maintains that the characters noted above and in Table 1 are variable elsewhere in the range of *Carapa*, they are quite constant in western Ecuador, where *C. megistocarpa* and *C. guianensis* clearly pass the test of sympatry.

In some characteristics *C. megistocarpa* is closer to *C. procera* than to *C. guianensis*, e.g., consistently slender-pedicellate flowers and ellipsoid fruit with valves lacking medial excrescences, but the 4- rather than 5-parted symmetry of its flowers and fruits seemed to relate *C. megistocarpa* definitively to *C. guianensis*. The fruit is the largest in the genus, the minimum length and width both always exceeding the maximum dimensions given for either species in the *Flora Neotropica* monograph, hence the epithet "megistocarpa."

Carapa megistocarpa was the fourth-commonest species in the Centinela forest, with 18 plants at least 2.5 cm dbh in a 1,000-m^2 sample area. Its amazing football-like cauliflorous fruits were one of the most characteristic features of this forest, famous for its high local endemism (Gentry, 1986; Dodson & Gentry, in prep.). Sadly, it may now be extinct, since the last remnants of the Centinela ridgetop have been converted to banana plantations.

PALMAE

Desmoncus cirrhifera Gentry & Zardini, sp. nov. TYPE. Colombia. Valle: Bahía Malaga, steep banks at edge of Mora swamp overlooking tidal stream, 0 m, 4°2′N, 76°15′W, 16 Dec. 1985, *A. Gentry, M. Monsalve, C. Restrepo and J. Gamboa 53392* (holotype, CUVC; isotypes, MO(2), COL, K). Figure 3.

Frutex scandens, sparse spinosus, spinis brevibus curvatis. Folia 25–60 cm longa, foliolis 5–9-jugatis, lanceolato-ellipticis, longicaudatis. Inflorescentia semel ramosa, 15–19 rachillis 1–3 cm longis. Fructus ellipsoideus vel subglobosus, 1.5–2 cm longus, 1–1.5 cm latus.

Spiny climbing palm (± erect when young) with stems (including the enclosing leaf sheath) 1–2 cm thick, the leaf sheath with occasional short thick-based spines < 4 mm long, these mostly ± recurved, glabrous except for small, appressed, irregularly branched reddish scales, extended above the node into an ocrea ca. 5 cm long, this unarmed or with an occasional small spine. Leaves 25–60 or more cm long, with 5–9 pairs of lanceolate-elliptic to narrowly elliptic, subopposite to definitely alternate, caudate-acuminate pinnae, these 6–21 cm long (not counting the acumen), 2–7 cm wide, the tendril-like linear acumen 4–11 cm long, pendent and often somewhat twisted when fresh, the surface glabrous except for minute scattered ± peltate scales, these mostly sessile and reddish, sometimes in part stalked, also with minute whitish scales or scalelike enations, the larger leaflets with somewhat larger, irregularly branching, appressed, reddish trichomes near margin below, the midvein prominent above and below, the other longitudinal veins relatively inconspicuous, the transverse veinlets slightly prominulous above in older leaflets; rachis with irregularly scattered thick-based straight or recurved spines 2–5 mm long; leaf apex linear and unarmed in juvenile state, in mature plants armed with small, strongly recurved spines 2.5–4 mm long, sometimes a few of these thicker and terminated with a reduced, very narrow, vestigial leaflet 4–6 cm long, this always thin and membranaceous; thick, elongate grappling hooks completely lacking at leaf apex. Inflorescence axillary, the peduncular inflorescence bract (spathe) caducous in fruit, the persistent basal part of the prophyll ca. 6–8 cm long, thin, unarmed, fibrous, fragmenting into the individual fibers; peduncle 11–14 cm long, the rachis once-branched with 15–19 rachillae, each 1–3 cm long, the lowermost progressively larger, the flowers not seen, loosely clustered along upper half to two-thirds of rachilla, this flattened and somewhat zigzag or twisted between adjacent flowers. Fruit 1-seeded, red, ellipsoid to subglobose, 1.5–2 cm long, 1–1.5 cm wide, subtended by a sessile 3-lobed cupule formed from the 3 persistent basally fused tepals, this ca. 5 mm across.

Endemic to the wet part of lowland coastal Colombia in Valle, Chocó, and (fide Galeano & Bernal, 1985) extreme northwestern Antioquia departments.

Additional specimens examined. COLOMBIA. VALLE: Bahía Malaga, Quebrada Alegria, trail along proposed route of new road to military base, 50 m, 4°2′N, 77°22′W, 15 Dec. 1985, *Gentry, Monsalve, Restrepo & Gamboa 53319* (CUVC, MO). CHOCÓ: Taparalito, Quebrada Taparal, N of Palestina, primary wet forest, 30 m, 4°15′N, 77°12′W, 30 Mar. 1985, *Gentry, Zardini, Monsalve & Caicedo 53795* (CUVC, MO); Quibdó–Tutunendó road ca. 3 km W of Tutunendó, pluvial forest, 80 m, 5°46′N, 76°35′W, 8 Jan. 1981, *Gentry, Mulampy, Hikes, Libenson, Olson & Cogollo 30363* (COL, MO).

Common name. Matamba.

The outstanding feature of the plant is its exceedingly long tendril-like leaflet apices. It belongs to Burret's (1934) section *Campylacanthium*, as indicated by its short curved spines, and it is the first record of that section in the trans-Andean Neotropics. John Dransfield, who examined a duplicate of one of the sterile collections cited above, identified it as a new species. Subsequently, this species was also recognized as undescribed by Gal-

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FIGURE 3. Desmoncus cirrhifera.—*A. Leaf and infructescence (*Gentry et al. 53392*).—B. Cut stems waiting to be made into baskets, Taparalito, Chocó, Colombia (*Gentry et al. 53795*).—C. Basket made from* D. cirrhifera, *Docordó, Colombia.*

eano & Bernal (1985) in their treatment of the palms of Antioquia Department. Again, sterile material prevented its description. Discovery of fruiting material finally makes possible its description.

Desmoncus cirrhifera is one of the most utilized palm species of the Pacific coast region of Colombia. It is used to make nets and shrimp traps (catangas) in the Bahía Malaga and Río San Juan delta areas (sub *Gentry et al. 53392*) and is prized by the Chocó Indians at Taparalito and Docordó who make their strongest baskets from it (Fig. 3C).

SAPINDACEAE

Allophylus dodsonii A. Gentry, sp. nov. TYPE. Ecuador. Los Ríos: Río Palenque Field Station, halfway between Quevedo and Santo Domingo de los Colorados, wet forest, 200 m, 21 Feb. 1974. *Gentry 10098* (holotype, MO; isotype, QCA; additional duplicates distributed as *A.* cf. *amazonicus*).

Arbor. Folia unifoliolata, elliptica vel obovato-elliptica, ad apicem obtusa vel subacuta, ad basim cuneata, margine subintegro. Inflorescentia axillaris, paniculata, ramis floriferis anguste racemosis, ascendentibus. Flores minuti, petalis intra pubescentibus. Fructus ellipsoideus, ca. 1 cm longus.

Tree 15–20 m tall, the branchlets ± glabrescently puberulous with mostly appressed trichomes. Leaves unifoliolate, elliptic or obovate-elliptic, the apex obtuse to acutish, the base cuneate, 6–28 cm long, 3–12 cm wide, membranaceous, the margin entire or inconspicuously crenulate-serrate near apex, almost glabrous, very sparsely and inconspicuously puberulous along midvein above and below, sometimes with few trichomes in axils of lateral nerves, with 10–14 secondary veins on a side, these curved and ascending; petiole 1–2 cm long to petiolule insertion, ± appressed puberulous, at least adaxially, apically jointed with flexed petiolular leaflet base. Inflorescence axillary, paniculate, the usually 3 elongate branches ascending and narrowly racemose, puberulous. Flowers (seen only in female condition) small, ca. 1 mm long and 2 mm across at full anthesis, white, on pedicels 1–2 mm long, the very broadly ovate sepals appressed-puberulous, the petals strongly pubescent inside, slightly pubescent outside, usually also ciliate-margined; stamens ca. 1 mm long, the tiny anthers presumably nonfunctional; pistil almost 2 mm long, the style apically forked to form 2 exserted stigmas almost 0.5 mm long. Fruits broadly ellipsoid, ca. 1 cm long, essentially glabrous.

Known only from the remnant patch of coastal Ecuadorian lowland wet forest at the Río Palenque Field Station.

Additional specimens examined. ECUADOR. LOS RÍOS: Río Palenque Field Station, 16 Feb. 1974 (st), *Gentry 9957* (MO), 7 Oct. 1976 (st), *Dodson & Gentry 6587* (MO, SEL), without date (fl), *Dodson 7343* (MO, SEL), 4 Apr. 1980 (fr), *Dodson & Gentry 10176* (MO, SEL).

This species was treated as *Allophylus* cf. *amazonicus* (Mart.) Radlk. in the *Flora of Río Palenque* (Dodson & Gentry, 1978). However, it differs conspicuously from that Amazonian species in the larger fruits, sparsely appressed puberulous branchlets, entire or subentire leaves, and especially the 3-branched rather than simply racemose inflorescence.

This was one of very few species in the Río Palenque flora interpreted as having a trans-Andean range disjunction, i.e., occurring on both sides of the Andes but not reaching Central America. Thus it is perhaps not surprising that the additional collections now available from both sides of the Andes prove the coastal plant specifically distinct.

LEGUMINOSAE

Pithecellobium paucipinnatum (Schery) Gentry & Dodson, comb. nov. *Albizia paucipinnata* Schery, Ann. Missouri Bot. Gard. 37: 400. 1950. TYPE. Ecuador. El Oro: Portovelo, *Steyermark 54035* (MO) . . . . as "*Albizzia.*"

This is a common tree species of the dry forests of the Guayaquil area of southwest Ecuador, especially in juvenile condition. At Capeira, 20 km N of Guayaquil (Dodson & Gentry, in press), there are about 10 trees at least 2.5 cm dbh per ha in the remnant patch of now highly disturbed dry forest. Although previously unreported from that country, it also occurs in adjacent northwestern Peru. At Capeira its common name is "compoño"; in Peru it is called "angolo."

This species was described as an *Albizia* by Schery, in the absence of fruiting material, and related by him to *Pithecellobium multiflorum* (HBK.) Benth. and *P. coripatense* Rusby of what is now generally known as *Pithecellobium* section *Arthrosamanea* (sometimes segregated as the genus *Cathormion*). These species grow mostly in swampy or riverine habitats and are characterized by a flattened segmented fruit that breaks apart transversely into numerous lomentlike segments, presumably adapted for water dispersal.

Generic delimitation in Mimosoideae is notoriously difficult, and Schery considered section *Arthrosamanea* as related to mostly wind-dispersed *Albizia* rather than mostly animal-dispersed *Pithecellobium*. Sometimes these taxa are accorded generic rank as *Arthrosamanea* (Britton & Rose, 1936) or *Cathormion* (Burkart, 1964). Others

(Brenan & Brummitt, 1965) suggested merging these taxa with *Enterolobium* instead. However, in nearly all neotropical floristic treatments, the indehiscent-fruited species of this alliance are nowadays included in *Pithecellobium* sensu lato (Macbride, 1943; Woodson & Schery, 1950), following Bentham (1875). Although a more recent summary (Nielsen, 1981) returns these plants to *Albizia* (along with some other segregates of *Pithecellobium*), we prefer to retain the indehiscent-fruited non-wind dispersed relatives in *Pithecellobium* following Barbosa (1984 and pers. comm.) and the long-standing tradition.

Vegetatively the taxa of *Pithecellobium* section *Arthrosamanea* are characterized by oblong, sessile, asymmetric leaflets with strongly ascending, almost palmate venation. *Pithecellobium* section *Arthrosamanea* is represented in the Guayaquil area by *P. daulense* Spruce ex Benth., which is vegetatively strikingly similar to *P. paucipinnatum* but has more-elliptic leaflets that are glabrous rather than puberulous as in *P. paucipinnatum*. That species, like other bona fide members of section *Arthrosamanea*, occurs in swampy, poorly drained areas along the Río Daule at Capeira, while *P. paucipinnatum* occurs in the upland dry forest.

We were at first inclined to treat the upland plant at Capeira as a variant of *P. daulense*; however, a collection of its fruits (*Dodson & Gentry 12652*; MO, GUA, SEL) proves that it is only distantly related to *P. multiflorum* and its allies. Indeed, the indehiscent fruits are quite unlike those of any *Pithecellobium* known to us, although probably most closely related to the very different but similarly indehiscent fruits of *Pithecellobium saman*. Superficially, there is a surprising resemblance to the fruits of *Hymenaea*, especially in the texture, color, and composition of their resinous-secreting surface.

The fruits of *P. paucipinnatum* are 12–14 cm long, 1.7–2 cm wide, straight, somewhat compressed, subwoody, reddish brown, glabrous, and pitted on the surface with minute resinous glands. Although obviously indehiscent, these fruits are interesting in that they break transversely rather easily, potentially indicating a shared ancestor with section *Arthrosamanea*. Since the fruits of this species are completely unlike the thin wind-dispersed fruits of *Albizia*, transfer to *Pithecellobium* seems appropriate.

Additional specimens examined. ECUADOR. GUAYAS: Capeira, 22 km N of Guayaquil 2°S, 79°58′W, 20–150 m, *Gentry & Dodson 54812* (MO); same locality, *Dodson & Gentry 12652* (MO). MANABI: base of Montecristi, 180 m, *Dodson & Thien 1716* (MO). EL ORO: Río Amarillo upstream from Portovelo, *Steyermark 54035* (MO). PERU. TUMBES: Zarumilla, Dtto. Matapalo, 550 m, Camino Caucho–Campo Verde km 79, *I. Canales P. 15* (MO, MOL).

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STUDIES IN NEOTROPICAL PALEOBOTANY. V. THE LOWER MIOCENE COMMUNITIES OF PANAMA— THE CULEBRA FORMATION[1]

Alan Graham[2]

Abstract

The lower Miocene Culebra Formation of central Panama consists of lignites and lignitic shales in a predominantly estuarian sandstone sequence. Forty-one palynomorphs have been identified from the lignites, and the following ten are most abundant: Monolete fern spore type 2 (20%), Manicaria*-type palm pollen (10%),* Cyathea *(8%),* Cryosophia*-type palm pollen (8%),* Selaginella *(7%),* Synechanthus*-type palm pollen (6%),* Rhizophora *(6%), monolete fern spore type 1 (5%),* Hampea/Hibiscus *(4%), and* Lycopodium *(2%). Ferns constituted 25% of the fossil flora, palms 24%, and lowland vegetation types totaled 71%. The most prominent paleocommunities were the tropical moist forest represented by 30 genera that can occur in this vegetation type (including an only moderately developed mangrove swamp), premontane wet forest (25 genera), tropical wet forest (22 genera), and possibly some form of the premontane moist forest (12 genera). Communities of higher elevations and dry to arid habitats (including savannahs) were poorly represented to absent. Paleoenvironments were similar to those of the present, including annual rainfall estimated at about 275–325 cm (107–128 inches). The rainfall probably decreased slightly with elevation, similar to the pattern shown in a transect from sea level to about 1,172 m from present-day Atlantic Costa Rica (353.6–188.9 cm). Annual temperature probably ranged between about 21°C and 32°C, as on adjacent Barro Colorado Island today. These estimates are consistent with the general paleotemperature curve derived from ^{18}O studies of marine invertebrates, and with emerging paleobotanical data from other Central America Tertiary floras. The geographic affinities of the Culebra flora are distinctly Central and North American, with all of the 41 taxa identified represented in the modern flora of Panama. Pollen of the Gramineae and shrubs of open, drier habitats continue to be rare or absent in Tertiary formations from southern Central America.*

The geologic formations of central Panama provide an opportunity to trace vegetational and paleoenvironmental history through five segments of Tertiary time. The Gatuncillo Formation exposed near Alcalde Díaz is of middle(?) to late Eocene age, and study of this paleoflora has been completed (Graham, 1985). The Culebra, Cucaracha, and La Boca formations are of lower Miocene age, and the Gatun Formation is upper Miocene/Pliocene in age (a recent estimate by Vokes, pers. comm., 1988, is that the Gatun Formation may be as young as middle Pliocene). All are known to contain fossil pollen and spores. These studies, together with those of Bartlett & Barghoorn (1973) on Quaternary vegetation, and information on the modern vegetation (Croat, 1978; D'Arcy, 1987; the recently completed *Flora of Panama*; and the Flora Mesoamericana project) will eventually provide a more complete data base for the vegetation of Panama and its Cenozoic evolution than for any other area in the Neotropics.

Concepts on the history of neotropical vegetation are being developed at a time when important new information is also becoming available on other aspects of the biotas. This allows comparison of the paleobotanical data with global paleotemperature and sea-level curves (Savin, 1977; Savin & Douglas, 1985; Savin et al., 1975; Vail & Hardenbol, 1979; Vail et al., 1977; Haq et al., 1987) and studies on marine invertebrates (Jones & Hasson, 1985) and terrestrial vertebrates (e.g., see papers in Stehli & Webb, 1985). This allows in-

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terpretation within an increasingly precise paleophysiographic context (Buskirk, 1985; Coney, 1982; Gose, 1985; Smith, 1985).

Other than a few megafossil studies done earlier in the century (see literature in Graham, 1973, 1979, 1982, 1986), the plant microfossils of the Culebra Formation provide only our second insight into lower Miocene vegetation of northern Latin America. The other is an assemblage from the lower Miocene Uscari sequence of Costa Rica (Graham, 1987a).

THE COLLECTING LOCALITY

The Culebra Formation belongs to a complex of lower Miocene strata in the Canal region of Panama (Graham et al., 1985: 489). Material was obtained from a well (Hole No. GH-9) drilled in January 1958 by the Panama Canal Commission. The site was near Gold Hill on the west side of the Canal at latitude 9°02′N, longitude 79°38′W. Fifty-seven samples were taken from lignites or lignitic shales along the 154-m core between levels 491.6 and 377, and 21 yielded pollen and spores. Eleven were selected for study from the following depths (in feet, following the original log data): 377, 407, 415.5, 425, 456, 469.8, 470.6, 488, 490.6, 491, and 491.6.

The 57 samples totaled approximately 9.5 feet of coalified lignite and lignitic shale (avg. ca. 2 inches/sample), with numerous narrow bands adding another ca. 1.5 feet (9.6%). The rest of the core was mostly sandstone (Graham et al., 1985: 489–491, tables 1, 2), and constituted ca. 103 feet (90.4%). Swift (1977) has studied Holocene sedimentation rates in the Panama Basin, but there have been no studies on the Culebra or other Tertiary formations. In general, near-shore sandstones and lignites deposited in an estuarian environment in tectonically active regions accumulate rapidly. In the absence of more precise data, the time span represented by the section is estimated at a few to several tens of thousands of years. Other details on the geology of the Culebra and related formations are given in Graham et al. (1985).

MATERIALS AND METHODS

Extraction and processing techniques are described in Graham (1985). Slides are labeled Pan Core, Culebra, with depth and slide number cited. Location of specimens on the slides is by England Slide Finder coordinates (e.g., ESF L-39, 1). All materials are deposited in the palynology collections at Kent State University.

SYSTEMATICS

Forty-one palynomorphs were identified from the Culebra Formation, and a number of others were recovered whose biological affinities could not be established. Some of the more distinctive and/or common ones are listed as Unknown types 1–14 in Table 1. Further details of the identification procedures are given in Graham (1985: 507–508).

LYCOPODIACEAE

Lycopodium (Figs. 1–3). Amb oval-triangular, apices rounded; trilete, laesurae straight, narrow, ca. 20 μm long, extending to and occasionally branching at spore margin, inner margin entire; distal surface with numerous circular punctae ca. 1 μm diam., proximal surface laevigate; wall ca. 1.5–2 μm thick; 35–37 μm.

These spores are similar to the modern *L. reflexum* Lam./*L. linifolium* L. type (cf. Tryon & Tryon, 1982: 811, fig. 22), presently growing in moist shaded habitats in Panama. Similar spores have been reported from the lower Miocene Uscari shale sequence in Costa Rica (Graham, 1987a).

SELAGINELLACEAE

Selaginella (Fig. 4). Spherical to nearly bilateral, amb circular to reniform; trilete, laesurae frequently obscured by wall thickness and sculpture elements, straight, narrow, ca. 20–22 μm long, extending nearly to spore margin, inner margin entire; echinate, echinae short (ca. 2 μm), occasionally curved, dense, bases broad; wall ca. 2 μm thick (excluding echinae); 26–30 μm.

Microspores of *Selaginella* vary in size, and specimens from the Culebra Formation are relatively small (26–30 μm) and thick-walled. They are common in the Gulf/Caribbean Tertiary and have been reported from all formations studied in the present project (Eocene Gatuncillo Formation of Panama, Graham, 1985; Oligocene San Sebastian Formation of Puerto Rico, Graham & Jarzen, 1969; lower Miocene Uscari sequence of Costa Rica, Graham, 1987a; lower Miocene Culebra Formation of Panama, present report; and upper Miocene Paraje Solo Formation of Veracruz, Mexico, Graham, 1976). *Selaginella* is widely distributed in tropical regions in shaded, humid habitats.

CYATHEACEAE

Cyathea (Figs. 7–9). Amb oval-triangular, apices rounded; trilete, laesurae straight, narrow, 14–16 μm long, extending to spore margin, inner

TABLE 1. *Identification and numerical representation of fossil palynomorphs from the lower Miocene Culebra Formation, Panama. Figures are percentages based on counts of 200, except levels 377–425, which are based on 100 due to lower concentration and only fair preservation of the specimens; these levels also contain high percentages of fungal spores.*

	491.6	491	490.6	488	470.6	469.8	456	425	415.5	407	377
Lycopodiaceae											
Lycopodium	12	1	—	—	3.5	—	—	3	4	—	—
Selaginellaceae											
Selaginella	13	5	6.5	6.5	7	9	2	12	10	5	3
Cyatheaceae											
Cyathea	9	9.5	12	7.5	5.5	7	7.5	5	8	—	—
Pteridaceae											
Pteris	—	—	—	2	—	—	1.5	—	—	—	—
Schizaeaceae											
Lygodium	—	—	2	3.5	—	—	1	—	—	—	—
Vittariaceae											
cf. *Antrophyum*	2	1.5	2	2	2	—	1	—	—	—	—
Trilete fern spores											
Type 1	—	—	1	—	1.5	—	—	—	1	—	—
Type 2	3	—	2	—	1.5	0.5	1	—	—	—	—
Type 3	—	—	—	—	2	—	2	—	—	—	—
Type 4	—	—	—	—	1	—		—	—	—	—
Marattiaceae											
Danaea	—	—	—	—	0.5	—	1	—	—	—	—
Monolete fern spores											
Type 1	9.5	8	5	8.5	2.5		5	4	1	2	—
Type 2	15.5	37	28	15.5	12.5	19	12.5	24	12	32	20
Type 3	—	—	—	—	—	0.5	1	—	—	—	—
Gramineae	—	—	0.5	—	—	—	0.5	—	—	1	—
Palmae											
Cryosophila-type	7.5	4.5	7.5	5	8.5	9	10	13	10	8	5
Desmoncus-type	—	—	—	1	0.5	—	—	—	—	—	—
Manicaria-type	—	8.5	7.5	10	5	22	7.5	10	15	15	15
Synechanthus-type	5.5	10.5	2.5	4.5	2		1.5	12	11	3	30
Aquifoliaceae											
Ilex	—	—	—	0.5	2.5	0.5	2.5	—	1	—	—
Chenopodiaceae/ Amaranthaceae	—	—	—	—	1	—	—	—	—	—	—
Combretaceae											
Combretum/Terminalia	—	—	—	0.5	3	—	1	—	—	—	—
Compositae	—	—	—	0.5	—	—	—	—	—	—	—
Connaraceae											
cf. *Rourea*	—	—	—	—	1.5	0.5	1	—	—	—	—
Dilleniaceae											
cf. *Doliocarpus*	—	—	—	—	—	0.5	0.5	—	—	—	—
Dioscoreaceae											
Dioscorea/Rajania	—	—	—	—	0.5	—	—	—	—	—	—

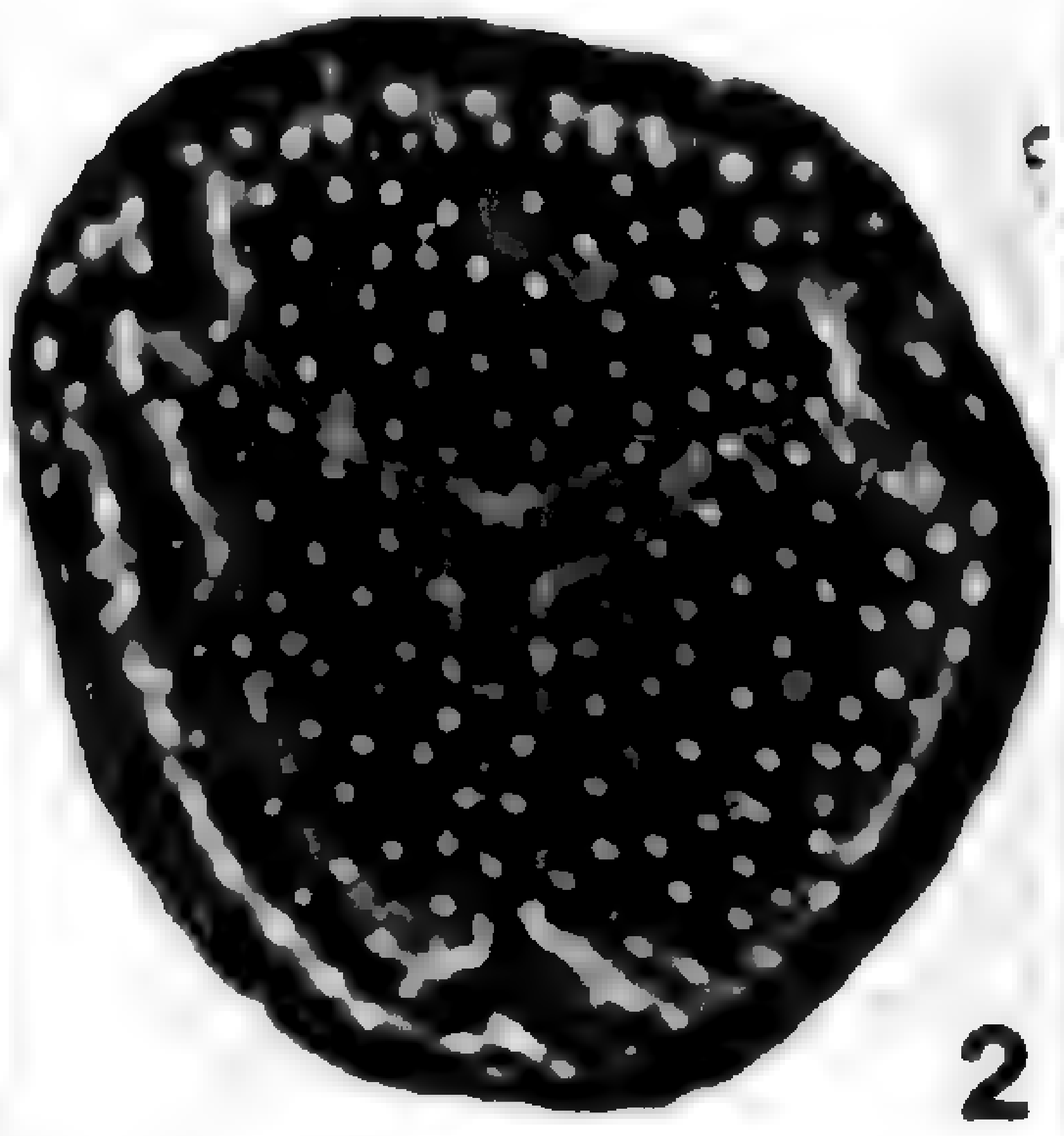
TABLE 1. *Continued.*

	491.6	491	490.6	488	470.6	469.8	456	425	415.5	407	377
Euphorbiaceae											
Alchornea	—	—	—	—	—	1.5	0.5	—	—	—	—
Sapium	—	—	—	—	—	—	2.5	—	—	—	—
Tetrorchidium	—	—	—	1	1.5	—	1.5	—	—	1	—
Flacourtiaceae											
Casearia	—	—	—	—	1.5	—	—	—	—	—	—
Leguminosae											
Mimosoideae											
Acacia	—	—	—	0.5	—	—	0.5	—	—	—	—
Malpighiaceae	—	—	—	2	1	—	—	—	1	—	—
Malvaceae											
Hampea/Hibiscus	7.5	4	4.5	4	3.5	5	1	2	1	3	3
Myrtaceae											
Eugenia/Myrcia	—	—	—	0.5	1.5	—	—	—	—	—	—
Rhizophoraceae											
Rhizophora	10.5	4	3.5	8.5	5.5	1.5	2.5	5	9	8	6
Rubiaceae											
Sabicea	—	—	—	—	—	—	0.5	—	—	—	—
Sapindaceae											
Allophylus	—	—	1	—	—	1	0.5	—	—	—	—
Cupania	0.5	—	—	—	—	—	0.5	—	—	—	—
Matayba	0.5	—	—	—	0.5	—	—	—	—	—	—
Sapotaceae											
cf. *Pouteria*	—	—	—	—	0.5	—	—	—	—	—	—
Sterculiaceae											
cf. *Guazuma*	—	—	—	—	—	—	0.5	—	—	—	—
Unknown											
Type 1	—	—	—	—	0.5	—	—	1	—	—	—
Type 2	—	—	0.5	—	—	—	1	—	—	—	—
Type 3	—	0.5	4.5	4.5	6	11.5	7.5	2	—	4	4
Type 4	—	—	—	0.5	—	—	—	—	—	—	—
Type 5	—	—	—	—	1.5	—	2	—	—	—	—
Type 6	—	—	—	—	—	—	0.5	—	—	—	—
Type 7	—	—	—	—	—	0.5	—	—	—	—	—
Type 8	—	—	—	0.5	—	—	1.5	—	—	—	—
Type 9	—	—	—	—	—	—	0.5	—	—	—	—
Type 10	—	—	—	0.5	—	1	1.5	—	—	—	—
Type 11	—	—	0.5	2	1.5	0.5	3.5	1	2	—	—
Type 12	—	—	—	—	—	—	0.5	—	—	—	—
Type 13	—	—	—	—	1	—	1.5	—	—	—	—
Type 14	—	—	—	1	1.5	1	1.5	—	—	—	—
Other unknowns	4	6	9	7	7	8	8	6	14	18	14

margin entire, bordered by lip 2–3 μm wide with punctae 1 μm diam.; distal surface finely punctate, proximal surface more laevigate near laesurae; wall 1.5–2 μm thick; 32–36 μm.

The classification of tree ferns differs among various authors, and reference slides with spores similar to the fossil specimens come from herbarium material labeled as *Alsophila* and *Cyathea*. As


1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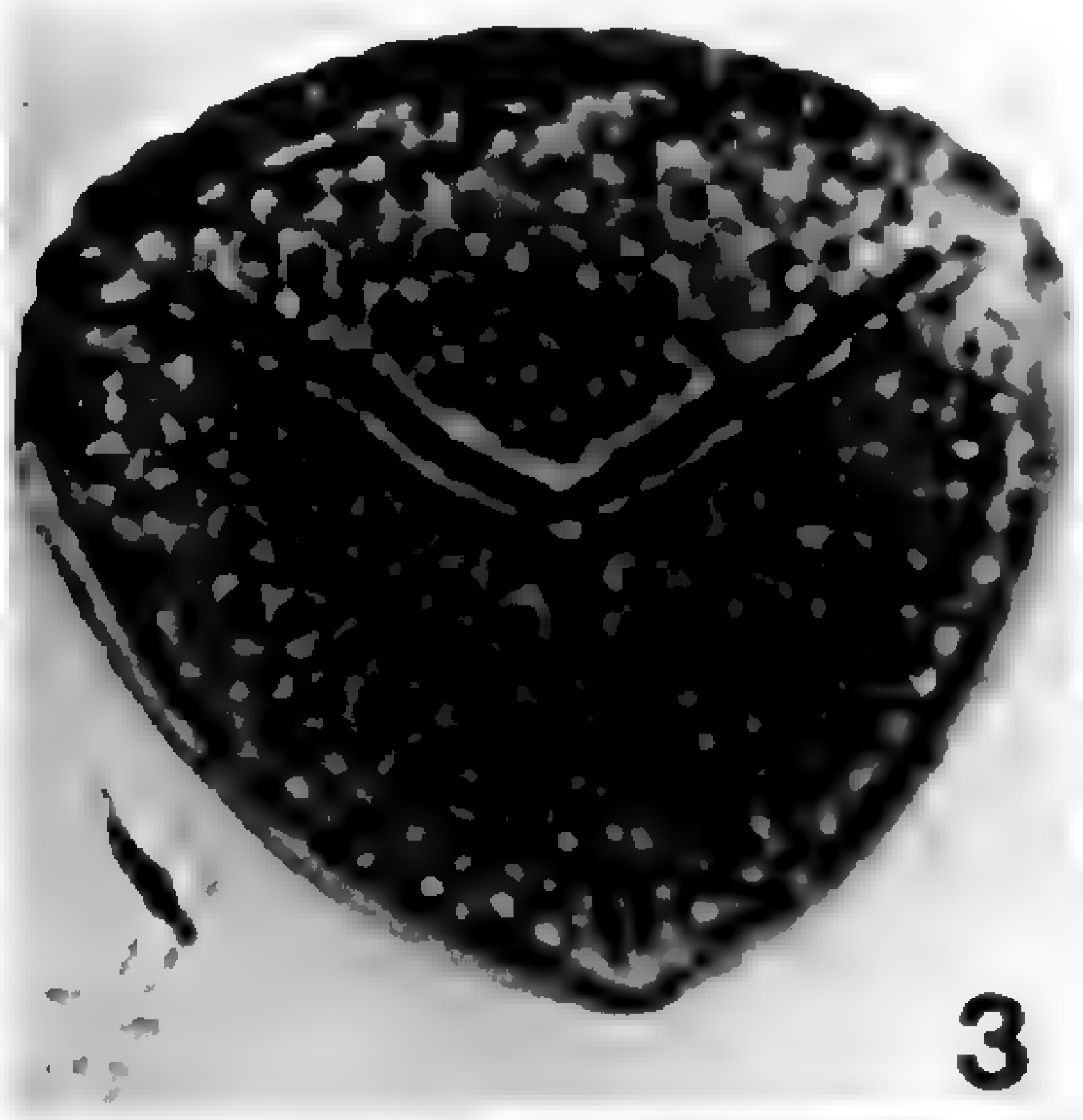
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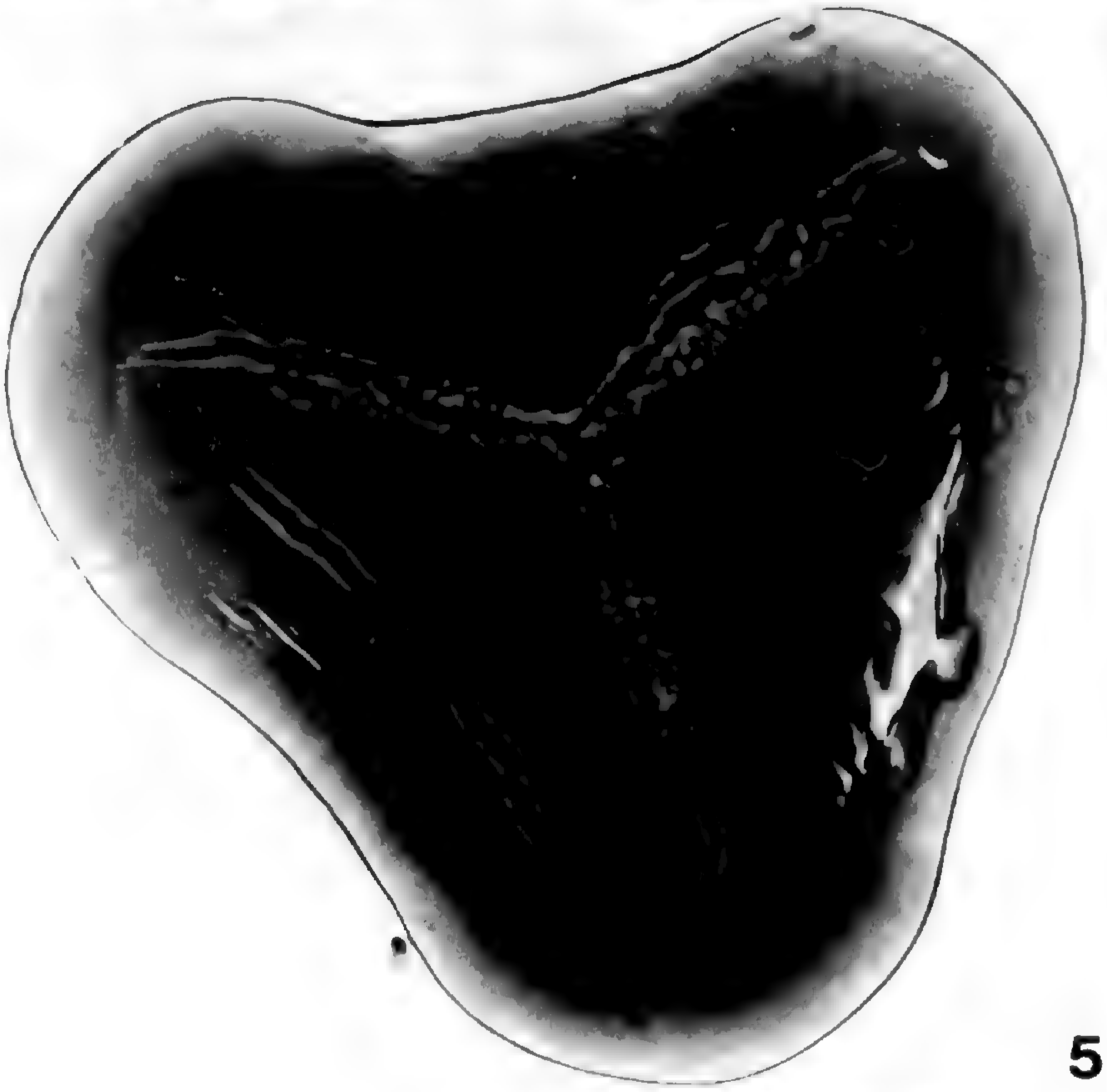
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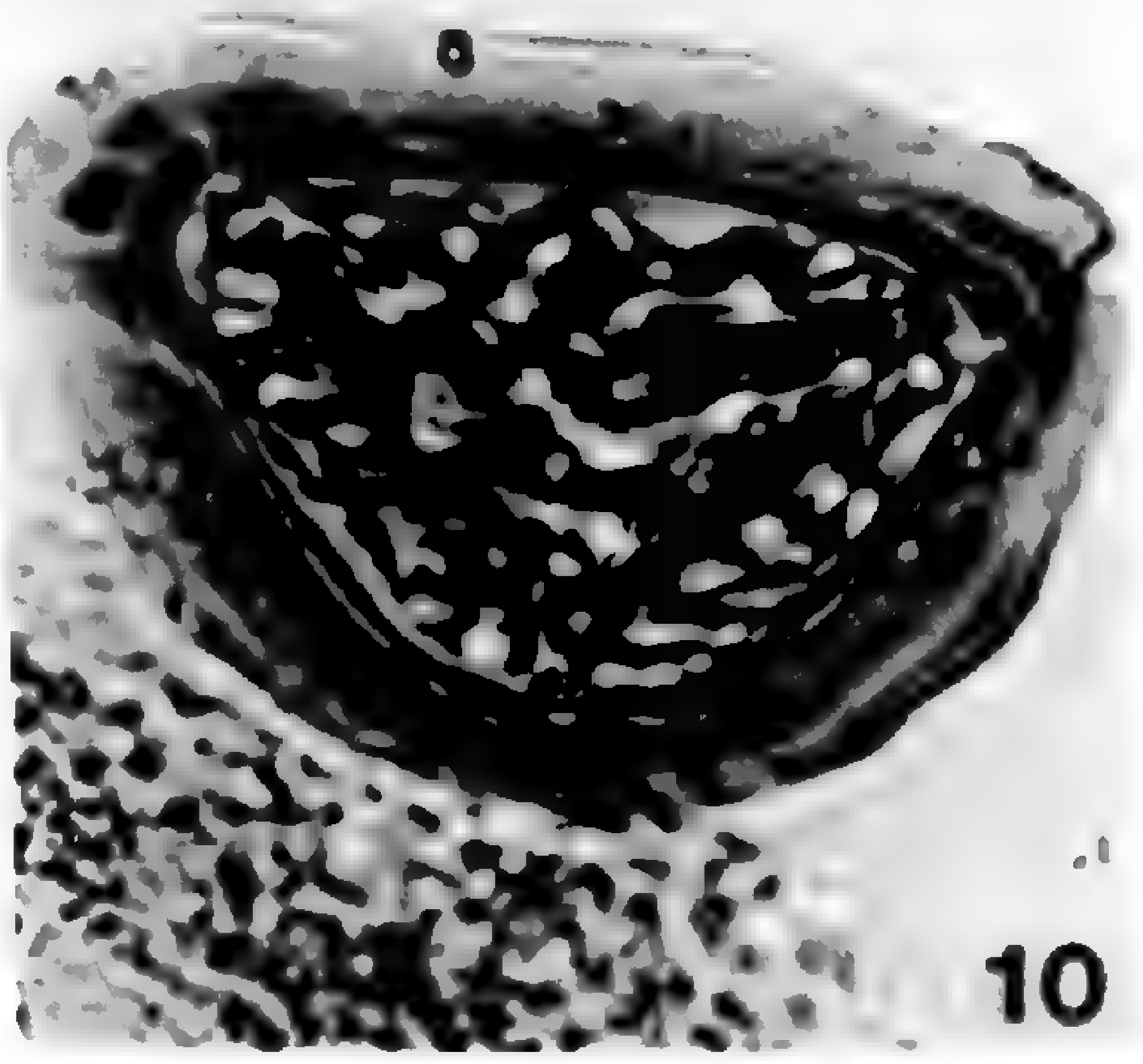
10

noted by Tryon & Tryon (1982: 204), "The name *Cyathea* has been variously applied to genera of widely different scope and definition, sometimes including nearly all members of the family." In illustrations of spores of neotropical tree ferns (Gastony & Tryon, 1976; Tryon & Tryon, 1982: 207), the micropunctate forms are referred to *Cyathea.*

The genus consists of 40 species of the American tropics growing primarily in montane forests and cloud forests, and also in low rain forests in Central America, usually at 1,500–2,000 m, but as low as 500 m (Tryon & Tryon, 1982: 204–205). Fossil spores are common in Gulf/Caribbean Tertiary deposits.

PTERIDACEAE

Pteris (Fig. 10). Amb triangular, apices rounded; trilete, laesurae straight, narrow, 18–22 μm long, extending to spore margin, inner margin entire; distal surface with coarse, irregular verrucae, proximal surface more laevigate, flange ca. 5–6 μm wide, hyaline; wall 2 μm thick; 42–48 μm.

Pteris includes about 200 species, with approximately 55 occurring in the American tropics (Tryon & Tryon, 1982: 334). The plants typically grow in wet forests or in openings along stream banks at low elevations (sea level to 2,000 m). Fossil spores are frequent, but in low percentages in Gulf/Caribbean Tertiary deposits.

SCHIZAEACEAE

Lygodium (Figs. 5, 6, 11, 12, 17). Amb triangular to concavo-triangular, apices rounded; trilete, laesurae ± straight, narrow, 34–38 μm long, extending nearly to spore margin, apices frequently branched, inner margin entire; laevigate to faintly verrucate; wall 2–4 μm thick; 80–100 μm.

Lygodium is a genus of about 30 species, with six to eight in the American tropics. According to Tryon & Tryon (1982: 71): "*Lygodium* characteristically occurs in open forest especially along the borders where the climbing leaves can reach well-lighted situations. In tropical America, it sometimes grows in rain forests, but more commonly in gallery forests, shrubby savannahs or along the borders of streams or river banks. It most commonly occurs from sea level to about 350 m, as a characteristic element of the low, humid tropics, and less often grows up to 1,000 m."

The specimens are large (up to 100 μm in diameter) and somewhat diverse in morphology; more than one biological species may be represented. The most notable variation is in the dark coloration that can occur at the apices. This is not found in our modern reference material, but in the fossil specimens it ranges from absent (Figs. 5, 6) to quite prominent (Fig. 17). Spores of *Lygodium,* but of a different morphological type, have been reported from the upper part of the lower Miocene in northern South America (Germeraad et al., 1968) under the artificial generic name *Crassoretitriletes.* Spores similar to the Culebra specimens are also known under the name *Matonisporites* described by Couper (1958; see especially pl. 20, figs. 15, 16) from the Jurassic and Lower Cretaceous of England. Dettmann (1963, pl. 11, figs. 1, 2) emended the description to include the thickened apices and reported the genus from Lower Cretaceous deposits of southeastern Australia. She noted (p. 59) possible affinities with *Dicksonia* (*D. sellowiana* Hook., *D. antarctica* Labill.), but our modern reference material of these species, and others in the genus, is different (see illustrations in Tryon & Tryon, 1982: 148). Recently Jameossanaie (1987, fig. 10, #5) described similar spores (*Matonisporites*) from the Upper Cretaceous of New Mexico. The Culebra specimens are the first of the type illustrated in Figures 5, 6, 11, 12, and 17 for the Gulf/Caribbean region.

VITTARIACEAE

Cf. *Antrophyum* (Figs. 18, 20). Amb triangular, apices rounded; trilete, laesurae relatively small in relation to spore diameter, straight, narrow, 10–14 μm long, extending ca. ⅔ distance to spore margin, inner margin entire; laevigate; wall ca. 1.5 μm thick; 52–65 μm.

Approximately ten of the ca. 40 species of *Antrophyum* occur in the Neotropics from Hidalgo, Mexico, through Central America and the Antilles,

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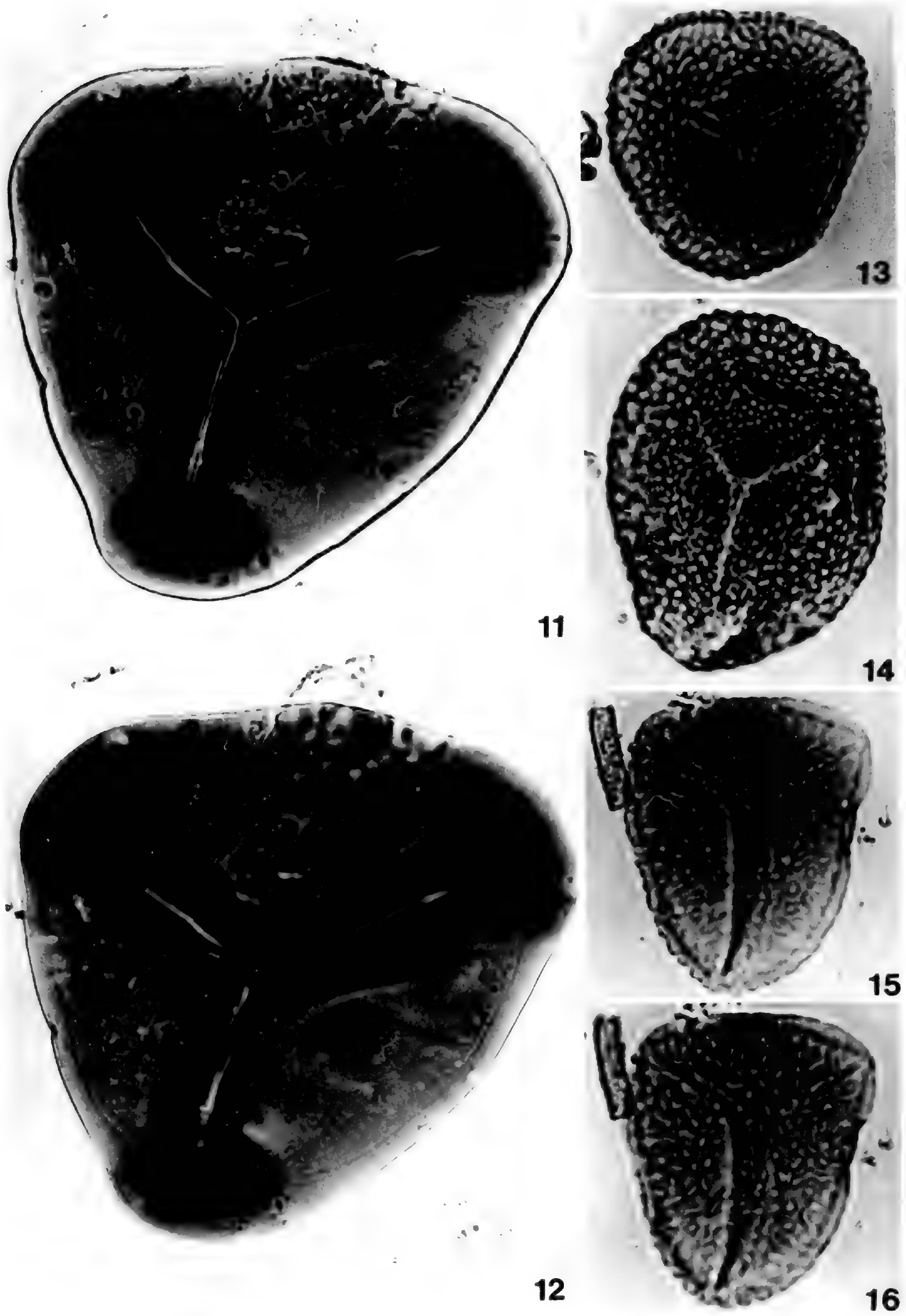
FIGURES 1–10. *Fossil spores from the Culebra Formation, Panama. 1–3.* Lycopodium.—*1, 2. Pan core 470.6, slide 3a, ESF L-39, 1.—3. Pan core 470.6, slide 3a, ESF W-31, 2.—4.* Selaginella. *Pan core 470.6, slide 3a, ESF K-28, 1.—5, 6.* Lygodium. *Pan core 488, slide 1, ESF Q-32, 4. 7–9.* Cyathea.—*7. Pan core 456, slide 3, ESF M-16, 1–2.—8, 9. Pan core 456, slide 3, ESF B-13, 304.—10.* Pteris. *Pan core 488, slide 1, ESF D-18, 3.*



FIGURES 11–16. *Fossil spores from the Culebra Formation, Panama.—11, 12.* Lygodium. *Pan core 488, slide 1, ESF L-14.—13. Trilete fern spore type 1. Pan core 490.6, slide 1, ESF H-36, 1.—14. Trilete fern spore type 2. Pan core 456, slide 4, ESF F-22, 3.—15, 16. Trilete fern spore type 3. Pan core 470.6, slide 2a, ESF E-35, 1–2.*

to northern Argentina and southeastern Brazil. The genus grows in rain forests and cloud forests, usually at elevations of 100–1,500 m. The specimens are laevigate, while modern spores often have a delicate sculpture ("echinate rods and surface strands," Tryon & Tryon, 1982: 360–361). Tryon & Tryon believe, however, that a perispore is present, and in fossil specimens this ornamental covering would not be preserved. Similar large, trilete, laevigate spores are known from the Eocene of Panama (Graham, 1985, figs. 13, 16) and the Miocene of Veracruz, Mexico (Graham, 1976, fig. 227).

OTHER TRILETE FERN SPORES

Several trilete fern spores were recovered for which biological affinities could not be determined. Four of the more distinctive ones are described below.

Type 1 (Fig. 13). Amb oval-triangular; trilete, laesurae straight, narrow, ca. 20 μm long, extending to spore margin, inner margin ± entire; finely reticulate to micropunctate (width of muri equals diameter of lumen, ca. 1 μm), sculpture less dense near laesurae; wall ca. 1.5 μm thick; 42 μm.

Type 2 (Fig. 14). Amb oval-triangular to ± circular; trilete, laesurae straight, narrow, 20–22 μm long, extending ca. ⅔ distance to spore margin, inner margin entire; finely reticulate; wall 1.5 μm thick; 45–55 μm.

Type 3 (Figs. 15, 16). Amb oval-triangular to wedge-shaped, apices rounded; trilete, laesurae straight, narrow, 22–26 μm long, extending to spore margin, inner margin entire; punctate, punctae circular (ca. 1 μm) to elongated (2–4 μm) and slitlike and sinuous; wall 2 μm thick; 42 × 36 μm (slightly compressed).

Type 4 (Fig. 19). Amb irregular, ± oval-triangular, apices rounded; trilete, laesurae straight, narrow, 34–36 μm long, extending to spore margin, inner margin entire, conspicuous lip 12 μm wide (maximum, conspicuousness augmented by folds?); low, moundlike verrucae ca. 2–3 μm diam.; wall ca. 3 μm thick; 72 × 64 μm (compressed).

MARATTIACEAE

Danaea (Fig. 21). Amb circular to ± reniform; monolete, laesurae straight, narrow, 18–20 μm long, extending nearly to spore margin, inner margin entire; echinate, echinae ca. 2 μm long, relatively dense; wall 1 μm thick; 28–32 μm (excluding spines).

Danaea is a neotropical genus of about 20 species, which presently grows from southern Mexico, through Central America and the Antilles, into Venezuela, the Guianas, Bolivia, and the Amazon Basin (Tryon & Tryon, 1982: 47). It grows in moist habitats, wet forests, and rain forests from sea level to about 2,300 m. Fossil spores have not been reported previously from Tertiary deposits in the Gulf/Caribbean region.

OTHER MONOLETE FERN SPORES

Type 1 (Fig. 22). Reniform; monolete, laesura straight, narrow, 22–26 μm long, extending ca. ¾ spore length, inner margin entire; laevigate; 41 × 22 μm.

These spores likely represent the Blechnaceae (e.g., *Blechnum*) and Polypodiaceae (e.g., *Asplenium, Thelypteris*) without the delicate ornamented perispore. They are common in fossil deposits, recognized under the artificial generic name *Laevigatisporites*, and range from Paleozoic to Recent.

Type 2 (Fig. 23). Reniform; monolete, laesura straight, narrow, 22–26 μm long, extending ¾ spore length, inner margin entire; verrucate, verrucae moderately low and conspicuous, shape irregular, ca. 2 × 4 μm; wall 2–3 μm thick; 56–58 × 39–41 μm.

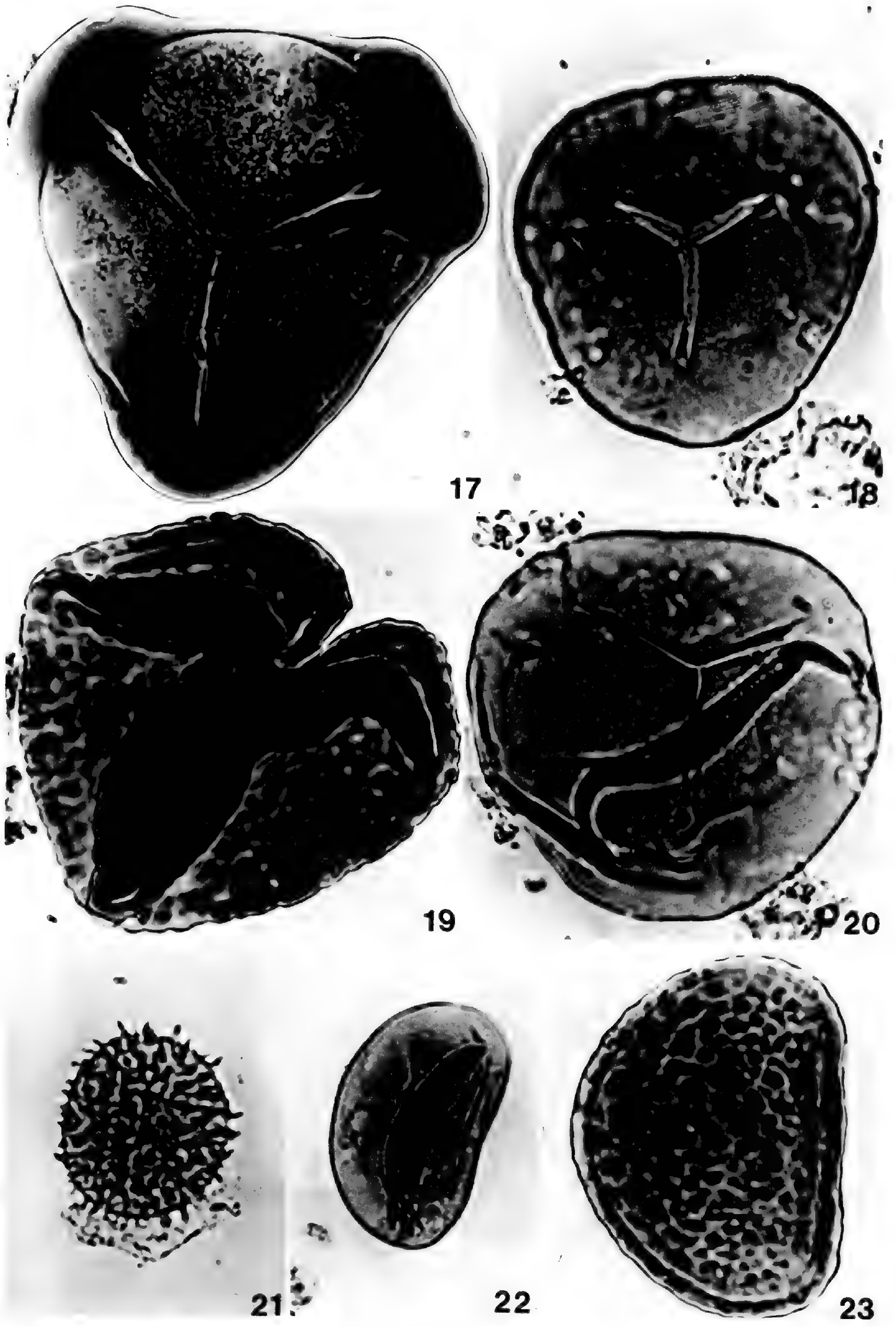
These spores are produced by species of several genera of the Polypodiaceae and Blechnaceae (e.g., *Blechnum, Microgramma*), bear the artificial generic name *Verrucatisporites*, and range from the Paleozoic to Recent.

Type 3 (Figs. 24–26). Reniform; monolete, laesura straight to curved, narrow, 32–36 μm long, extending ca. ½–⅔ spore length, inner margin entire; verrucate, verrucae distinct peglike structures, apices often flat, moderately to sparsely dense, ca. 2–3 μm diam.; 52–65 × 27–51 μm.

GRAMINEAE

(Fig. 27). Spherical, amb circular; monoporate, pore circular, 3 μm diam., inner margin entire, annulus ca. 2 μm wide, outer margin entire; tectate, wall ca. 2 μm thick; scabrate; 36–40 μm.

The Gramineae are stenopalynous, and the specimens cannot be referred to any single genus. Grass pollen has been reported from the Miocene of Veracruz (Graham, 1976) but not from the Eocene Gatuncillo Formation of Panama (Graham, 1985) or the lower Miocene Uscari sequence of Costa Rica (Graham, 1987a). Germeraad et al. (1968) listed its range in the Gulf/Caribbean region as base of the middle Eocene to Recent, but Muller



FIGURES 17–23. *Fossil spores from the Culebra Formation, Panama.—17.* Lygodium. *Pan core 456, slide 4, ESF K-11, 2. 18, 20. Cf.* Antrophyum.—*18. Pan core 456, slide 1, ESF U-14, 3–4.—20. Pan core 456, slide*

(1981) cited reports extending it back into the Paleocene of Brazil.

PALMAE

Palm pollen is one of the most common plant microfossils in the Culebra Formation. Four types are described, and it is likely that more than one genus may be represented by each.

Cryosophila-type (Figs. 29–32). Prolate, amb oval; monocolpate, colpus straight, 24–26 μm long, extending entire length of grain, margin entire; tectate-perforate, wall 2 μm thick; reticulate, muri relatively broad (ca. 1–1.5 μm), flat, lumen ca. 2 μm diam. on distal side, smaller approaching colpus; 34–38 × 24–32 μm.

This is one of the most common types of palm pollen in the Culebra Formation (Table 1). It is very similar to that of *Cryosophila warscewiczii* (H. Wendl.) Bartl., a tree up to 10 m tall distributed from Belize to Panama. In Panama it is known from the "tropical moist forest on both slopes of the Canal Zone and in Panamá and Darién; known also from premontane wet forest in Coclé (El Valle) and Panamá (Cerro Campana) and from tropical wet forest in Darién" (Croat, 1978: 171). Palm pollen is usually abundant in Gulf/Caribbean Tertiary deposits, but this is the first report of the *Cryosophila* type. Bartlett & Barghoorn (1973: 230, figs. 5, 6) reported a more finely reticulate form from the Quaternary of Panama.

Desmoncus-type (Figs. 33, 34). Prolate; monocolpate, colpus straight, broad, boatlike, apices rounded, 26–28 μm long, extending nearly entire length of grain, inner margin entire; tectate-perforate, wall ca. 1.5 μm thick; finely reticulate (diameter of lumen ca. 1 μm or slightly less); 30 × 18 μm.

This kind of pollen is produced by several palms, and *Desmoncus* is used primarily as an example of a morphologically similar type. A climbing palm known from Mexico to South America, it grows in Panama in tropical moist forests in the Canal region, in the provinces of Panamá and Darién, and in the tropical wet forest in Colón (Croat, 1978: 171).

Manicaria-type (Figs. 37, 38). Prolate; monocolpate, colpus straight to occasionally bent, 36–40 μm long, extending nearly entire length of grain, inner margin entire; finely reticulate (diameter of lumen ca. 1 μm or slightly less); tectate-perforate, wall ca. 1 μm thick; 40–45 × 21–27 μm, widest part just off equator of grain.

Manicaria is used as an example of a palm producing pollen morphologically similar to the specimens. It is a tree up to 10 m tall with three species in the Antilles, Central America, and South America (fide Bailey, 1943) and often occurs in dense groves in wet places. Similar pollen of this general palm type has been reported from the Eocene of Panama (Graham, 1985, fig. 26).

Synechanthus-type (Figs. 35, 36). Prolate; monocolpate, colpus straight, 28–30 μm long, extending entire length of grain, inner margin entire; scabrate (to possibly microreticulate); tectate, wall 1.5–2 μm thick; 28–34 × 22–26 μm.

Synechanthus is representative of modern palms producing morphologically similar pollen (cf. also *Aiphanes*, the West Indian *Thrinax*). It is a tree to 6 m tall distributed from Costa Rica to Colombia and Ecuador, usually at low elevations. In Panama it is known from "tropical moist forest on both slopes in the Canal Zone and in San Blas and Darién, from premontane wet forest in Veraguas (Cerro Tute) and Panamá (Lago Cerro Azul), and from premontane rain forest in Panama (Cerro Jefe) and Darién (Cerro Pirre)" (Croat, 1978: 178).

AQUIFOLIACEAE

Ilex (Fig. 28). Oblate-spheroidal, amb circular; tricolporoidate, colpi straight, 9–11 μm long (pole to equator), tapering to acute apex, equatorially arranged, meridionally elongated, equidistant, extending within 7 μm of pole (P.I. 0.33), inner margin diffuse, pores obscure, diam. ca. 2–3 μm, circular, situated at midpoint of colpus; intectate, clavate, wall 3 μm thick; 25–30 μm.

Ilex is one of the most common microfossils in the Gulf/Caribbean Tertiary, and its stratigraphic range and ecology have been discussed previously (e.g., Graham, 1985: 514). Briefly, its geologic range is from Late Cretaceous to Recent (Muller, 1981), and in northern Latin America pollen has been recovered from all formations studied in the

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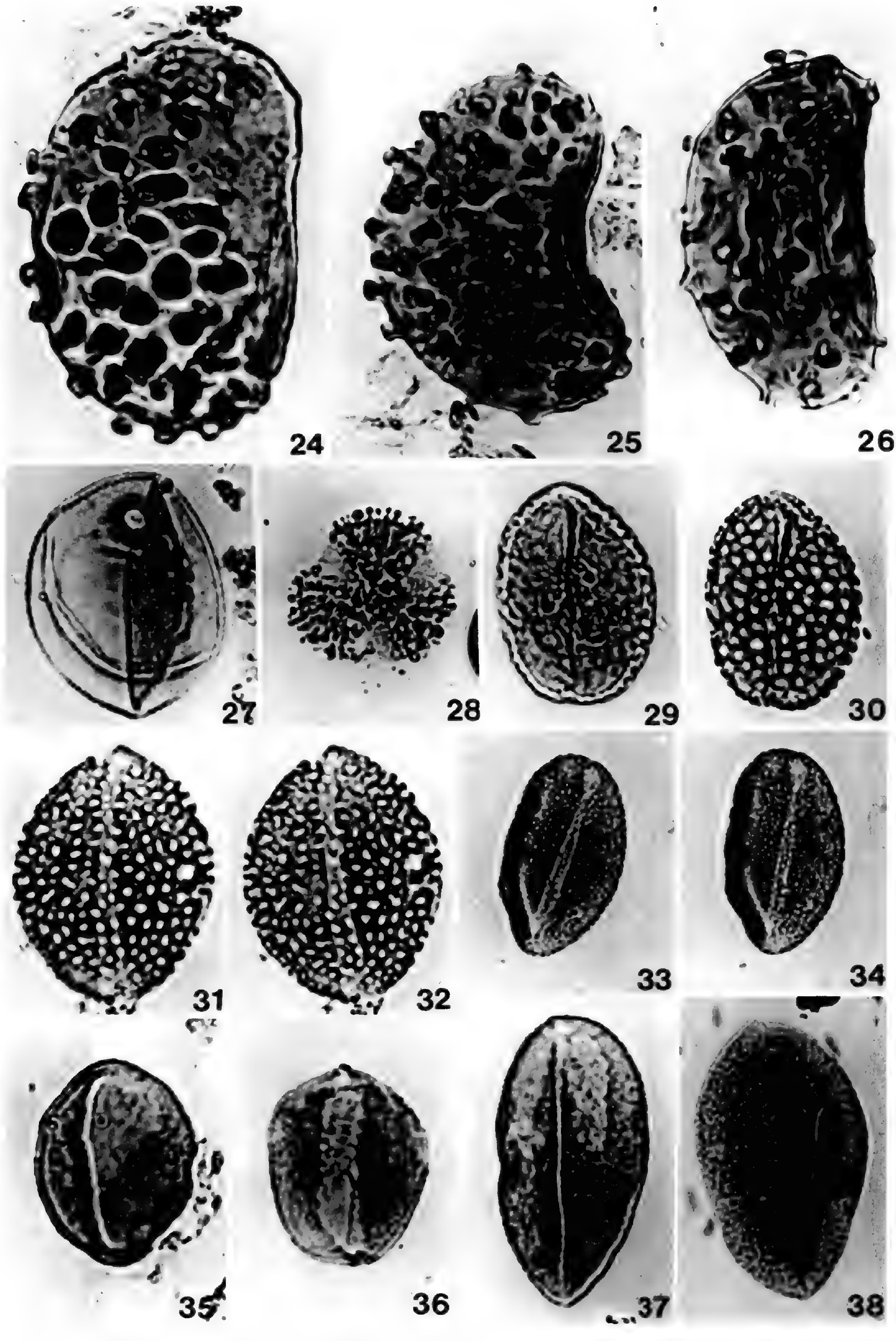
4, ESF J-27.—19. Trilete fern spore type 4. Pan core 470.6, slide 2a, ESF K-34, 1.—21. Danaea. *Pan core 456, slide 3, ESF K-7, 2.—22. Monolete fern spore type 1. Pan core 470.6, slide 2a, ESF T-31, 2.—23. Monolete fern spore type 2. Pan core 470.6, slide 2a, ESF S-28, 2–4.*



FIGURES 24–38. *Fossil spores and pollen from the Culebra Formation, Panama.—24–26. Monolete fern spore type 3. Pan core 456, slide 1, ESF R-25, 1–3; Pan core 470.6, slide 2a, ESF L-18; Pan core 470.6, slide 2a,*

present project (Eocene to Recent). In the modern flora it grows at mid altitudes in moist to slightly drier habitats.

CHENOPODIACEAE/AMARANTHACEAE

(Fig. 39). Spherical, amb circular; periporate, pores circular, evenly distributed, distance between pores ca. 6–8 μm, estimated number ca. 40, diam. 3 μm, inner margin entire; tectate, wall relatively thick (3 μm); psilate; 21–23 μm.

Pollen of genera in these two families cannot be distinguished consistently, and the specimens serve only to record the family (or families) in the lower Miocene vegetation of Panama.

COMBRETACEAE

Combretum/Terminalia (Figs. 40, 41). Prolate to prolate-spheroidal; tricolporate with 3 pseudocolpi, colpi straight, 15 μm long, apices blunt, equatorially arranged, meridionally elongated, equidistant, inner margin entire, pore frequently obscure, circular, diam. 2–3 μm, situated at midpoint of colpus; tectate, wall 1.5–2 μm thick; psilate to faintly scabrate; 14–16 × 18–20 μm.

The occurrence of *Combretum/Terminalia* in Gulf/Caribbean deposits has been discussed recently by Graham (1985). Pollen of the two genera cannot be distinguished consistently (Graham, 1980), and the morphological type ranges from Eocene to Recent in the region. Both genera are found in moist to wet habitats, although individual species may range into drier habitats.

COMPOSITAE

(Figs. 42, 43). Spherical to oblate-spheroidal, amb circular; tricolporate, colpi straight, short (ca. 4–6 μm pole to equator), equatorially arranged, meridionally elongated, equidistant, pore obscure, ca. 2 μm diam., situated at midpoint of colpus; vesiculate (air cavities evident in equatorial mesocolpial region); tectate, outer wall 3–4 μm thick; echinate, spines short (ca. 3 μm), base broad, moderately dense (distance between spines ca. 3–4 μm); 24–26 μm.

These vesiculate Compositae pollen grains are typical of later Cenozoic deposits and have not been reported previously in our studies, although other Compositae pollen types are known from the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976). The Culebra specimens are of the Heliantheae type (e.g., *Ambrosia*, *Franseria*, *Iva*) but cannot be referred to any one genus.

CONNARACEAE

Cf. *Rourea* (Figs. 44, 45). Prolate; tricolpate, colpi straight, 16–18 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire to appearing minutely dentate due to overlying sculpture elements; tectate, wall ca. 1 μm thick; finely reticulate; 20–24 × 14–18 μm.

These prolate, tricolpate reticulate grains are a generalized type but compare most closely to members of the Connaraceae, especially *Rourea*. The genus is represented in Panama by three species (fide Woodson & Schery, 1950a), the most common being *R. glabra* Aubl., distributed from southern Mexico, through Central America and the Antilles, to the Guianas and Brazil. In Panama it is "known principally from tropical moist forest in the Canal Zone, San Blas, Veraguas, Los Santos, Panamá, and Darién; known also from tropical dry forest in Coclé and Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Colón and Panamá" (Croat, 1978: 423).

DILLENIACEAE

Cf. *Doliocarpus* (Figs. 46–48). Prolate to prolate-spheroidal; tricolporate, colpi straight, 23–25 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi ca. 3 μm wide, pore obscure, circular, ca. 3 μm diam., situated at midpoint of colpus; tectate perforate, wall 2.5–3 μm thick; reticulate, muri smooth, about as wide as lumen; 30–34 × 20–24 μm.

Four species of *Doliocarpus* presently occur in the vicinity of the collecting site: *D. dentatus* (Aubl.) Standley, *D. major* J. F. Gmel., *D. multiflorus* Standley, and *D. olivaceus* Sprague & L. O. Williams ex Standley. The specimens are most similar to *D. dentatus*, but there is some variation in the

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ESF R-22, 1.—27. Gramineae. Pan core 456, slide 4, ESF N-9, 3–4.—28. Ilex. *Pan core 488, slide 1, ESF S-9, 1–2.—29–32.* Cryosophila*-type. Pan core 488, slide 1, ESF S-10, 2–4; Pan core 456, slide 3, ESF V-10, 1.—33, 34.* Desmoncus*-type. Pan core 470.6, slide 3a, ESF J-24.—35, 36.* Synechanthus*-type. Pan core 456, slide 1, ESF U-35, 2–4; Pan core 469.8, slide 2, ESF U-16, 3.—37, 38.* Manicaria*-type, Pan core 456, slide 3, ESF S-12, 1; Pan core 470.6, slide 3a, ESF N-27, 3–4.*


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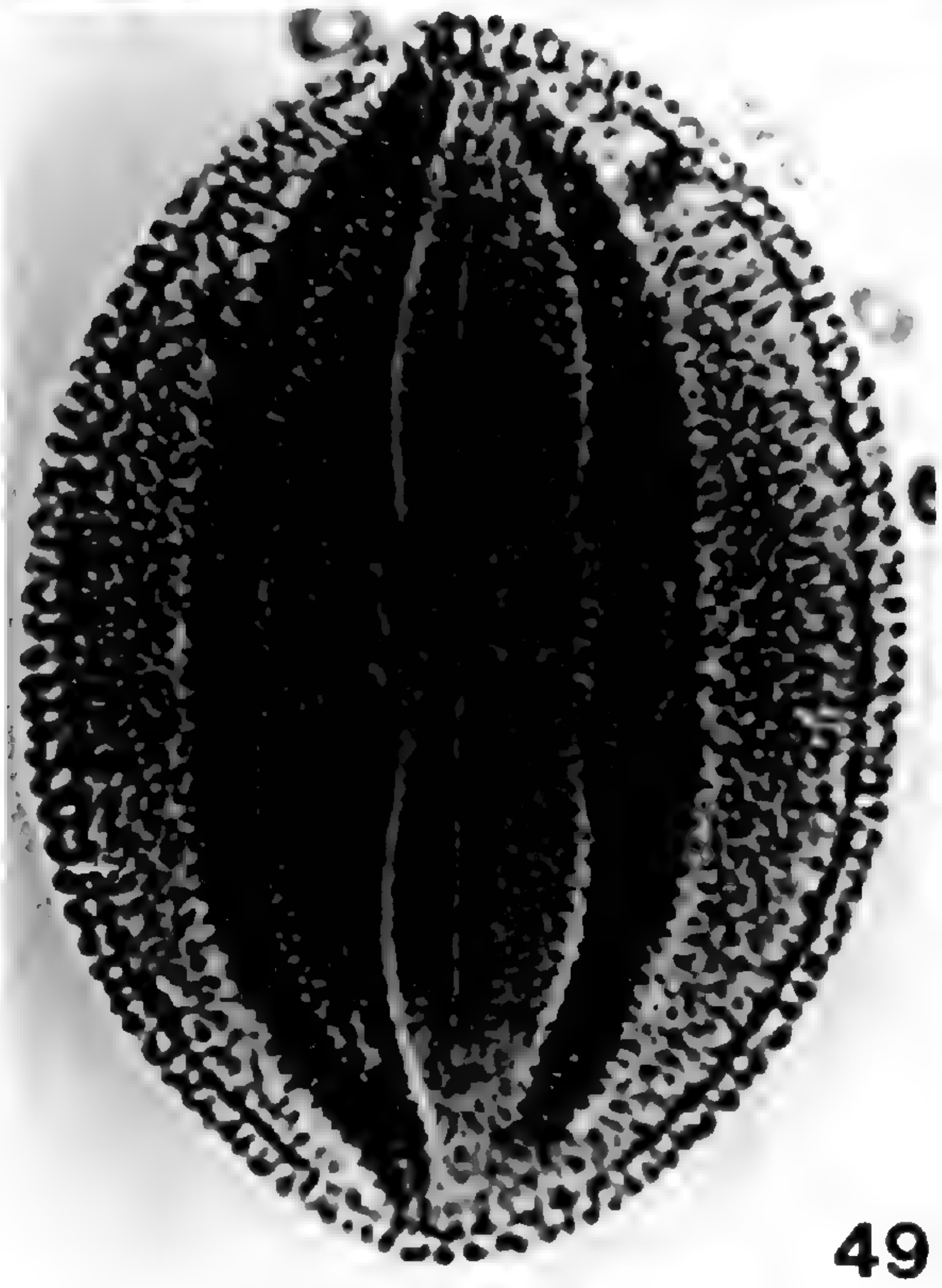
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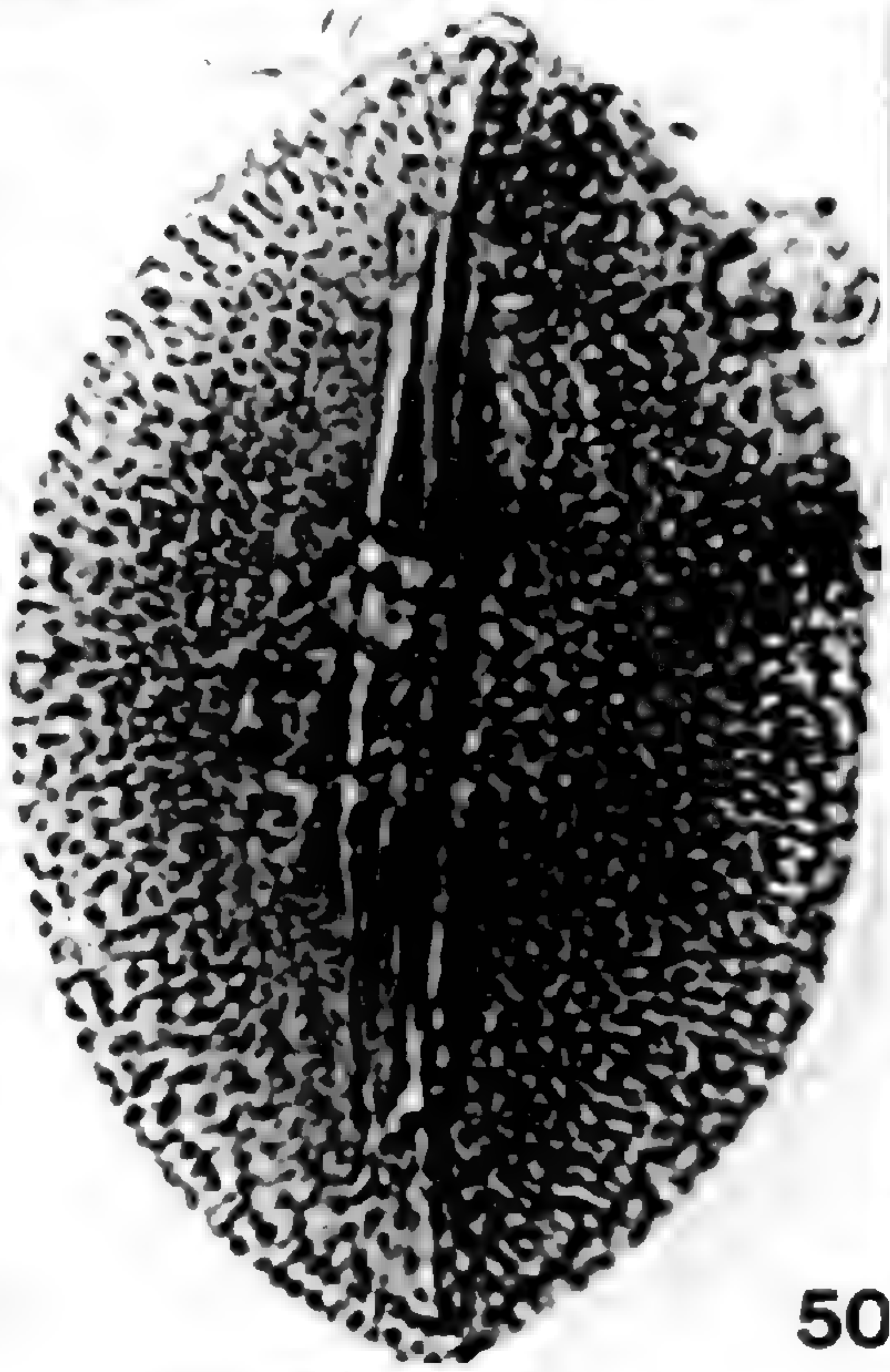
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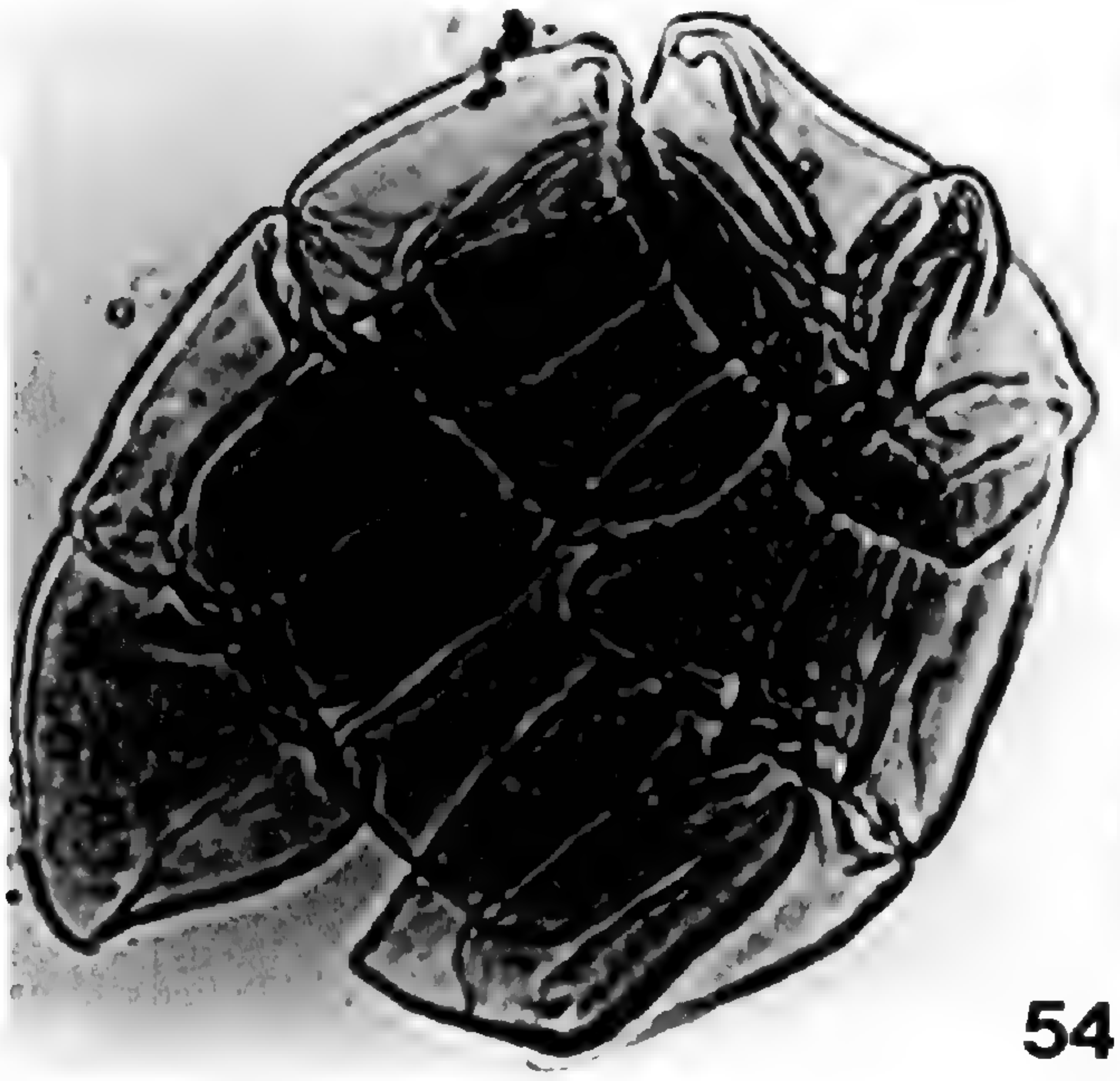
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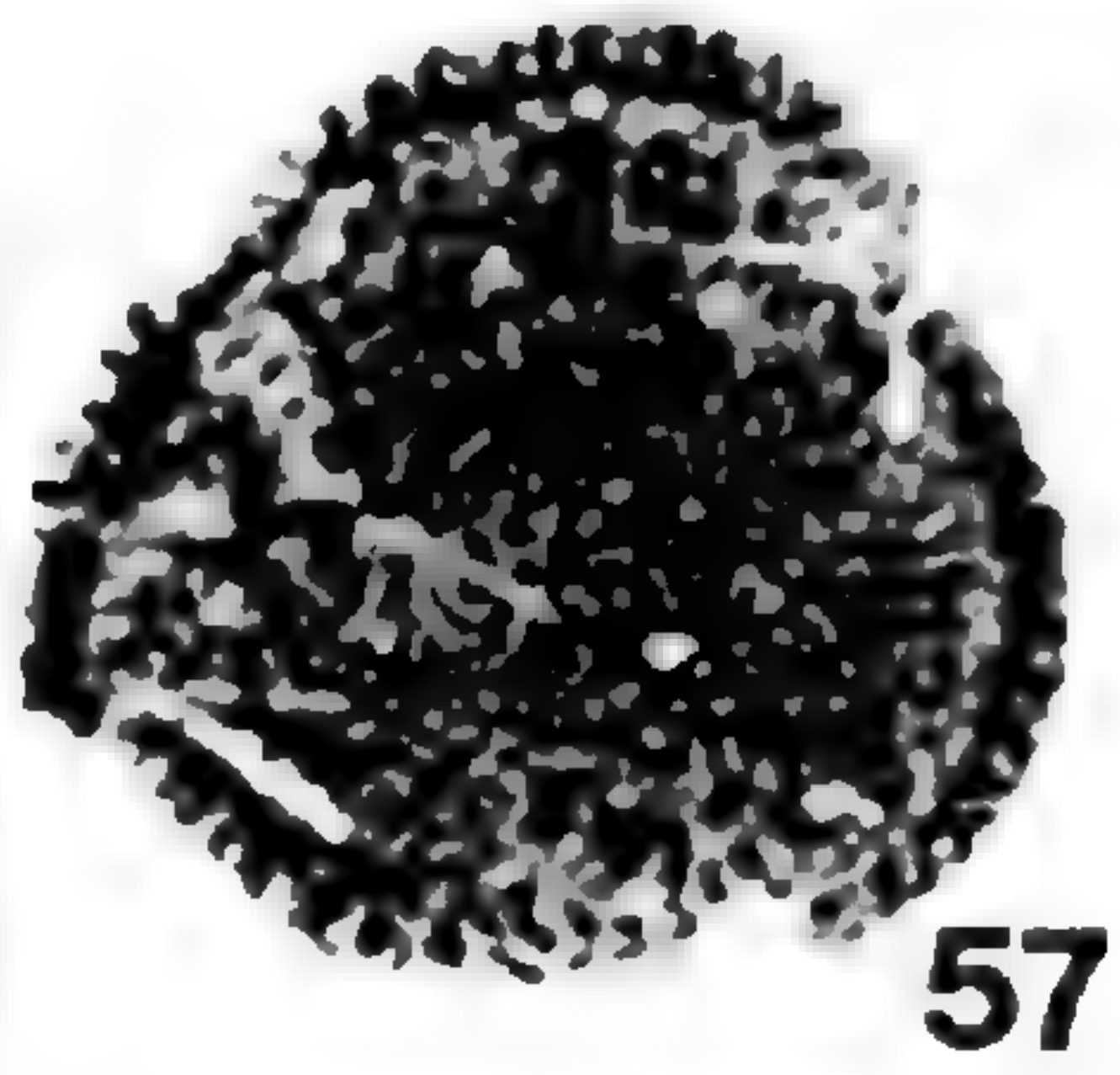
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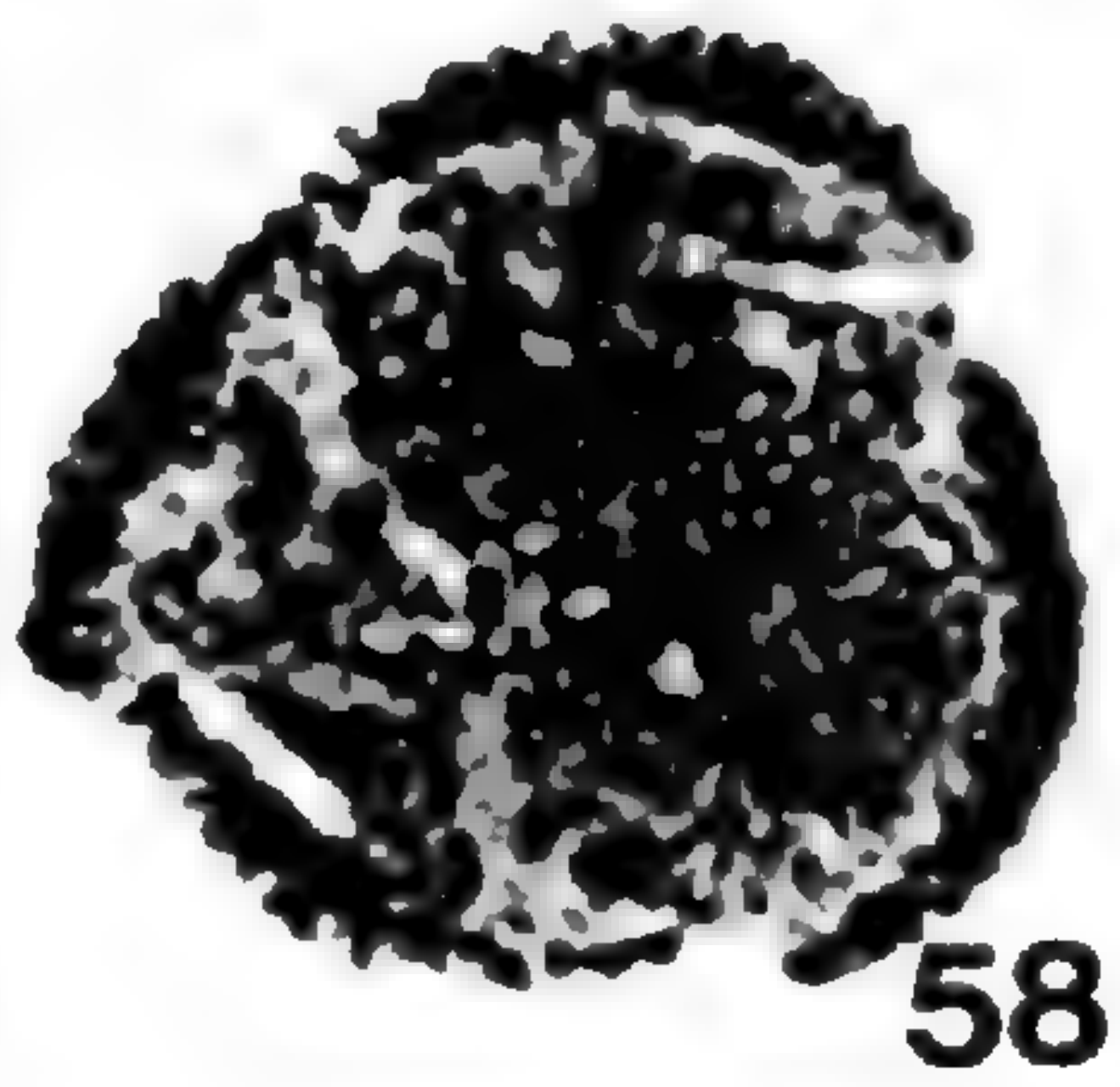
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modern pollen among individual herbarium collections. In the collection *Lewis et al. 722A* (Chiriquí, Panama, MO) the reticulum is slightly coarser (muri broader) like the specimens, while in the collection *Proctor et al. 27037* (Nicaragua, CR) the reticulum is finer. Consequently the fossil specimens are presently identified only as cf. *Doliocarpus.*

Doliocarpus dentatus occurs from Mexico through Central America to Paraguay and is scattered in the Antilles. In Panama it grows in the tropical moist forest, tropical dry forest, premontane moist forest, and premontane wet forest (Croat, 1978: 599).

DIOSCOREACEAE

Dioscorea/Rajania-type (Fig. 51). Prolate; tricolpate, colpi frequently sinuous, irregular, 21–23 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire; tectate-perforate, wall relatively thin (ca. 1.5 μm); finely reticulate; 26–28 × 17–19 μm.

Eleven native species of *Dioscorea* are listed for Panama by Morton (1945), and Croat (1978) listed five native Central American species for Barro Colorado Island. *Dioscorea* is found primarily in the tropical moist, premontane moist, premontane wet, and tropical wet forests. *Rajania* is a West Indian segregate of *Dioscorea.* Similar pollen has been reported from the Miocene of Veracruz, Mexico (Graham, 1976).

EUPHORBIACEAE

Alchornea (Fig. 52). Oblate, amb circular; tricolpate, colpi straight, 6–8 μm long (pole to equator), equatorially arranged, meridionally elongated, equidistant, extending within 5–6 μm of pole, inner margin entire, distinct operculum; tectate, wall 1.5 μm thick; psilate to faintly scabrate; 20 μm.

Pollen of *Alchornea* is frequent in Gulf/Caribbean Tertiary deposits and ranges from the lower and middle Eocene (Colombia; González Guzmán, 1967) to Recent (Muller, 1981). Its distribution and ecology for the region have been summarized by Graham (1987a), based on Croat (1978) and Webster & Burch (1967). Briefly, it grows in the tropical moist, premontane wet, and premontane rain forest, with a wide altitudinal range of 300 to 2,000 m. Pollen of the family has been described by Punt (1962).

Sapium (Figs. 49, 50). Prolate; tricolporate, colpi straight, 62–66 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi 4–6 μm wide, margo present (formed by reticulum becoming finer bordering the colpi), pore large (12–14 μm diam.), oval, situated at midpoint of colpus; tectate-perforate, wall 3 μm thick, individual columellae distinct; finely reticulate; 76–80 × 52–56 μm.

Sapium is a genus of about 120 species (fide Willis, 1966) of trees and shrubs widely distributed in tropical and subtropical regions of the New World. Webster & Burch (1967) listed four species for Panama, and Croat (1978) recorded two for Barro Colorado Island. It grows in the tropical moist, premontane wet, and lower montane wet forests. Hartshorn (1983: 143–144) described its occurrence within the Monteverde Reserve in Costa Rica (cove, leeward cloud, windward cloud, and swamp forests).

There is considerable range in size of *Sapium* pollen, and the smaller forms (48 μm) have been described from the Quaternary of Panama (Bartlett & Barghoorn, 1973). Slightly larger specimens (58 μm) occur in the upper Miocene Paraje Solo Formation of Veracruz, Mexico (as cf. *Sapium*; Graham, 1976). The Culebra specimens are exceptionally large (80 μm) and are matched by a collection labeled *S. haematospermum* Muell.-Arg. (*Rocha 3666*, Argentina, TEX). It is not possible to refer the specimen to any one modern species, but pollen identical to the specimens in size and fineness of the reticulum apparently does occur in the genus.

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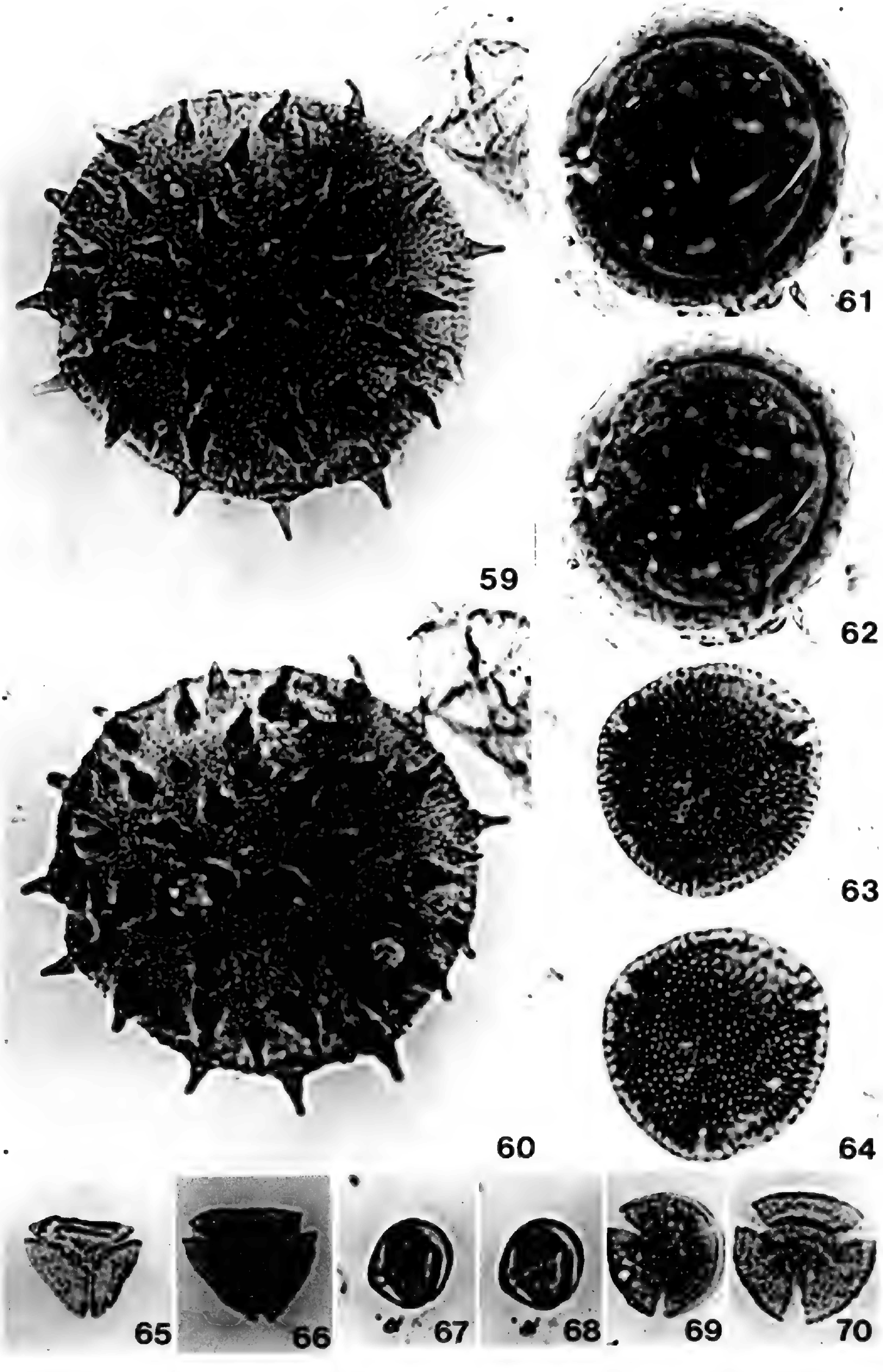
FIGURES 39–58. *Fossil pollen from the Culebra Formation, Panama.—39. Chenopodiaceae/Amaranthaceae. Pan core 470.6, slide 3a, ESF Q-39, 1.—40, 41.* Combretum/Terminalia. *Pan core 470.6, slide 2a, ESF O-16, 2–4; Pan core 456, slide 4, ESF W-15, 4.—42, 43. Compositae. Pan core 488, slide 1, ESF J-14, 4.—44, 45. Cf.* Rourea. *Pan core 456, slide 4, ESF T-32, 2–4; Pan core 456, slide 3, ESF W-23.—46–48. Cf.* Doliocarpus. *Pan core 469.8, slide 2, ESF K-23, 1–2; Pan core 456, slide 1, ESF L-26, 2–4.—49, 50.* Sapium. *Pan core 456, slide 4, ESF K-15; Pan core 456, slide 4, ESF G-12, 3.—51.* Dioscorea/Rajania *type. Pan core 470.6, slide 2a, ESF F-38, 3.—52.* Alchornea. *Pan core 469.8, slide 2, ESF T-15, 2–4.—53.* Casearia. *Pan core 470.6, slide 2a, ESF L-21.—54.* Acacia. *Pan core 488, slide 1, ESF R-34.—55–58.* Tetrorchidium. *Pan core 488, slide 1, ESF T-33, 2–4; Pan core 470.6, slide 2a, ESF Q-35, 2–4.*



FIGURES 59–70. *Fossil pollen from the Culebra Formation, Panama.*—*59, 60.* Hampea/Hibiscus. *Pan core 488, slide 1, ESF C-29.*—*61, 62. Malpighiaceae. Pan core 488, slide 1, ESF B-26, 3.*—*63, 64.* Sabicea. *Pan*

Tetrorchidium (Figs. 55–58). Oblate-spheroidal, amb circular; tricolpate, colpi straight, 12–14 μm long (pole to equator), equatorially arranged, meridionally elongated, equidistant, inner margin finely dentate; intectate, finely baculate to nearly echinate, wall ca. 1.5 μm thick; 26–30 μm.

According to Webster & Burch (1967), there are about ten species of *Tetrorchidium* in the New World (five in Africa), and two are listed for Panama (*T. euryphyllum* Standley, rainforests of Costa Rica and Panama; *T. gorgonae* Croizat). Hartshorn (1983) mentioned *Tetrorchidium* sp. in the swamp forests of the Monteverde Reserve in Costa Rica (associated with *Alchornea* and *Sapium*). Pollen wall thickness varies among the species of *Tetrorchidium*, and the specimens are similar to the thinner-walled forms in our collection (e.g., *T. rotundatum* Standley, Nicaragua). Similar pollen has been reported from the Oligocene of Puerto Rico (Graham & Jarzen, 1969) and the Miocene of Veracruz, Mexico (Graham, 1976).

FLACOURTIACEAE

Casearia (Fig. 53). Prolate; tricolporate, colpi straight, 18–20 μm long, apices acute, equatorially arranged, meridionally elongated, equidistant, inner margin entire, narrow costae colpi, pore equatorially elongated (colpi transversalis), 1.5–2 × 4–5 μm, situated at midpoint of colpus; tectate, wall 1.5 μm thick; sculpture subdued, appearing psilate; 23–25 × 16–18 μm.

Casearia pollen records in the Gulf/Caribbean Tertiary have recently been reviewed by Graham (1985). Briefly, it is known from the middle(?) to late Eocene (Gatuncillo Formation, Panama) to Recent. The modern plants are trees and shrubs widely distributed in tropical and subtropical regions, with eight species listed for Panama (Robyns, 1968). They are most typical of moist forest types but can range into somewhat drier habitats (Croat, 1978). Pollen of the family has been studied by Keating (1973).

LEGUMINOSAE–MIMOSOIDEAE

Acacia (Fig. 54). Solid sphere, 16-celled polyad, amb circular; nonaperturate; individual cells ± cubical, ca. 20 μm; tectate, wall 1.5 μm thick; faintly scabrate; 52–54 μm.

Woodson & Schery (1950b) listed 12 species of *Acacia* for Panama, and Croat (1978) recorded five for Barro Colorado Island. They grow mainly in the tropical moist forest (in contrast to the familiar savannah habitats of African and Australian species) but can range into drier vegetation types. *Acacia* pollen has been reported from the Oligocene San Sebastian Formation of Puerto Rico (Graham & Jarzen, 1969), and a similar grain was recovered from the Quaternary of Panama (as Mimosoideae; Bartlett & Barghoorn, 1973).

MALPIGHIACEAE

(Figs. 61, 62). Spherical, amb circular; periporate, pores circular, 4–5 μm diam., inner margin entire; tectate, wall thick (3–4 μm); scabrate; 38–42 μm.

Only two poorly preserved specimens of the Malpighiaceae were recovered from the Culebra Formation and serve only to record the family in the assemblage.

MALVACEAE

Hampea/Hibiscus (Figs. 59, 60). Spherical, amb circular; periporate, pores circular, 3–4 μm diam., inner margin entire, narrow annulus; tectate, wall 2 μm thick; echinate, spines 4–5 μm long, broadened at base, moderately dense (distance between spines ca. 6–8 μm); 48–70 μm.

Robyns (1964a) and Croat (1978) listed one species of *Hampea*, *H. appendiculata* (Donn. Sm.) Standley, for Panama and Barro Colorado Island. It is a shrub to mid-size tree growing in Honduras, Costa Rica, and Panama in the tropical moist, premontane moist, tropical wet, and premontane rain forests. *Hibiscus* is represented by 14 species in Panama (fide Robyns, 1965), and on Barro Colorado Island by three species (Croat, 1978). *Hibiscus sororius* L.f. is a herb to small suffrutex that is common in marshy areas as a component of floating masses of marshy and swamp vegetation (Croat, 1978: 583). Hartshorn (1983) listed it as a member of the coastal strand vegetation in Costa Rica. Although insect pollinated, with large (to 70 μm) echinate pollen, the plant grows in habitats that would be immediately marginal to the Culebra depositional basin, and fossil specimens are frequent in the deposits.

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core 470.6, slide 3a, ESF U-31, 3.—65, 66. Eugenia/Myrcia. *Pan core 470.6, slide 3a, ESF Q-22, 4; Pan core 470.6, slide 3a, ESF D-26, 2–4.—67–70.* Rhizophora. *Pan core 456, slide 4, ESF J-17, 1; Pan core 456, slide 4, ESF Q-11, 3–4; Pan core 488, slide 1, ESF V-12, 3.*

The *Hampea/Hibiscus* pollen type is recorded under the artificial generic name *Echiperiporites* and ranges globally from the upper Eocene to Recent. It is known from the upper Eocene of Venezuela (Muller, 1981), upper Miocene of Veracruz, Mexico (Graham, 1976), and the Quaternary of Panama (Bartlett & Barghoorn, 1973).

MYRTACEAE

Eugenia/Myrcia (Figs. 65, 66). Oblate; amb triangular; tricol(poroid)ate; colpi straight, 6–8 μm long (pole to equator), equatorially arranged, meridionally elongated, equidistant, inner margin entire, syncolpate, pores vaguely defined, located at apices of grain at midpoint of colpus; tectate, wall ca. 1.5 μm thick; scabrate; 12–16 μm.

Occurrences of *Eugenia/Myrcia* in the Gulf/Caribbean Tertiary have been discussed recently by Graham (1985, 1987a). It is frequent in the sediments, although not in high percentages, and ranges from the middle Eocene to Recent. Study of the modern pollen (Graham, 1980) indicates that isolated microfossils cannot be referred consistently to any one genus of the family, and the specimens serve only to document the Myrtaceae as a prominent component of the lower Miocene vegetation of Panama.

RHIZOPHORACEAE

Rhizophora (Figs. 67–70). Prolate to prolate-spheroidal; tricolporate, colpi straight, 14–16 μm, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi ca. 2–3 μm, pores elongated equatorially (colpi transversalis), 1 × 4 μm, constricted at midpoint of colpus; tectate-perforate, wall 2–3 μm thick; finely reticulate; 16–20 × 14–19 μm.

Records of *Rhizophora* pollen in the Gulf/Caribbean Tertiary have been summarized by Graham (1985: 519, 1987a). The Culebra specimens further document its widespread occurrence and often dominant percentages in sediments such as lignites deposited under warm-temperate to subtropical, coastal, brackish-water conditions. It ranges from late Eocene to Recent in tropical American sediments (often reported under the artificial generic name *Zonocostites*), and in older deposits is replaced by its presumed ecological counterpart, *Brevitricolpites* of unknown biological affinity. Other aspects of modern and fossil mangrove pollen have been discussed by Langenheim et al. (1967), Leopold (1969), and Muller & Caratini (1977).

RUBIACEAE

Sabicea (Figs. 63, 64). Oblate, amb oval-triangular to nearly circular; tricolpate/porate (apertures short, slitlike, ca. 2:1 length/width ratio), 4–6 × 2–3 μm, equatorially arranged, meridionally elongated, equidistant, inner margin faintly dentate (due to overlying sculpture elements), faint costae colpi; tectate-perforate, wall 2–3 μm thick; finely reticulate, muri smooth, width about same as diameter of lumen (ca. 0.5–1 μm); 32–36 μm.

The presence of *Sabicea* pollen in the Culebra assemblage has been reported recently by Graham (1988a). Briefly, the genus presently grows from Mexico to northern South America and is represented in Panama by three species and two varieties common in tropical moist and premontane wet forests. *Sabicea* has not been reported previously in the fossil record.

SAPINDACEAE

Allophylus (Figs. 71–75). Oblate to peroblate, amb distinctly triangular; triporate, pore slightly elongated meridionally, ca. 5 × 3 μm, equatorially arranged, equidistant, inner margin entire, faint costae colpi; tectate, wall 2 μm thick; scabrate to microreticulate; 14 × 24 μm.

Allophylus is a mostly South American genus of about 190 species of shrubs or small trees with six species in Mexico and Central America, and three in Panama (fide Croat, 1976). It typically grows at low to moderate elevations (ca. 1,000 m) and ranges through several forest types—tropical dry, tropical moist, tropical wet, premontane moist, and premontane wet forests. It has been reported previously from the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976).

Cupania (Fig. 76). Oblate to peroblate, amb triangular; tricolpor(oid)ate, colpi straight, 7–8 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, syncolpate; tectate, wall 2 μm thick; psilate to faintly scabrate; 12–16 μm.

Cupania is a genus of about 45 tropical American species of trees and shrubs. The nine species listed for Panama (Croat, 1976) grow primarily in the tropical moist, tropical wet, and premontane wet forests. The genus has been reported from the upper Miocene Paraje Solo Formation of Mexico (Graham, 1976) and from the Quaternary of Panama (Bartlett & Barghoorn, 1973).

Matayba (Fig. 77). Oblate, amb triangular;

tricolpor(oid)ate; colpi straight, 12–14 μm long, apices branched with triangular sexine area included at poles, equatorially arranged, meridionally elongated, equidistant, inner margin entire; tectate, wall 2 μm thick; scabrate; 23–27 μm.

Croat (1976: 433) noted that *Matayba* is not always easily separable from *Cupania*. The pollen is also similar. *Matayba* pollen, however, commonly has branched colpi that include a triangular segment of the sexine at the poles, while in *Cupania* the colpi most frequently are unbranched or, when branched, do not usually include the triangular segment of sexine.

Matayba consists of about 45 species of trees and shrubs in tropical America, four of which are recorded for Panama (Croat, 1976), where it is found in the tropical dry, tropical moist, tropical wet, premontane moist, and premontane wet forests. *Matayba* has been reported from the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976).

SAPOTACEAE

Cf. *Pouteria* (Figs. 78, 79). Prolate; tricolporate, colpi straight, equatorially arranged, meridionally elongated, equidistant, inner margin entire, narrow costae colpi, pores elongated equatorially, 2–3 × 4–5 μm, situated at midpoint of colpus, narrow annulus; tectate, wall relatively thick (2–3 μm); faintly scabrate; 26–28 × 20–22 μm.

Pouteria is a genus of about 100 species of trees and shrubs found chiefly in tropical America. Included are a number of segregates that "are probably sound and deserve recognition at least at the subgeneric level. Unfortunately many of the segregate genera themselves are poorly defined, being based on relatively few specimens. As more material is collected, the generic limits may have to be shifted. This is particularly true among American species" (Pilz, 1981: 186).

The pollen is also similar to other members of the family, including *Sideroxylon*, which is a genus of trees and shrubs of the New and Old World tropics growing in Mexico, northern Central America, and Colombia but is not listed for Panama (Blackwell, 1968; Croat, 1978; D'Arcy, 1987). Species previously assigned to *Sideroxylon* from Panama are now mostly referred to *Pouteria* (e.g., *S. sapota* Jacq. = *P. sapota* (Jacq.) Moore & Stearn; *S. uniloculare* Donn. Smith = *P. unilocularis* (Donn. Smith) Baehni; Pilz, 1981). Collections at MO are rare from Mexico (one collection) and South America (two collections) but common from Asia, Africa, and Oceanica (Ricketson, pers. comm., 1987), suggesting a possible Old World origin. It is the only genus in the Culebra assemblage with this pattern of distribution, hence the provisional reference of the fossil specimens to *Pouteria*.

STERCULIACEAE

Cf. *Guazuma* (Fig. 80). Prolate; tricolporate, colpi straight, 16–18 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, narrow costae colpi, pores obscure, slitlike, ca. 1 × 3 μm, situated at midpoint of colpus; tectate-perforate, wall 2 μm thick; finely reticulate; 22–24 × 20–22 μm.

Guazuma is a genus of trees and shrubs consisting of three species with only *G. ulmifolia* Lam. listed for Panama (Robyns, 1964b). The latter species grows from Mexico to Panama and in the West Indies. It is ecologically variable and in Panama grows in the tropical moist, premontane wet, premontane moist, premontane dry, and tropical dry forests (Croat, 1978: 594).

UNKNOWNS

A number of specimens were recovered that could not be identified. Some of the more distinctive and/or abundant ones are illustrated and briefly described below.

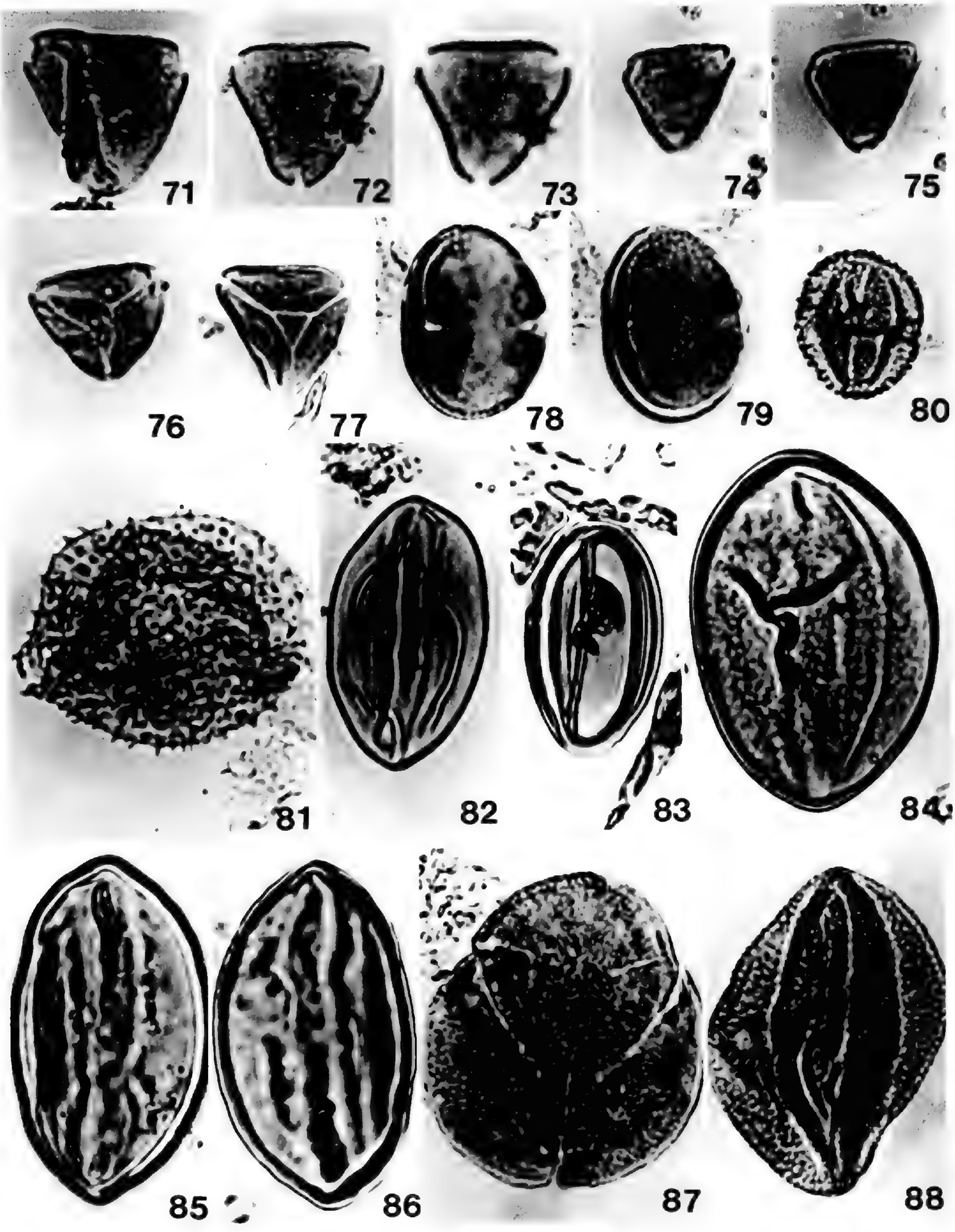
Type 1 (Fig. 81). Spherical, amb circular; nonaperturate; intectate, wall thin (ca. 1.5 μm); echinate, spines short (ca. 2–3 μm), dense; 36 μm.

Type 2 (Figs. 82–86). Prolate; tri(?)colpate, colpi sinuous, 28–46 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire; tectate, wall 2–3 μm thick, homogeneous and hyaline; psilate to faintly textured (scabrate?); 32–50 × 19–34 μm.

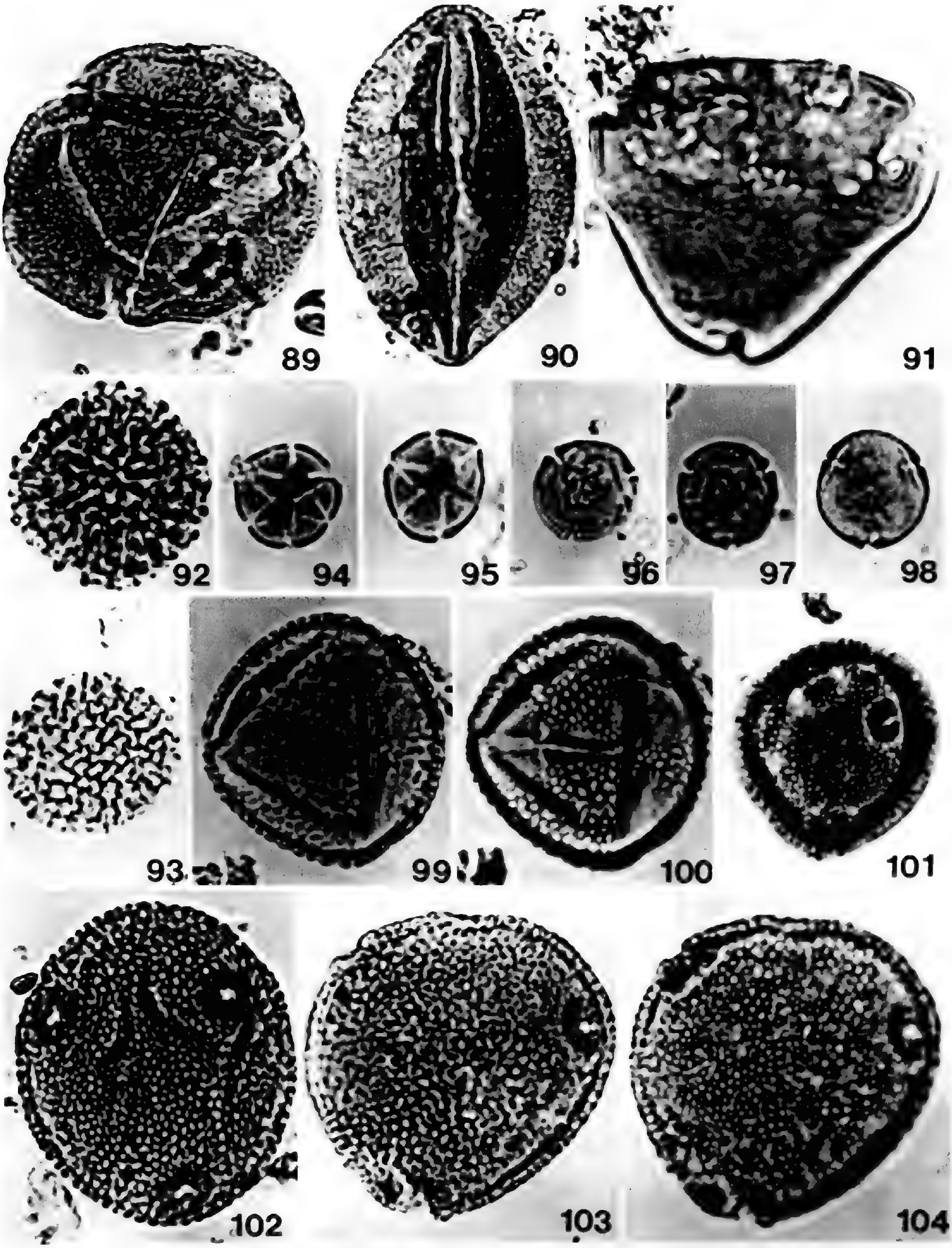
These specimens are characterized by a glass-like, hyaline wall and possibly represent an unknown fungal spore.

Type 3 (Figs. 87–90). Prolate; tricolporate, colpi straight, 40–46 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi 5–9 μm wide, pore slightly oval, 3 × 5 μm, situated at midpoint of colpus; tectate-perforate, wall 2 μm thick; finely reticulate; 42–55 × 32–43 μm.

These specimens are similar to pollen of several genera of the Anacardiaceae but also resemble



FIGURES 71–88. *Fossil pollen from the Culebra Formation, Panama.—71–75.* Allophylus. *Pan core 469.8, slide 1, ESF J-14, 1–3; Pan core 469.8, slide 2, ESF W-24, 2; Pan core 456, slide 3, ESF G-27, 1–3.—76.* Cupania. *Pan core 456, slide 3, ESF F-30.—77.* Matayba. *Pan core 470.6, slide 3a, ESF T-25, 2.—78, 79. Cf.* Pouteria. *Pan core 470.6, slide 3a, ESF J-35, 1–3.—80. Cf.* Guazuma. *Pan core 456, slide 4, ESF O-29, 4.—81. Unknown type 1. Pan core 470.6, slide 3a, ESF Q-18, 4.—82–86. Unknown type 2. Pan core 490.6, slide 1, ESF Y-32, 1; Pan core 456, slide 1, ESF H-12, 4; Pan core 456, slide 3, ESF V-18, 4; Pan core 456, slide 1, ESF R-19, 3.—87, 88. Unknown type 3. Pan core 469.8, slide 1, ESF R-23, 1–2; Pan core 469.8, slide 1, ESF Q-30, 3–4.*



FIGURES 89–104. *Fossil pollen from the Culebra Formation, Panama.—89, 90. Unknown type 3. Pan core 456, slide 1, ESF U-22, 1; Pan core 456, slide 3, ESF L-14, 2.—91. Unknown type 9. Pan core 456, slide 3, ESF R-26, 4.—92. Unknown type 14. Pan core 470.6, slide 3a, ESF F-36, 3–4.—93. Unknown type 13. Pan core 456, slide 1, ESF Q-37, 4.—94, 95. Unknown type 5. Pan core 456, slide 4, ESF F-17, 3–4; Pan core 456, slide 3, ESF P-25.—96–98. Unknown type 8. Pan core 456, slide 4, ESF K-30, 1; Pan core 456, slide 4, ESF P-25, 2–4.—99, 100. Unknown type 7. Pan core 469.8, slide 2, ESF U-25, 3–4.—101. Unknown type 12. Pan core 456, slide 4, ESF N-10.—102–104. Unknown type 11. Pan core 456, slide 3, ESF G-33; Pan core 488, slide 1, ESF V-27, 3.*

some Bignoniaceae and Euphorbiaceae. They are common in the Culebra assemblage and in several other Gulf/Caribbean Tertiary formations (e.g., Eocene Gatuncillo Formation, Panama; Graham, 1985, figs. 138–144).

Type 4 (Fig. 107). Oblate-spheroidal, amb circular; tetracolporate, colpi straight, equatorially arranged, meridionally elongated, equidistant, inner margin entire, pores equatorially elongated, ca. 1 × 4 μm, situated at midpoint of colpus; tectate, wall 2 μm thick; psilate to faintly scabrate; 23 μm.

Type 5 (Figs. 94, 95). Oblate to oblate-spheroidal; amb circular; stephanocolpate, colpi 6, straight, 6 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, pores equatorially elongated, ca. 1 × 4 μm, situated at midpoint of colpus; tectate, wall 2 μm thick; psilate; 14–16 μm.

Type 6 (Figs. 105, 106). Oblate-spheroidal, amb circular; tricolpor(oid)ate, colpi straight 15 μm long, equatorially arranged, meridionally elongated, equidistant, margin diffuse; tectate, wall 3 μm thick; scabrate, some sculpture elements more pointed, approaching echinae; 36 μm.

These specimens are generally similar to *Valeriana*, but no exact match could be found among the species examined.

Type 7 (Figs. 99, 100). Prolate-spheroidal; tricolpate, colpi straight, 22–24 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi ca. 3 μm wide, pores circular, 3 μm diam., situated at midpoint of colpus; tectate-perforate, wall 3 μm thick; reticulate, muri smooth, slightly narrower than the lumina; 36 μm.

These rare specimens may represent obliquely preserved specimens of *Coccoloba*.

Type 8 (Figs. 96–98). Oblate, amb spherical; tricolporate, colpi straight, short (4–6 μm), equatorially arranged, meridionally elongated, equidistant, inner margin entire, pores elongated equatorially (colpi transversalis), 1 × 5–6 μm, situated at midpoint of colpus; tectate, wall 1.5 μm thick; psilate to faintly scabrate; 14–20 μm.

Type 9 (Fig. 91). Oblate, amb triangular; tricolpate/porate (length/width ratio ca. 2:1), equatorially arranged, meridionally elongated, equidistant, inner margin entire, situated at apices of triangular grain; tectate, wall 2–3 μm thick; scabrate; 45 μm.

Type 10 (Fig. 108). Oblate to peroblate, amb oval-triangular to circular; tricolpate, colpi short (3–4 μm), equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi ca. 3 μm wide; tectate-perforate, wall 2 μm thick; finely reticulate; 24–28 μm.

These specimens are similar to several Bombacaceae and related families (Tiliaceae, Sterculiaceae), but a precise identification could not be made.

Type 11 (Figs. 102–104). Oblate, amb circular; triporate, pores circular, 2–3 μm diam., equatorially to slightly subequatorially arranged (grains heteropolar), equidistant, inner margin entire, annulus 3–4 μm wide; tectate-perforate, wall 2 μm thick; finely reticulate; 43–50 μm.

These distinctive specimens are common in the Culebra Formation and probably represent a plant that was and likely still is common in the tropical American flora. The specimens are similar to *Bocconia arborea* S. Wats., but the modern pollen is periporate with only an occasional triporate grain, while the numerous specimens are all triporate.

Type 12 (Fig. 101). Oblate-spheroidal to spherical, amb circular; tri- to periporate, pores circular, 2 μm diam., conspicuous annulus 2–3 μm wide; tectate-perforate, wall thick (ca. 4 μm); finely reticulate; 35 μm.

Type 13 (Fig. 93). Spherical, amb circular; tricolpate (colpi short, obscure); tectate-perforate, wall thick (4–5 μm); reticulate, muri smooth, fine and slightly sinuous; 25–28 μm.

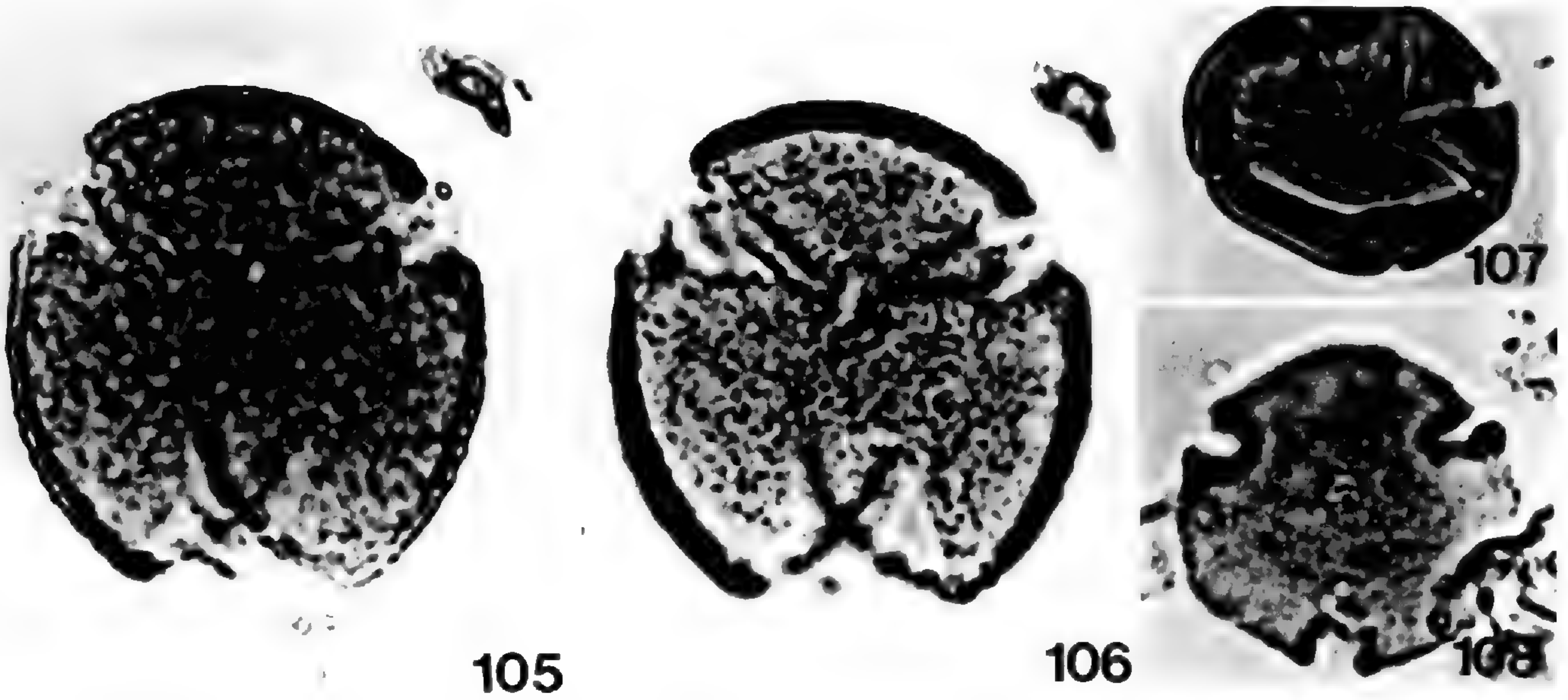
Type 14 (Fig. 92). These specimens are similar to Type 13, but the muri and walls are slightly thicker. Both are similar to pollen in some Rubiaceae (*Chomelia, Terebraria*) but do not match exactly any species in our reference collection.

In addition to these unknowns, there is also present the usual assortment of generalized small, prolate, tricolpate/colporate, finely reticulate forms common in Gulf/Caribbean Tertiary deposits. These are illustrated in Graham (1985, figs. 117–128). It is difficult to distinguish among these similar, intergrading types and they cannot presently be identified.

NUMERICAL REPRESENTATIONS

A total of 1,800 palynomorphs were tabulated from the Culebra material (200 each from levels 491.6–456, and 100 each from levels 425–377; Table 1). The ten most abundant types are as follows:

Monolete fern spore type 2: 367 specimens (20%)



FIGURES 105–108. *Fossil pollen from the Culebra Formation, Panama.—105, 106. Unknown type 6. Pan core 456, slide 3, ESF M-15, 3–4.—107. Unknown type 4. Pan core 488, slide 1, ESF J-13, 4.—108. Unknown type 10. Pan Core 456, slide 3, ESF F-25, 3.*

Manicaria-type palm pollen: 176 (10%)
Cyathea: 140 (8%)
Cryosophila-type palm pollen: 140 (8%)
Selaginella: 128 (7%)
Synechanthus-type palm pollen: 109 (6%)
Rhizophora: 100 (6%)
Monolete fern spore type 1: 84 (5%)
Hampea/Hibiscus: 68 (4%)
Lycopodium: 40 (2%)
Total ferns: 25%
Total cryptogams (ferns, *Lycopodium*, *Selaginella*): 40%
Total palms: 24%
Total lowland vegetation types (ferns, other cryptogams, palms, *Rhizophora*, *Hampea/Hibiscus*): 71%.

The composition of the Culebra flora clearly reflects a lowland tropical vegetation. Since the flora is derived from lignites deposited under lowland, coastal, brackish-water, warm-temperate to tropical conditions, there is a tendency to emphasize, possibly to over-emphasize, the potential bias toward this vegetation type. The actual bias is more in quantitative representation, with lowland communities over-represented and upland communities usually under-represented. Direct comparison of the fossil assemblage with modern vegetation types can be complicated further by differential preservation, insect versus wind pollination, and other factors. Thus attempts to quantify the paleocommunities in terms of relative abundance or aerial extent would be speculative, particularly in the absence of modern studies on pollen rain. Any impression, however, that major components of the vegetation, such as upland communities or savannahs, are *a priori* missing from paleofloras derived from lignites is inconsistent with existing data. The middle to upper Oligocene San Sebastian flora of Puerto Rico (Graham & Jarzen, 1969) and the upper Miocene Paraje Solo of southeastern Mexico (Graham, 1976), both preserved in lignites, contain many representatives of inland and highland communities in the form of pollen and spores blown or washed into the lowland basins of deposition. The data show rather convincingly that virtually any tropical vegetation type can be represented in and recognized from palynofloras such as the Culebra. An exception may be paramo, since the pollen of some important components, such as Gramineae, Compositae, and Cyperaceae, cannot be differentiated from non-paramo species. In general, however, when the characteristic and defining members of a community are missing from a diverse and well-preserved palynoflora, this is likely due to the absence or poor representation of the community in the region rather than to an absolute bias in the depositional process.

Features traditionally examined in core material are the first and last appearances of distinct types, changes in percentages of individual types through the section, and similar data on groups or assemblages of types. The purpose is to assess the possibility of subdividing or zoning the section for more precise comparison with other sections or formations (stratigraphic correlation). Such analysis is difficult for the Culebra section because of the uneven quality of preservation along the core. For example, the lowermost (oldest) samples from 491.6 and 491 feet contain palynomorphs of only fair preservation and of low diversity (14 and 12 types of palynomorphs, respectively; Fig. 109). There

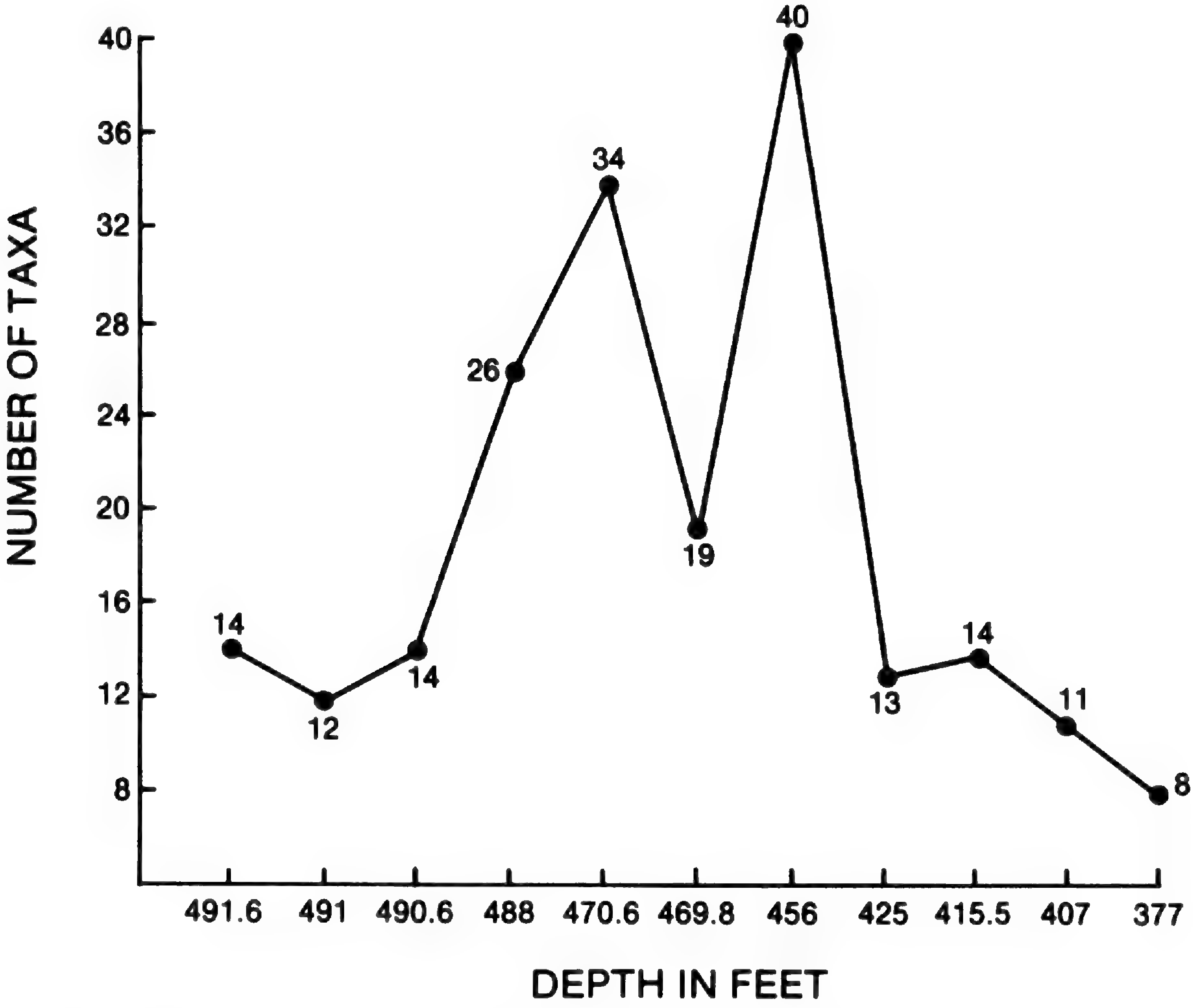


FIGURE 109. *Number of palynomorphs in each of the 11 samples from the Culebra core. Diversity and preservation were lowest at levels 491.6, 491, 490.6, 425, 415.5, 407, and 377, which also contained abundant fungal spores. Levels 470.6 and especially 456 contained the largest number of well-preserved palynomorphs and are probably most representative of the Culebra vegetation.*

are abundant thick-walled fern spores, suggesting possible differential preservation. Beginning with level 490.6, both the quality of preservation and diversity increase, which continue through level 456 (40 types), with the exception of a drop in diversity at level 469.8 (19 types). The remaining four samples (425, 415.5, 407, 377) are poor, with large numbers of thick-walled fern spores and fungal spores. It has been my experience in Gulf/Caribbean Tertiary deposits that abundance of fungal spores usually coincides with a decrease in the quality, abundance, and diversity of pollen.

In light of the differences in preservation along the core, the facts that *Lycopodium* first appears at level 490.6, or *Pteris* and Malpighiaceae at level 488, probably do not carry much stratigraphic or paleoecological significance. In instances where a particular microfossil appears confined to a single level or narrow zone (e.g., *Desmoncus*-type, Chenopodiaceae/Armaranthaceae, Compositae, cf. *Doliocarpus*, *Alchornea*, *Casearia*, *Acacia*, *Eugenia/Myrcia*, *Sabicea*, cf. *Pouteria*, cf. *Guazuma*), the percentages are very low, and the zone is usually between levels 488 and 456, where diversity and preservation are generally high. One quantitative feature of the section that does appear real is the very high percentage of *Synechanthus*-type palm pollen at level 377. Not only are these grains numerically abundant, but many occur in dense, anther-size clusters, indicating that this layer likely was deposited under or immediately adjacent to a dense stand of these palms. Similar clusters of *Rhizophora*, *Pelliceria*, and monolete, verrucate fern spores (Polypodiaceae, Blechnaceae) occur in other Gulf/Caribbean Tertiary deposits.

Other than the unusual, and probably fortuitous, abundance of *Synechanthus*-type palm pollen at level 377, the quantitative features of the assem-

TABLE 2. *Distribution of taxa identified from the lower Miocene Culebra Formation among comparable modern community types in Panama. Placement is according to principal or most common occurrence (s), and most range through more than one community.*

TROPICAL MOIST FOREST (30 genera)
Lycopodium, Selaginella, cf. *Antrophyum, Cyathea, Danaea, Lygodium, Pteris, Cryosophila*-type, *Desmoncus*-type, *Manicaria*-type, *Synechanthus*-type, *Acacia, Alchornea, Allophylus, Casearia, Combretum, Cupania, Dioscorea,* cf. *Doliocarpus, Eugenia, Hampea, Matayba, Myrcia,* cf. *Pouteria, Rhizophora,* cf. *Rourea, Sabicea, Sapium, Terminalia, Tetrorchidium*

PREMONTANE WET FOREST (25 genera)
Lycopodium, Selaginella, cf. *Anthophyum, Cyathea, Danaea, Lygodium, Pteris, Cryosophila*-type, *Manicaria*-type, *Synechanthus*-type, *Alchornea, Allophylus, Casearia, Combretum, Cupania, Dioscorea,* cf. *Doliocarpus, Eugenia,* cf. *Guazuma, Matayba,* cf. *Rourea, Sabicea, Sapium, Terminalia, Tetrorchidium*

TROPICAL WET FOREST (22 genera)
Lycopodium, Selaginella, cf. *Antrophyum, Danaea, Lygodium, Pteris, Cryosophila*-type, *Desmoncus*-type, *Manicaria*-type, *Allophylus, Casearia, Combretum, Cupania, Dioscorea, Eugenia, Hampea, Hibiscus, Matayba, Myrcia,* cf. *Pouteria, Terminalia, Tetrorchidium*

PREMONTANE MOIST FOREST (12 genera)
cf. *Antrophyum, Lygodium, Allophylus, Combretum, Dioscorea, Eugenia,* cf. *Guazuma, Hampea, Ilex, Matayba,* cf. *Rourea, Terminalia*

TROPICAL DRY FOREST (7 genera)
Lygodium, Allophylus, Casearia, Combretum, cf. *Guazuma, Matayba,* cf. *Rourea*

LOWER MONTANE WET FOREST (6 genera)
Lycopodium, Selaginella, Cyathea, Pteris, Manicaria-type, *Sapium*

LOWER MONTANE MOIST FOREST (5 genera)
Lycopodium, Selaginella, Cyathea, Pteris, Manicaria-type

PREMONTANE RAIN FOREST (5 genera)
Synechanthus-type, *Alchornea, Casearia, Hampea,* cf. *Pouteria*

PREMONTANE DRY FOREST (4 genera)
Casearia, Combretum, Eugenia, cf. *Guazuma*

LOWER MONTANE RAIN FOREST (none)
MONTANE WET FOREST (none)
MONTANE RAIN FOREST (none)

blage do not suggest any distinct zones or significant change in vegetation other than the expected spatial reshuffling of local communities with minor changes in the landscape. The assemblage is best considered as a unit, with levels 488 to 456 most representative of the Culebra vegetation. The tabulations in Tables 1 and 2 provide the most complete listing presently available of plants and paleocommunities occurring on the volcanic islands constituting Central America ca. 20 Ma.

PALEOCOMMUNITIES

Genera identified from the Culebra Formation are arranged according to paleocommunities in Table 2. These are only approximations because the microfossils are mostly identifiable to genus, and many genera range through more than one community. On the other hand, recognition of the paleocommunities is based on the presence of characteristic genera and on the total number of genera indicative of a given assemblage rather than on single "key" members. Thus, the impact of any one assignment is reduced. Also, as data accumulate from other Tertiary fossil floras in northern Latin America, there is increasing consistency, both between floras and between the paleobotanical data and evidence derived from other independent lines of inquiry (see discussions in Graham, 1987a, b, 1988c, d) regarding the kinds of vegetation likely present in the Gulf/Caribbean region. As noted earlier, the prominent representation of wet- to moist-lowland communities, compared with higher-altitude and drier savannah-type vegetation, cannot be ascribed solely to bias in the depositional environment, because the latter communities are recorded in Gulf/Caribbean Cenozoic palynofloras.

Four paleocommunities are prominent in the Culebra flora (Table 2). The tropical moist forest is represented by 30 genera that presently occur in this community. Included is *Rhizophora*, establishing the presence of the mangrove swamp, although pollen was not abundant in this section. The maximum percentage was 10.5% at level 491.6, with an average of 5.8% for the 11 levels. This is in contrast to percentages as high as 96% in one sample from the Paraje Solo Formation of southeastern Mexico (Graham, 1976: 803, table 1). The absence of other mangrove genera such as *Avicennia*, *Conocarpus*, *Laguncularia*, and *Pelliceria* suggests: 1) the community was present but not dominant in the vicinity of the depositional basin at this time, and 2) that these sediments accumulated in an estuarian fern/palm marsh environment behind the mangrove zone. The record of *Rhizophora* can be quite variable through a section, however, reflecting changes in land/sea relationships in this tectonically active region. In January 1984, core material was received from another well drilled on the east bank of the Panama Canal just north of Gold Hill. The base of the core penetrated into the uppermost part of the Culebra Formation. The microfossils were similar to those from the core used in this study, but at level 171.65–171.9, near the transition between the Culebra and the overlying Cucaracha formations (slightly higher in the Culebra section than the material reported here), the assemblage was virtually 100% *Rhizophora*. These rapid changes in the abundance of mangrove pollen are useful in defining the position of former shorelines, and were used by Bartlett & Barghoorn (1973) to trace the history of Quaternary fluctuations in sea level in Panama. Mangrove vegetation was likely common throughout the Gulf/Caribbean region from the late Eocene onwards, even though its representation at a given locality varied with physiographic conditions.

The premontane wet forest potentially includes 25 genera, and the tropical wet forest 22 genera. Some form of the premontane moist forest (12 genera) was probably present, although the evidence is not as strong as for other lowland forests. Representation of vegetation types characteristic of higher altitudes and drier habitats (including savannahs) drops off significantly, and there is no palynological evidence for their presence. This is also true for the middle(?) to late Eocene Gatuncillo flora (Graham, 1985), and the Cucaracha (Graham, 1988b) and La Boca floras of Panama (Graham, in prep.).

Thus, the vegetation of the low-lying volcanic islands constituting present-day southern Central America ca. 20 Ma consisted of a fringing zone of mangrove vegetation, with fern and palm swamps occupying the estuaries where fresh water diluted the brackish-water habitat of the mangroves. On adjacent, better-drained slopes were versions of the tropical wet, tropical moist, premontane wet, and premontane moist forests. Very local, edaphically controlled, temporal habitats supporting drier vegetation may have been present, but there is no paleobotanical evidence for these communities in the Culebra flora.

PALEOENVIRONMENTS

Of the 41 taxa recognized for the Culebra flora, all grow in southern Central America at present. The vegetation clearly grew under climatic conditions comparable to those presently prevailing in the coastal, lowland, and moderate-altitude habitats. It is not possible to quantify precisely the lower Miocene climates of the region, but the data from Barro Colorado Island cited by Croat (1978: 3–5) and from Costa Rica cited by Coen (1983) and Fleming (1986) provide approximations of the rainfall and temperature. For Barro Colorado Island, "Under the Köppen system of climatic classifications, BCI's climate is Am, or tropical Monsoon Climate. Annual rainfall on BCI ranges from 190 to 360 cm (76 to 143 inches); between 1924 and 1962 it averaged 275 cm (107.3 inches). This compares with an average 328 cm (128 inches) at Colón, on the Atlantic coast of the Canal Zone, and 177 cm (68 inches) at Balboa on the Pacific coast, during the same period" (Croat, 1978: 3; data from Rubinoff, 1974). The vegetation of the Culebra Formation is most similar to that of the present Atlantic coast of Panama. It is obvious that the existing climatic differentiation between a moist Atlantic side and a drier Pacific side did not prevail, at least to the same degree, in the lower Miocene when the present-day isthmus consisted of a series of islands. Regarding temperature, "The atmospheric temperature may vary from as low as 16.5°C (61.7°F) to as high as 35.5°C (95.9°F), with the lowest temperature being recorded within the forest during the rainy season and the highest at the Laboratory Clearing in the dry season. With rare exceptions the temperature ranges between 21 and 32°C (70° and 90°F) throughout the year, and the average ambient temperature in the Laboratory Clearing is 27°C (77°F). The seasonal variation in monthly averages is just 2.2°C" (Croat, 1978: 3).

Fleming (1986) presented similar rainfall data for ten sites in Costa Rica. Three of these form a transect from the Atlantic coast (site 10, Limón, elevation 5 m) up the Cordillera Central (site 8, Turrialba, elevation 602 m) to the Central Valley (site 6, San José, elevation 1,172 m). The mean annual rainfall is 353.6, 264.1, and 188.9 cm for the respective sites. These elevations and climatic conditions are considered similar to those prevailing on the islands of southern Central America during the lower Miocene. A generalized illustration of my concept of the spatial distribution of lower Miocene communities in southern Central America is shown in Wake (1987: 255, fig. 14), truncated at about 1,000–1,500 m elevation.

Estimates of general climate can be evaluated to some extent by comparison with ocean surface-water temperature curves derived from ^{18}O analysis of foraminifera and other marine invertebrates (Savin, 1977; Savin & Douglas, 1985; Savin et al., 1975). The curves have been discussed recently by Graham (1987b) in relation to emerging paleobotanical data for northern Latin America. The curve shows that during the lower Miocene temperatures were generally high, consistent with the tropical conditions suggested by the Culebra (Panama) and Uscari (Costa Rica) floras. A sharp drop occurred at the end of the Miocene, and this is clearly reflected in the composition and paleoecology of the late Miocene Paraje Solo flora of southeastern Mexico (Graham, 1976).

The affinities of the Culebra flora are distinctly Central and North American. There are no exclusively South American elements present, and those growing in South America are plants widespread throughout the neotropics (e.g., *Rhizophora*). This is the expected pattern of geographic affinity because the latest connection between the North and South American continents formed only in late Pliocene times, about 3 Ma (Stehli & Webb, 1985).

These data illustrate the consistency beginning to emerge between results from paleobotanical studies in the Neotropics and data derived from other independent sources. The paleoenvironmental reconstructions and biogeographic patterns, presently based on the Uscari and Culebra palynofloras, can be further evaluated and refined when studies on two additional lower Miocene floras are completed. These are the Cucaracha and La Boca floras from the Canal region of central Panama.

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STUDIES IN NEOTROPICAL PALEOBOTANY. VI. THE LOWER MIOCENE COMMUNITIES OF PANAMA—THE CUCARACHA FORMATION[1]

Alan Graham[2]

ABSTRACT

*The Cucaracha microfossil flora is the third in a series of four lower Miocene assemblages studied from southern Central America (Uscari—Costa Rica; Culebra, Cucaracha, La Boca—Panama). Nineteen palynomorphs have been identified (*Selaginella, *monolete fern spores types 1–3,* Cyathea, Ceratopteris, Pteris, *cf.* Antrophyum, *trilete fern spores types 1–2,* Crysophila *and* Manicaria*-type palm pollen,* Ilex, *Compositae,* Alchornia, Alfaroa/Engelhardia, Crudia, Eugenia/Myrcia, *and* Rhizophora*). The paleocommunities include a fern marsh, with associated palms, fringed seaward by mangroves, and bordered on the surrounding uplands by versions of the tropical wet, tropical moist, and premontane forests. Evidence for higher-altitude vegetation and communities of drier to arid aspect (open forests, savannahs) continues to be meager for Tertiary floras in the region. Affinities of the flora are distinctly Central and North American, consistent with other paleontological and biogeographic data, as well as paleophysiographic reconstructions for southern Central America. Paleoclimatic conditions were similar to those presently prevailing in coastal, lowland, and mid-altitude (1,200–1,500 m) habitats. Frequent and extensive volcanic activity documented for the region likely disrupted the vegetation, resulting in a shifting mosaic of short-term, more open communities. This may account for a paleobotanical record reflecting primarily dense forests on the slopes, while the few fossil mammalian faunas contain remains of browsers and grazers, suggesting more open forests and savannahs.*

The Cucaracha Formation is lower Miocene in age and outcrops along both sides of the Panama Canal between Hodges Hill and the Pedro Miguel Locks (Stewart & Stewart, 1980). It belongs to a complex of three Tertiary formations similar in age and lithology known to contain plant microfossils. The lowermost is the Culebra, and study of these palynomorphs has been completed (Graham, 1988). The Cucaracha Formation lies directly on the Culebra in local areas, and thus stratigraphic relationships are relatively clear, even though the region is considerably faulted. The position of the La Boca Formation is more difficult to determine because nowhere does it lie directly on the Cucaracha. However, the Pedro Miguel does overlie the Cucaracha, and in other areas it interfingers with the La Boca. Thus the three formations are presently considered sequential in age, with the Cucaracha being intermediate between the slightly older Culebra and slightly younger La Boca formations. For more detailed discussion of the geology of the pollen-bearing strata see Graham et al. (1985).

The Cucaracha Formation consists mainly of bentonitic clay shales, tuffaceous siltstones, and sandstones with lenses of conglomerates, carbonaceous shales, and lignite. A well was drilled through the formation in 1958 (Hole No. PA-33, latitude 9°01′N, longitude 79°38′W, Cucaracha Reach Widening Studies, Panama Canal Commission), and the log shows the above sequence repeated many times through the 40.8-m section. Near the base is a conglomerate containing abundant oyster shells. The sequence is typical of a tectonically active, coastal, estuarine environment, and the lignites

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TABLE 1. *Identification and numerical representation of fossil palynomorphs from the lower Miocene Cucaracha Formation, Panama. Figures are percentages based on counts of 100. Samples 57–59 are from the lower lignite in the section, and samples 62–66 are from the upper lignite. Samples 57 and 66 contained abundant fungal spores, and preservation of pollen and other spores was fair to poor.*

	Sample Number						
	57	58	59	62	63	65	66
Selaginellaceae							
Selaginella	—	—	—	—	—	—	5
Monolete fern spore							
Type 1	16	6	62	7	14	1	3
Type 2	3	—	—	—	1	1	7
Type 3	6	65	16	72	77	77	38
Cyatheaceae							
Cyathea	—	—	—	—	—	—	3
Pteridaceae							
Ceratopteris	—	—	1	—	—	—	—
Pteris	—	—	1	—	—	—	—
Vittariaceae							
cf. *Antrophyum*	—	3	3	—	—	—	—
Trilete fern spore							
Type 1	—	—	—	—	—	—	4
Type 2	—	—	—	—	—	—	3
Palmae							
Crysophila-type	—	—	—	—	—	—	2
Manicaria-type	11	13	8	6	6	4	13
Aquifoliaceae							
Ilex	—	—	—	—	—	—	1
Compositae	—	—	—	2	—	—	—
Euphorbiaceae							
Alchornea	—	—	1	1	—	1	—
Juglandaceae							
Alfaroa/Engelhardia	—	—	—	1	—	—	—
Leguminosae Caesalpinioideae							
Crudia	—	—	—	—	—	—	2
Myrtaceae							
Eugenia/Myrcia	—	—	—	—	—	—	2
Rhizophoraceae							
Rhizophora	60	13	7	9	—	11	17
Unknowns							
Type 1	3	—	—	—	—	—	—
Type 2	1	—	1	2	2	5	—

indicate warm-temperate to tropical conditions. Extensive vulcanism is indicated by the tuffs (waterlain volcanic ash) and the basalt that caps the section.

THE COLLECTING LOCALITY

Samples were obtained from a roadside exposure along road K-2, about 0.8 km northwest of the intersection with K-15 in the Gaillard Cut section of the Canal. At this site there is a small utility building, and about 4 m above and to the left is a conspicuous conglomerate layer about 1 m thick (see figs. 7, 8 in Graham et al., 1985). This layer terminates abruptly and continues on the other side of the building about four meters lower in the section. This is one of the many minor faults in the region and is a convenient marker for the locality. Ten samples were collected (our locality C, samples 57a–66) and seven contained plant microfossils. Three of these (57–59) came from a 0.6-m layer of lignitic shale about six meters below the conglomerate and to the right (facing the slope) of the utility building. Four (62, 63, 65, 66) came from a similar lignitic shale about four meters above the conglomerate; all samples were spaced horizontally about two meters apart. About 0.7 km further to the right (NW) is the site from which Whitmore & Stewart (1965) reported a mammalian fauna from the Cucaracha Formation, all with distinct North American affinities.

MATERIALS AND METHODS

Extraction and processing techniques are described in Graham (1985). Slides are labeled Pan C, Cucaracha, sample, and slide number (e.g., Pan C, Cucaracha, 66, 1). Location of specimens on the slides is by England Slide Finder coordinates (e.g., ESF R-34, 3–4). All materials are deposited in the palynology collections at Kent State University.

SYSTEMATICS

Nineteen palynomorphs have been identified from the Cucaracha assemblage (Table 1), and two others were recovered whose biological affinities could not be established (unknowns types 1 and 2). Illustrations, descriptions, and other data are provided for each pollen/spore type, but since all have been recovered from other Gulf/Caribbean Tertiary formations, the information is synoptic, and references are provided to more detailed discussions. These formations, with references, are as follows: Gatuncillo (middle(?) to late Eocene, Panama; Graham, 1985), San Sebastian (middle to late Oligocene, Puerto Rico; Graham & Jarzen, 1969), Uscari (early Miocene, Costa Rica; Graham, 1987a), Culebra (early Miocene, Panama; Graham, 1988), and Paraje Solo (late Miocene, southeastern Veracruz, Mexico; Graham, 1976). A map of the geographic distribution and a chart summarizing the age of the formations are given in Graham (1987b; for other aspects of the identification procedures see Graham 1985: 507–508). Present ranges of the modern analogs within the Neotropics and ecological data are summarized after each description, with more detailed summaries provided in the paleobotanical publications previously cited. These data are based on field observations, personal communication with specialists in the various plant groups, and the literature, especially Croat (1978), D'Arcy (1987), Hartshorn (1983), Tryon & Tryon (1982), and Woodson & Schery (1943–1980). Terminology for vegetation types follows Holdridge (1947; Holdridge et al., 1971), used by Croat (1978) and Hartshorn (1983) for describing the plant communities of Panama and Costa Rica.

SELAGINELLACEAE

Selaginella (Figs. 1, 2). Spherical, amb circular to oval-triangular; trilete, laesurae frequently obscured by dense sculpture and appearing monolete, straight, narrow, ca. 20–24 μm long, extending nearly to spore margin; echinate, echinae short (ca. 2–3 μm), occasionally curved, dense, bases broad; wall ca. 2 μm thick (excluding echinae); 26–30 μm.

Other occurrences. Gatuncillo, San Sebastian, Uscari, Culebra, Paraje Solo formations.

Distribution. Widespread; usually moist, shaded habitats; typically low to mid altitudes but widespread altitudinally.

MONOLETE FERN SPORES

These spore types are produced by many members of the Blechnaceae and Polypodiaceae and cannot be referred to any one modern genus, especially in the absence of the ornamented exospore or perine. They are often assigned to the artificial genera *Laevigatosporites* (smooth forms) or *Verrucatosporites* (verrucate forms), and these range from Paleozoic to Recent. They occur in all of our Gulf/Caribbean Tertiary deposits studied to date, and multiple biological species are likely represented by each of the spore types described below.

Type 1 (Figs. 3, 4). Reniform; monolete, laesurae straight, narrow, 24–28 μm long, extending ca. ¾ spore length, inner margin entire; laevigate; 40–50 × 30–40 μm.

This is one of the most abundant spores in the Cucaracha Formation, although percentages vary widely among the samples (Table 1). Figure 4 is a low-magnification view of part of a single field (negative-size portion) typical of samples where the spore is dominant. Ten specimens are evident in this field, and a thousand or more may occur on a slide.

Type 2 (Figs. 5, 6). This spore differs from Type 1 in having a slightly thicker wall and, therefore, is more consistently reniform in shape. The specimens range in size from 35 × 20 μm (Fig. 5) to 42 × 32 μm (Fig. 6).

Type 3 (Figs. 7–11). Reniform; monolete, laesura straight, narrow, 30–45 μm long, extending ¾ spore length, inner margin entire; verrucate, verrucae moderately low, conspicuous and dense, grading into less dense, widely spaced verrucae, shape irregular, ca. 3 × 6 μm; wall 2–3 μm thick; 35–55 × 25–35 μm.

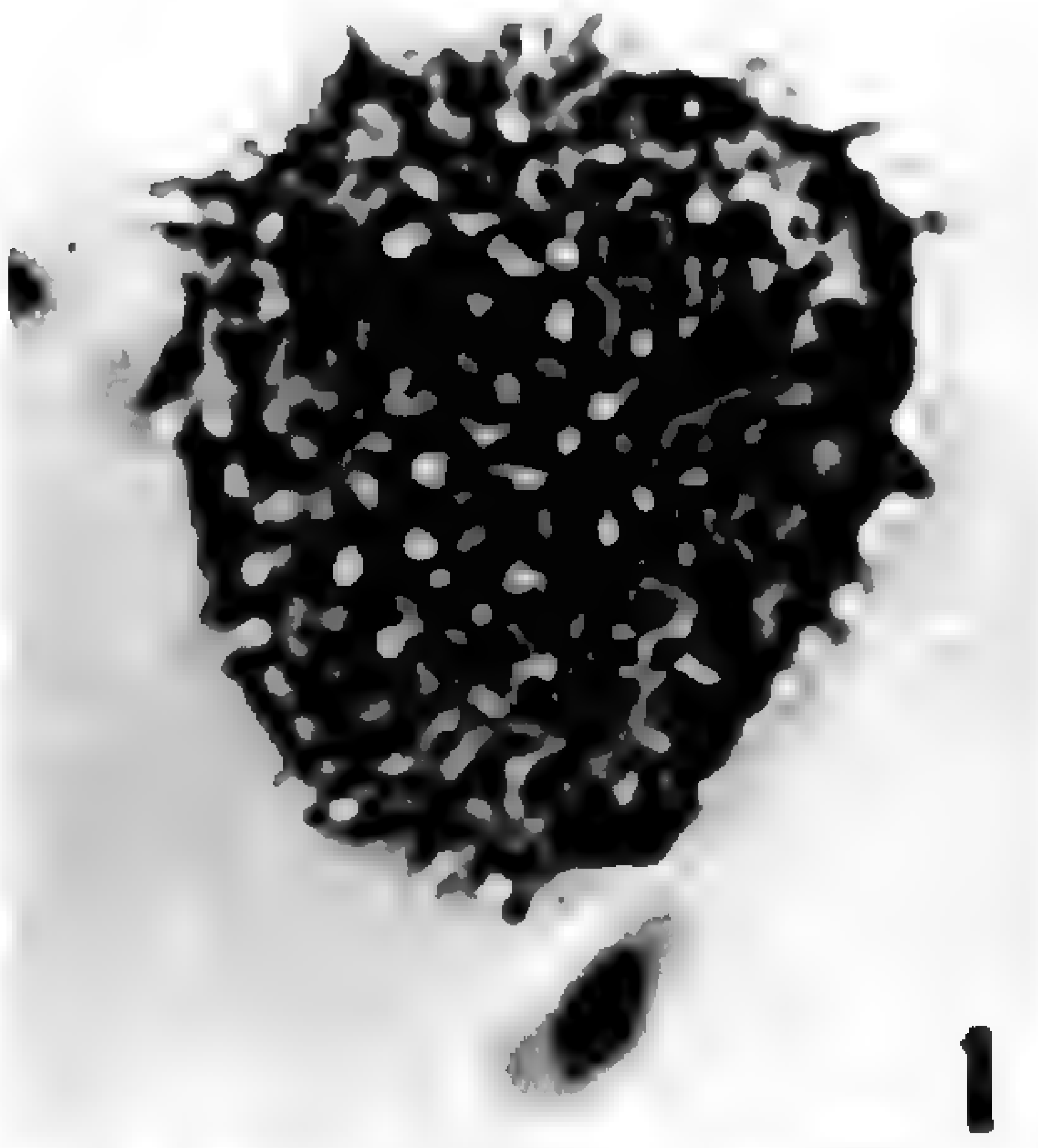
This is another spore that is dominant in several samples, almost to the exclusion of other microfossils (Table 1). In addition to individual specimens, many clusters of 5–20 loosely aggregated spores were evident on the slides (Fig. 7). This indicates that the Cucaracha sediments at this locality were accumulating directly under or immediately adjacent to a fern marsh, with little transport of the specimens.

The spores vary in size and density of the verrucae. Figure 8 illustrates a small specimen (ca. 37 μm), and Figure 9 a larger one (ca. 54 μm), while comparison of Figure 8 with Figure 11 shows the variation in the number of verrucae. Similar spore variation occurs within species as well as among species and genera of modern Blechnaceae and Polypodiaceae. As noted previously, more than one biological species, or genus, is likely represented by this spore type.

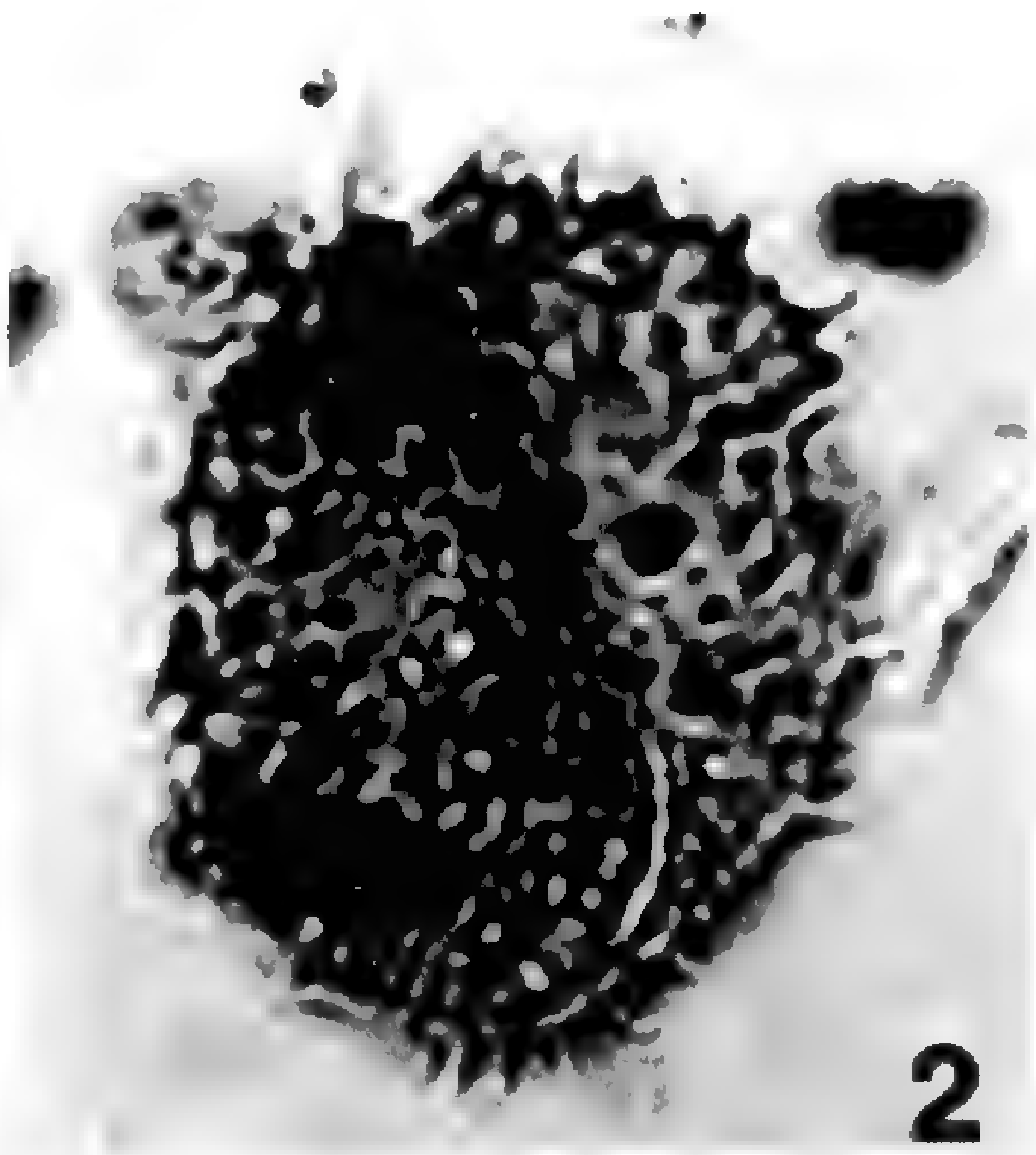
TRILETE FERN SPORES

Cyatheaceae

Cyathea. Amb oval-triangular, apices rounded; trilete, laesurae straight, narrow, 14–16 μm long, extending to spore margin, inner margin entire, bordered by lip 2–3 μm wide with punctae 1 μm diam.; distal surface finely punctate, proximal surface more laevigate near laesurae; wall 1.5–2 μm thick; 30–35 μm.



1



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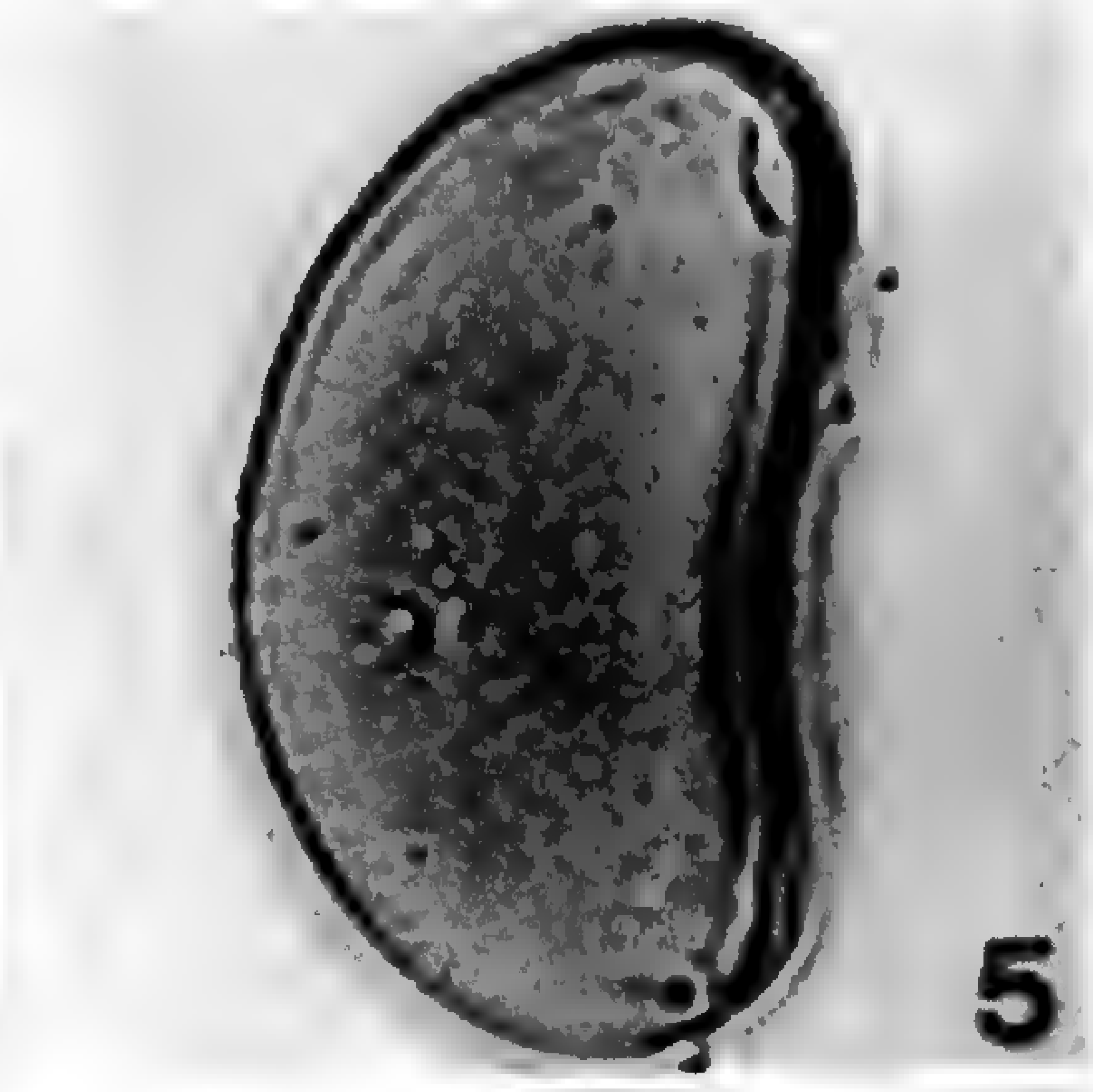

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7

8

A few poorly oriented specimens of *Cyathea* were recovered from sample 66, but the genus is frequent in other Caribbean Tertiary deposits. According to Gastony & Tryon (1976) and Tryon & Tryon (1982: 207), the micropunctate forms represent *Cyathea*, while similar but smooth (laevigate) types are referred to the closely related *Alsophila*.

Other occurrences. San Sebastian, Culebra, Paraje Solo formations.

Distribution. Widespread, primarily montane forests and cloud forests; in Central America low rain forests usually at 1,500–2,000 m, but as low as 500 m.

Pteridaceae

Ceratopteris (Figs. 14, 15). Amb oval-triangular, spore margin undulating due to projecting sculpture elements; trilete, laesurae straight, narrow, 28–32 μm long, extending to spore margin, inner margin entire; wall coarsely and conspicuously striate, striae psilate, 3–4 μm wide, prominently developed on distal surface, less distinct approaching laesurae; wall 2–3 μm thick; 75–90 μm.

Other occurrences. Gatuncillo, Paraje Solo formations.

Distribution. Widespread, southeastern U.S. (Texas to Florida), southern Mexico, Central America, Antilles, South America; frequently aquatic, ditches, lagoons, river/lake margins, brackish waters; sea level to ca. 300 m.

Pteris (Fig. 13). Amb triangular, apices rounded; trilete, laesurae straight, narrow, 15–18 μm long, extending to spore margin, inner margin entire; distal surface with coarse, irregular verrucae, proximal surface more laevigate, flange ca. 6 μm wide, hyaline; wall 2 μm thick; 42–48 μm.

Other occurrences. Gatuncillo, San Sebastian, Uscari, Culebra, Paraje Solo formations.

Distribution. Mexico, Central America, the Antilles, and South America; openings or along margins of wet or cloud forests; sea level to ca. 2,000 m.

Vittariaceae

Cf. *Antrophyum* (Fig. 12). Amb triangular, apices rounded; trilete, laesurae relatively small in relation to spore diameter, straight, narrow, 12–15 μm long, extending ca. ⅔ distance to spore margin, inner margin entire; laevigate; wall ca. 1.5 μm thick; 47–54 μm.

Other occurrences. San Sebastian (not figured in Graham & Jarzen, 1969), Culebra, and Paraje Solo formations.

Distribution. Hidalgo, Mexico, Central America, and the Antilles, to northern Argentina and southeastern Brazil; rain and cloud forests; elevations usually 100–1,500 m.

OTHER TRILETE FERN SPORES

Type 1 (Fig. 16). Amb oval-triangular; trilete, laesurae straight, narrow, 14–16 μm long, extending to or nearly to spore margin, inner margin entire; finely reticulate, reticulum becoming more irregular near laesurae; wall ca. 1.5 μm thick; 27–30 μm.

Other occurrences. Possibly Culebra Formation (larger specimen).

Type 2 (Figs. 17, 18). Amb oval-triangular; trilete, laesurae straight, narrow, 15–17 μm long, extending to or nearly to spore margin, inner margin entire; punctate, punctae circular (ca. 1 μm) to elongated (2–3 μm), slitlike and sinuous; wall 2 μm thick; 33–36 μm.

Other occurrences. Possibly Culebra Formation (larger specimen with more conspicuous slitlike punctae).

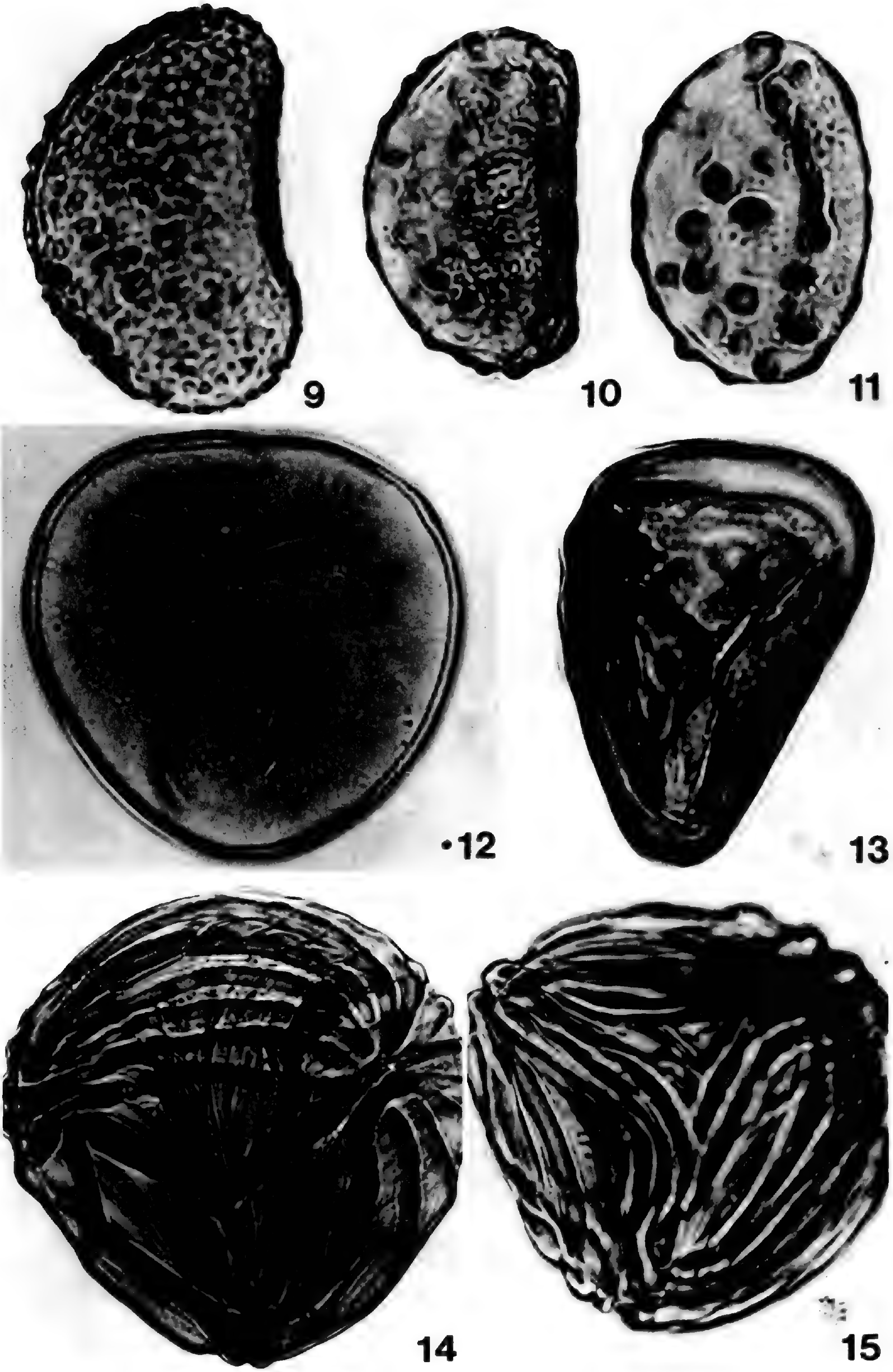
PALMAE

Crysophila-type (Fig. 19). Prolate, amb oval; monocolpate, colpus straight, 22–24 μm long, extending entire length of grain, margin entire; tectate-perforate, wall 2 μm thick; reticulate, muri relatively broad (ca. 1–1.5 μm), flat, lumen ca. 2 μm in diameter on distal side, smaller approaching colpus; 31–33 × 18–20 μm.

Other occurrences. Culebra Formation.

←

FIGURES 1–8. *Fossil spores from the Cucaracha Formation, Panama.—1.* Selaginella *(trilete scar evident). Pan C-66, 1, ESF R-34, 3–4.—2.* Selaginella *(trilete scar obscure, appearing monolete). Pan C-66, 1, ESF T-31. 3, 4. Monolete fern spore type 1.—3. Pan C-57, 1, ESF C-24, 4.—4. Overview (10×) in upper left corner of Pan C-59, 2 showing 10 monolete fern spore type 1 in single frame (partial field of view).—5. Monolete fern spore type 2 (small). Pan C-63, 1, ESF K-21, 2–4.—6. Monolete fern spore type 2 (large). Pan C-57, 1, ESF G-21, 2–4.—7. Loose cluster of monolete fern spore type 3. Pan C-62, 1, ESF G-33, 2.—8. Monolete fern spore type 3. Pan C-57, 1, ESF G-22, 1–3.*



FIGURES 9–15. *Fossil spores from the Cucaracha Formation, Panama.—9–11. Monolete fern spore type 3. Pan C-65, 1, ESF P-22, 3–4; Pan C-63, 1, ESF K-11, 2; Pan C-63, 1, ESF H-16, 1–2.—12. Cf.* Antrophyum.

Distribution. Belize to Panama; tropical wet, tropical moist, premontane wet forests; low altitudes.

Manicaria-type (Figs. 20–22). Prolate; monocolpate, colpus straight, 30–36 μm long, extending nearly entire length of grain, inner margin entire; scabrate (to possibly microreticulate); trilete, wall 1.5 μm thick; 36–45 × 20–24 μm.

Other occurrences. Gatuncillo, Culebra formations.

Distribution. Antilles, Central and South America; wet places; low altitudes.

Another palm pollen of the *Manicaria*-type was recovered but differs in size (25 vs. 36–45 μm; Figs. 23, 24).

AQUIFOLIACEAE

Ilex (Fig. 25). Oblate-spheroidal, amb circular; tricolporoidate, colpi straight, 18 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin diffuse, pores obscure, situated at midpoint of colpus; intectate; clavate, wall ca. 3 μm thick (length of clavae); 27 × 22 μm.

Other occurrences. Gatuncillo, San Sebastian, Uscari, Culebra, Paraje Solo formations.

Distribution. Widespread; mesic to slightly drier habitats; low to mid altitudes; Costa Rica—tropical and premontane wet lowlands, montane rain forest.

COMPOSITAE

(Figs. 26–28). Spherical, amb circular; tricolporate, colpi straight, short (ca. 10 μm), equatorially arranged, meridionally elongated, equidistant, pore oval, ca. 4 × 2 μm, situated at midpoint of colpus; tectate, wall 2–3 μm thick; echinate, echinae short (ca. 2–3 μm), base broad, moderately dense (distance between spines ca. 3–4 μm); 23–27 μm.

Other occurrences. Uscari (rare), Culebra (rare), and Paraje Solo (relatively common) formations.

EUPHORBIACEAE

Alchornea (Fig. 29). Oblate, amb circular; tricolpate, colpi straight, 8–10 μm long (pole to equator), equatorially arranged, meridionally elongated, equidistant, extending within 6–7 μm of pole, inner margin entire, distinct operculum; tectate, wall 2 μm thick; psilate to faintly scabrate; 15–21 μm.

Other occurrences. San Sebastian, Uscari, Culebra, Paraje Solo formations.

Distribution. Widespread; Panama—tropical moist, premontane wet, premontane rain forests; Costa Rica—alluvial soil in tropical wet lowlands, mid-altitude wet and rain forests, altitude range 300–2,000 m.

JUGLANDACEAE

Alfaroa/Engelhardia (Fig. 30). Oblate, amb oval-triangular; triporate, pores circular, ca. 2 μm, inner margin entire, equatorially arranged, equidistant; tectate, wall 1.5 μm thick; psilate; 21 μm.

Other occurrences. Gatuncillo, San Sebastian, Paraje Solo formations.

Distribution. Mexico, Central America; typically associated with lower to mid-altitude temperate forests.

LEGUMINOSAE

Caesalpinioideae

Crudia (Fig. 31). Prolate; tricolporoidate, colpi narrow, straight, 25 μm long, extending nearly entire length of grain, equatorially arranged, meridionally elongated, equidistant, pore area faint, circular, situated at midpoint of colpus; tectate but with occasional separation between sculpture elements, wall 1.5 μm thick; distinctly and coarsely striate, striae generally oriented parallel to long axis of grain, surface psilate, margins entire, occasionally appearing beaded from underlying pores in foot layer/endexine; 32 × 20 μm.

Other occurrences. Gatuncillo Formation.

Distribution. Mainly Amazonian, often riverine; low altitude.

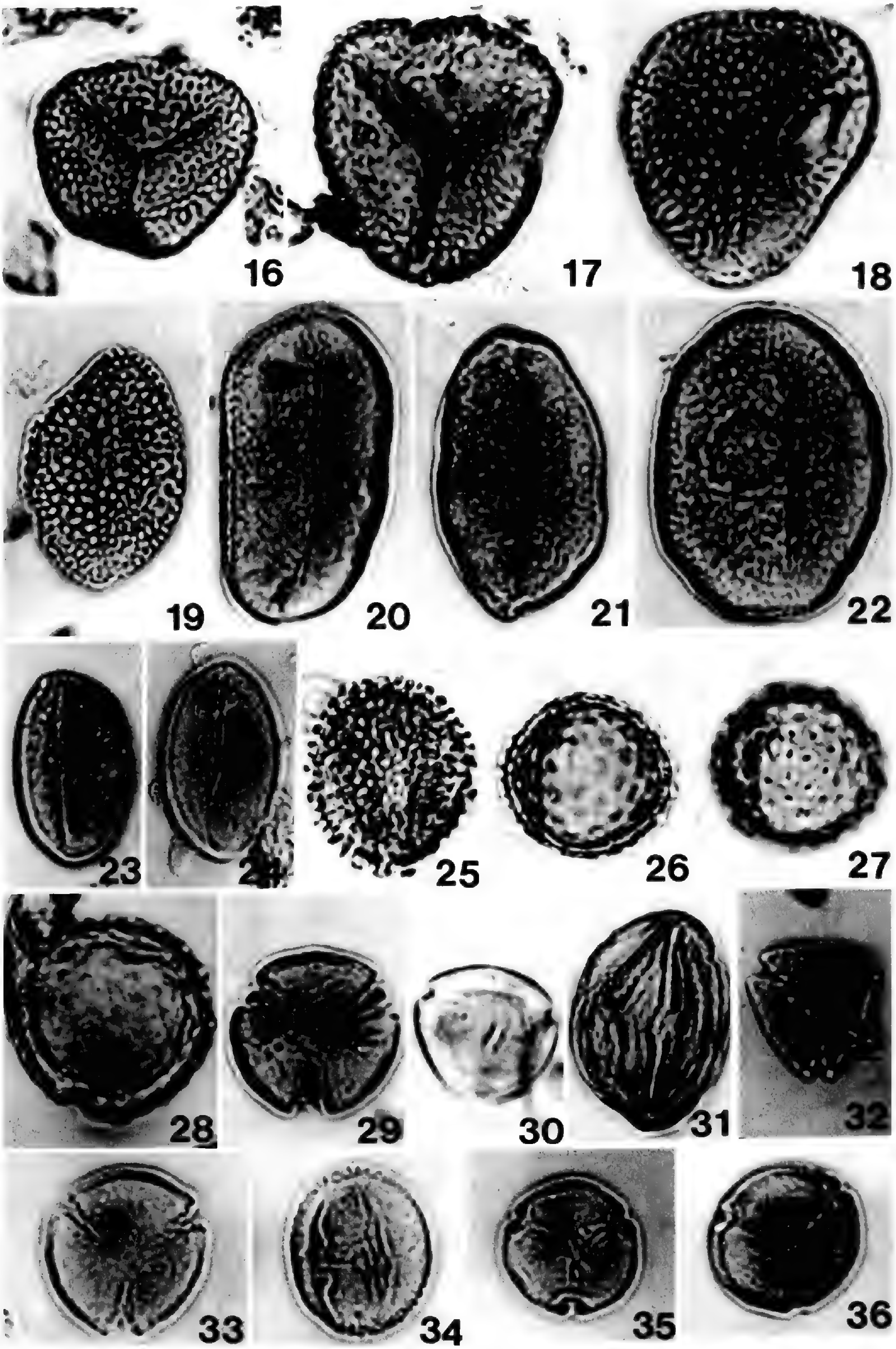
MYRTACEAE

Eugenia/Myrcia (Fig. 32). Oblate to peroblate, amb triangular; tricolporate, colpi narrow, straight, 9 μm long, equatorially arranged, meridionally elongated, equidistant, syncolpate, pore ca. 1 μm diam., situated on equator at midpoint of colpus; tectate, wall thin (ca. 1.5 μm); faintly scabrate; 18 μm.

Other occurrences. Gatuncillo, San Sebastian, Uscari, Culebra, Paraje Solo formations.

←

Pan C-59, 2, ESF X-20, 1–2.—13. Pteris. *Pan C-59, 2, ESF R-34, 2–4.—14, 15.* Ceratopteris. *Pan C-59, 2, ESF X-45, 1–3; Pan C-59, 2, ESF H-33.*



FIGURES 16–36. *Fossil spores and pollen from the Cucaracha Formation, Panama.—16. Trilete fern spore type 1. Pan C-66, 1, ESF K-35, 1.—17, 18. Trilete fern spore type 2. Pan C-66, 1, ESF G-53, 3; Pan C-66, 1, ESF X-31, 1–3.—19.* Cryosophila-*type palm pollen. Pan C-66, 1, ESF P-33, 3.—20–22.* Manicaria-*type palm*

FIGURES 37-39. *Fossil pollen from the Cucaracha Formation, Panama. Unknown type 2. Pan C-59, 2, ESF Q-41, 1; Pan C-59, 2, ESF V-48, 3-4; Pan C-57, 1, ESF M-19, 1-3.*

RHIZOPHORACEAE

Rhizophora (Figs. 33, 34). Prolate to prolate-spheroidal; tricolporate, colpi narrow, straight, 14-16 µm, apices acute, equatorially arranged, meridionally elongated, equidistant, costae colpi ca. 3 µm, pores elongated equatorially (colpi transversalis), 1 × 4 µm, constricted at midpoint of colpus, inner margin entire; tectate-perforate, wall 2-3 µm thick; finely reticulate; 18-25 × 16-20 µm.

Other occurrences. Gatuncillo, San Sebastian, Uscari, Culebra, and Paraje Solo formations.

Distribution. Widespread, southeastern U.S. to South America; warm-temperate to tropical habitats, coastal brackish waters; sea level.

UNKNOWNS

Type 1 (Figs. 35, 36). Oblate, amb circular; tricolporate, colpi narrow, straight, 6-8 µm long, equatorially arranged, meridionally elongated, equidistant, syncolpate, pores circular to slightly elongated equatorially, costae pori, situated on equator at midpoint of colpus; tectate-perforate, wall ca. 2 µm thick; finely reticulate; 16-20 µm.

Type 2 (Figs. 37-39). Prolate; tricolporate, colpi straight, 40-48 µm long, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi 5-7 µm wide, pore slightly oval, 3 × 5 µm, situated at midpoint of colpus; tectate-perforate, wall 2 µm thick; finely reticulate; 43-55 × 30-42 µm.

Other occurrences. Gatuncillo, Culebra, and Paraje Solo formations.

NUMERICAL REPRESENTATIONS

A total of 700 palynomorphs were tabulated from the Cucaracha material (100 from each of the seven samples; Table 1). Normally 200 pollen grains and spores are counted, but in the Cucaracha assemblage each sample was dominated by a single type, with all other forms collectively constituting only a small percentage of the flora. The most abundant microfossils were monolete fern spore type 3, monolete fern spore type 1, *Rhizophora*, and *Manicaria*-type palm pollen. Vascular cryptogams (ferns and *Selaginella*) totaled 71% of the flora, *Rhizophora* 17%, palms 9%, and all other angiosperm pollen 3%. Clearly, the sediments accumulated in a fern marsh with palms surrounding

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←
pollen (large). Pan C-59, 2, ESF N-43, 1-3; Pan C-59, 2, ESF K-28, 1-3; Pan C-59, 2, H-33, 4.—23, 24. Manicaria-*type palm pollen (small). Pan C-59, 2, ESF N-25; Pan C-57, 1, ESF U-11, 3.—25.* Ilex. *Pan C-66, 1, ESF E-34, 3-4.—26-28. Compositae, Pan C-62, 1, ESF R-40, 3-4; Pan C-62, 1, ESF F-48, 2-4.—29.* Alchornea. *Pan C-59, 2, ESF H-21.—30.* Alfaroa/Engelhardia. *Pan C-62, 1, ESF F-48, 2-4.—31.* Crudia. *Pan C-66, 1, ESF H-40, 3-4.—32.* Eugenia/Myrcia. *Pan C-66, 1, ESF S-31, 2-4.—33, 34.* Rhizophora. *Pan C-57, 1, ESF C-27, 1; Pan C-57, 1, ESF D-18, 3.—35, 36. Unknown type 1. Pan C-57, 1, ESF F-19, 4; Pan C-59, 2, ESF S-41, 1-3.*

and possibly intermingling with the ferns and with mangrove (*Rhizophora*) growing along the seaward margin of the depositional basin. It was a simple ecosystem in terms of community types, with little pollen of other associations being blown or washed into the basin from the surrounding landscape.

Another quantitative feature of the Cucaracha flora is the rapid change in this coastal vegetation over very short periods of time. Samples 57, 58, and 59 were from a lower lignite bed about 0.6 m thick. All samples were taken from about the middle of the seam and horizontally were about two meters apart. Yet sample 57 contained about 60% *Rhizophora* pollen, sample 58 had 65% type 3 monolete fern spores (with only 13% *Rhizophora*), and sample 59 had 62% type 1 monolete fern spore (with only 7% *Rhizophora* and 16% type 3 fern spore). The vertical difference between the samples was, at maximum, only a few centimeters, and in a rapidly accumulating, estuarine sedimentary basin this likely represents only a few to several hundred years. Within this brief time span, three different taxa dominated the site. The upper lignite layer was more uniform in composition, with monolete fern spore type 3 dominant in all samples (Table 1). Among the seven samples from the two lignite layers, *Rhizophora* ranged from absent (sample 63) to 60% (sample 57); monolete fern spore type 1 from 62% (sample 59) to 1% (sample 65); and monolete fern spore type 3 from 77% (samples 63, 65) to 6% (sample 57). There were apparently some habitat differences within and between the lignite layers, as well as differences in ecological preference between the ferns, because the percentages of monolete fern spore types 1 and 3 were reciprocal. These fluctuations evident in the pollen and spore assemblage are typical of estuarine habitats in tectonically unstable regions. Slight elevation of the land surface (or lowering of sea level) drains the lowlands marginal to the coast of salt water, and ferns dominate the freshwater habitats provided by inflowing rivers. With land subsidence marshes are inundated, the waters rendered brackish, and mangroves dominate the site. This sequence is repeated many times through the Culebra Formation, as evidenced by the alternating layers of lignites and lignitic shales; mud-, silt-, and sandstones; water-lain volcanic ash (tuffs); and the basal oyster-rich conglomerate.

PALEOCOMMUNITIES AND PALEOENVIRONMENTS

A limited number of paleocommunities are revealed by the Cucaracha flora. A fern marsh, with associated palms and the floating fern *Ceratopteris*, are well represented. This freshwater assemblage was fringed seaward by mangroves (*Rhizophora*). Some indication of the inland vegetation is provided by a few spores of the tree ferns *Cyathea* and *Pteris*, and small amounts of pollen of *Alchornea*, *Alfaroa/Engelhardia*, Compositae, *Crudia*, *Eugenia/Myrcia*, and *Ilex*. These suggest tropical wet, tropical moist, and premontane forests on the adjacent slopes. It is likely that higher-altitude vegetation was meager, and its absence to poor representation in the microfossil record not just the result of exclusion from the sedimentary process. In other palynofloras (e.g., the San Sebastian flora of Puerto Rico and the Paraje Solo flora of Mexico), representatives from mid- to higher-altitude communities are common. Their poor representation in the Cucaracha flora is probably an accurate reflection of the kinds of communities occupying the low, insular landscape in the region at the time.

Pollen grains of the Gramineae, other species associated with savannah habitats, and dry to arid vegetation were not recovered, consistent with results from other Tertiary floras in Central America.

The paleoenvironment can only be characterized generally as tropical and probably similar to that presently prevailing at lower altitudes in the region (see Graham, 1985: 531–532). All palynomorphs recovered from the Cucaracha Formation occur in the modern vegetation of Panama.

TERTIARY FLORAS, FAUNAS, AND VOLCANISM IN SOUTHERN CENTRAL AMERICA

As data accumulate on the Tertiary floras of northern Latin America, it is becoming evident that little *paleobotanical* evidence is emerging for extensive savannah or open-forest habitats. The limited data do not preclude, however, more local, shifting, temporal stands of these communities in the Central American landscape. Such accommodation is necessary because of a seemingly anomalous situation developing between the kind of vegetation reflected in the Tertiary floras of Central America and the kind of habitats required by the few mammalian faunas known from the area. The palynofloras suggest that tall, dense tropical forests were prevalent on adjacent upland slopes, while the vertebrate faunas contain significant numbers of browsers (low open forests) and grazers (savannahs).

Tertiary palynofloras from Central America (see chart in Graham, 1987b) contain little or no grass pollen, or pollen of trees or shrubs characteristically associated with open forests or savannahs. An exception may be the few grains of *Acacia* pollen found in the Paraje Solo and Culebra floras. Bartlett & Barghoorn (1973) found little evidence for savannah or drier open forests in Quaternary sediments from Gatun Lake, Panama, but Leyden (1984) reported the presence of more arid vegetation from Pleistocene deposits in Guatemala. The latter report, and the very small amounts of grass and *Acacia* pollen in Tertiary sediments, indicate that the list of Cenozoic paleocommunities for the region is still being developed. Nonetheless, the principal communities in the Cucaracha flora were likely the tropical moist, tropical wet, and premontane forests, with mangroves and fern and palm marshes occupying coastal and swamp habitats.

In contrast, browsers and grazers are the prominent components in the two principal Tertiary vertebrate faunas reported from Central America. Olson & McGrew (1941) described a fauna from the Pliocene Gracias Formation, in the Mejocote Valley of Honduras. In addition to *Amphicyon*, *Procamelus* (camel), and *Blickotherium* (mastodon), the most common remains were of the horses *Pliohippus* and *Neohipparion*. Whitmore & Stewart (1965) described a fauna from the Cucaracha Formation, ca. 0.7 km from the plant microfossil locality. In addition to the marsh- and swamp-inhabiting turtle and alligator remains, they reported five browsing ungulates: Equidae (*Anchitherium*, *Archaeohippus*), Rhinocerotidae (*Diceratherium*), Merycoidodontidae (*Merycochoerus*), and Protoceratidae (a selenodont artiodacytyl).

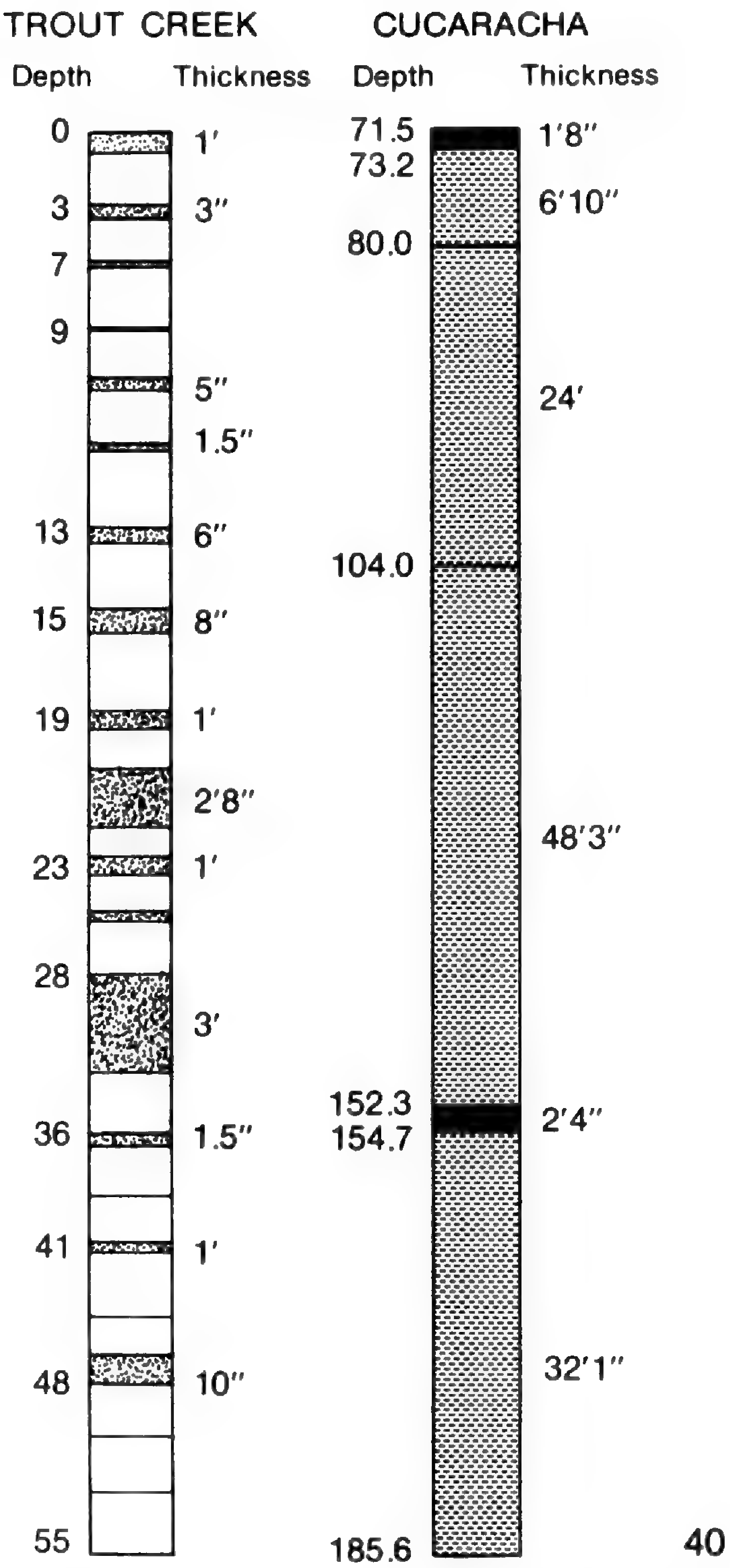
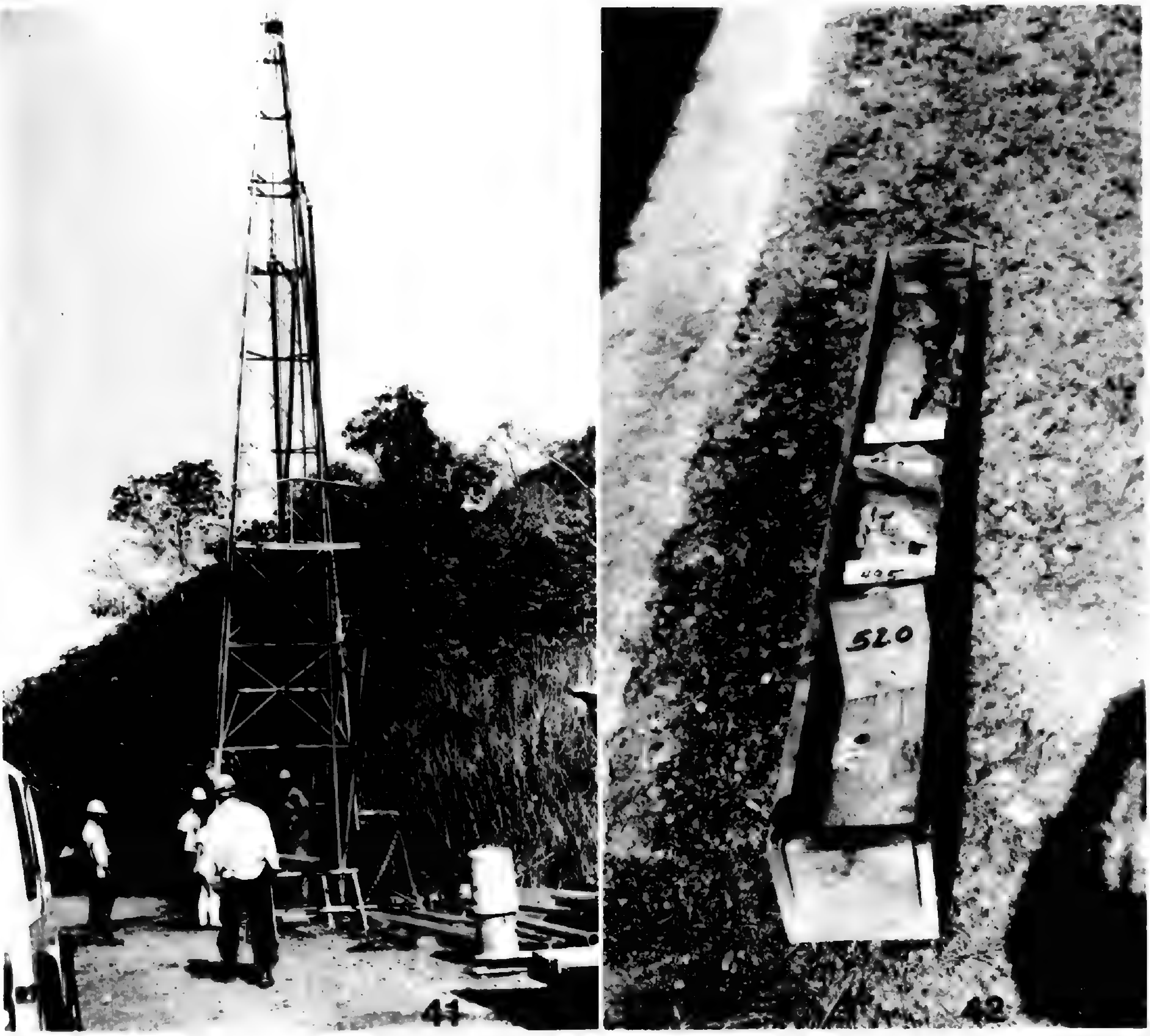


FIGURE 40. *Stratigraphic sections from the Trout Creek (late Miocene, Oregon) and Culebra (early Miocene, Panama) formations. White = diatomite; stippled = sandstone and sandy volcanic ash; black = lignite, lignitic shale, or highly carbonaceous clay-siltstone; dashed = tuffs (water-lain volcanic ash) or clay-siltstones derived from erosion of tuffs. In both sections the plant megafossils (Trout Creek) and microfossils (Culebra) are associated with sediments indicative of frequent and extensive volcanic activity.*

The situation wherein fossil floras suggest forest while faunas, including the near-contemporaneous and adjacent Cucaracha fauna, reflect open forest and savannah on the uplands, is similar to that in the Tertiary biota of the western United States. A tentative explanation suggested for that region may apply to southern Central America. In a study of the Miocene Trout Creek flora of southeastern Oregon (Graham, 1963, 1965), representative megafossil species were not uniformly distributed through the 17-m section. In the middle part of the section there were numerous layers of sand and volcanic ash. Toward the top and bottom, the number and thickness of the ash layers decreased (Fig. 40). Megafossils were abundant in the upper and lower portions and were much less common in the middle part, where volcanic activity was greatest. Clearly the plant communities were disrupted by ejection of quantities of volcanic ash, the deforestation allowing sands to wash into the depositional basin from the surrounding landscape. Taggart et al. (1982; Taggart, pers. comm., 1987) suggested that the browsing and grazing faunas that characterize the middle and late Tertiary of western North America were exploitive, flourishing during recovery periods when open habitats were more extensive. The reduced vegetation, unfavorable preservation conditions in the accumulating sandy ash layers, and the relatively brief time spans involved minimized the representation of this recovery vegetation in the plant fossil record. During intervening times when volcanic activity was less,



FIGURES 41, 42. *Drilling operations and resulting core from the Cucaracha Formation, Canal region, Panama.—41. Portable drill from truck bed.—42. Core from the Cucaracha Formation. Logs from these cores provide the descriptive lithologies (e.g., Fig. 40) used to characterize the general depositional environments of the microfossil assemblages. Photographs taken January 1986.*

forests became more extensive and contributed the abundant plant remains preserved in the diatomite. Another factor is the resistant nature of the faunal remains favoring preservation, transport, and accumulation in the depositional basin.

Figures 41 and 42 illustrate the coring device and the cores derived from the Cucaracha and other Tertiary formations in the Canal region of Panama. A description of the lithologies along these cores is kept by the Panama Canal Commission in the form of drill logs. A portion of one log from the Cucaracha Formation is presented by Graham et al. (1985: 495, table 3) and is summarized in Figure 40. It is clear that volcanic tuffs (water-lain volcanic ash) are common throughout the section (e.g., at levels 154.7′, 104.0′, 80′, and 73.2′), and the same is true for other Tertiary formations in Panama. Basalt also caps many of the sections. If the pattern of Tertiary faunas with significant numbers of browsing and grazing elements, and Tertiary floras reflecting forested vegetation, persists in future studies, a shifting mosaic of brief, open, recovery vegetation in this volcanically active region may afford a reasonable explanation for the apparent differences in habitats suggested by the floral and faunal evidence.

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CUPULAR STRUCTURE IN PALEOTROPICAL *CASTANOPSIS* (FAGACEAE)[1]

Robert B. Kaul[2]

ABSTRACT

The structure and some developmental aspects of the cupules of 22 species of paleotropical Castanopsis *are discussed and illustrated. Some species have cupules massively invested with strong, sharp spines, but others are less spiny, and some are nearly smooth. Most cupular armament results from spines produced axillary to the valvular scales and basally adnate to them. Columns of scales straddling the sutures between the cupular valves do not become spines, but the numerous scales elsewhere on the valves become somewhat spiny with age. Dehiscence in the spiny-valved species is mostly along the sutures. The smooth cupules of some species have scales in their early stages, but cupular expansion separates and tears them; such species are often indehiscent or only irregularly dehiscent and usually show nearly complete adnation of the cupule to the nut.*

Castanopsis is the third largest genus in the Fagaceae, after *Quercus* and *Lithocarpus* in their broad sense. Most of the approximately 120 species recognized by Camus (1929) and Barnett (1944) are paleotropical, but a few occur as far north as northeastern China, Korea, and Japan, and some ascend the Himalayas. For Malesia (the Malay Peninsula and all the islands from Sumatra to New Guinea and the Philippines) Soepadmo (1968, 1972) recognized 34 species and mapped species density. In Malesia, Borneo has the most species (21) and the most endemics (10); Sumatra and Java have 11 and 4 species, respectively, none endemic; and the Philippines have 4, including one endemic. Only two—*C. buruana* and *C. acuminatissima*—occur east of Wallace's Line between Bali and Lombok. Barnett (1942) found only one endemic species among the 16 she recognized for Thailand. About 25 are known from China, mostly from the southern provinces. The eight or nine mostly endemic Taiwanese species are taxonomically well studied (Li, 1963; Lin & Liu, 1965; Liao, 1971; Liu & Liao, 1976). One species (*C. cuspidata*), represented by two varieties, occurs in Japan (Ohwi, 1965). The one or two species outside Asia and nearby islands occur in western North America and are sometimes given their own genus, *Chrysolepis*, based largely upon cupular structure; palynologically they are indistinguishable from *Castanopsis* (Erdtman, 1943; Crepet & Daghlian, 1980), and foliar distinctions are weak (Jones, 1986). *Lithocarpus*, closely related and with perhaps 300 species, has a remarkably similar geographic distribution, including a single species in western North America.

Castanopsis in Malesia is characteristic of forests without strongly seasonal climates, but in Java and Thailand some species occur in seasonal climates (Hjelmqvist, 1968; Soepadmo, 1972). Twelve of the 34 Malesian species are restricted to lowland forests, and the others are in lowland and montane forests. Barnett (1942) and Hjelmqvist (1968) noted that the species of Thailand are found mostly in the uplands. Most paleotropical species of *Castanopsis* grow in mixed forests that often include *Lithocarpus* and *Quercus*, but *C. acuminatissima* forms nearly pure stands in New Guinea (Soepadmo, 1972; Whitmore, 1975; Paijmans, 1976). The genus is prominent in subtropical forests of China (Wang, 1961). The northeastern Asiatic and western North American species are sometimes abundant in the forests and are, of course, subjected to more seasonal climates than are most paleotropical species.

Pollination by small insects is suggested by their abundance around the rather strong-smelling, conspicuous staminate flowers, but some pollen might be wind-transported. It is not clear how the incon-

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spicuous, presumably odorless pistillate flowers attract insects; perhaps they are pollinated only incidentally to insect movements among the far more numerous staminate flowers around them.

The published infrageneric classifications of *Castanopsis* are based mostly upon fruit characters, as is the case for other fagaceous genera. Camus (1929) recognized three sections in *Castanopsis*: *Eucastanopsis* (cupule spiny, dehiscent or indehiscent, the nuts not fused to it); *Callaeocarpus* (cupule with or without spines, the nuts fused to it for most of their length); and *Pseudopasania* (cupule thin, dehiscent, containing a single free nut). The last group includes *C. acuminatissima.*

Barnett (1944) saw the genus as comprising 11 groups in Asia and nearby islands, but she did not give them formal taxonomic rank. She defined them by degree of adnation of the cupule to the nuts, ornamentation of the cupule, size of the scar of the nuts, size of the fruits, and foliar characters. She included the small "*fissa*-group" in *Castanopsis,* noting that it forms a connecting link to *Lithocarpus*; Forman (1966a, b) also aligned the *fissa*-group with *Castanopsis,* noting its strong alliance with *C. acuminatissima,* but Camus (1929) placed those species in *Lithocarpus* subg. *Pseudocastanopsis.* Thus these authors recognized the close affinity of *Castanopsis* to *Lithocarpus,* and Barnett (1940) suggested that recognition of two genera is perhaps more artificial than natural. Jones (1986) supported the placement of the *fissa*-group in *Castanopsis,* based upon his detailed study of foliar characteristics in the family.

Camus (1929) suggested that *Castanopsis* is closer to *Lithocarpus* than *Lithocarpus* is to *Quercus,* and recent foliar and palynological evidence supports her interpretation (Jones, 1986; Zavada & Dilcher, 1986). (*Lithocarpus* and *Quercus* are usually interpreted as distinct from each other, but exhibit many parallel traits.) The affinity of *Castanopsis* to *Castanea* is undoubtedly close.

Hjelmqvist (1948, 1968) and Forman (1966a, b) saw *Castanopsis* and *Lithocarpus* as distinct, noting the differences between the dichasium-cupule, which encloses all the flowers of a cymule in *Castanopsis,* and the flower-cupule enclosing individual flowers of a cymule in *Lithocarpus.* They interpreted the dichasium-cupule as a product of phylogenetic fusion of flower-cupules, and the dichasium-cupule of the one-flowered cymules of the *fissa*-group and other species thus as indistinguishable from a flower-cupule. The valveless cupules of *Lithocarpus* and *Quercus* are apparently morphologically identical also, but Forman (1966a) suggested that they are convergently derived, the cupule of *Lithocarpus* being a true flower-cupule and that of *Quercus* being a one-flowered dichasium-cupule whose lateral flowers have disappeared. However, there is no direct evidence for that in *Quercus*; rather, it was based upon comparative study of other genera, especially *Trigonobalanus daichangensis.* Some species of *Lithocarpus* show partial to nearly complete fusion of flower-cupules in the cymules, resulting in partial dichasium-cupules (examples illustrated in Kaul, 1987), which Forman (1966a) interpreted as phylogenetically parallel to the dichasium-cupules of *Castanopsis.*

In *Castanopsis* the cupular primordia are rather well developed by anthesis (but less so than in *Castanea*). The mature cupule encloses the one to seven nuts and often has distinct vertical sutures that define the cupular "valves," at the edges of which dehiscence often occurs (such features are not found in *Lithocarpus* and *Quercus*). However, variations in these and other characteristics occur within and between species.

The origin and structure of the fagaceous cupule have had various interpretations; Abbe (1974), Okamoto (1982), and Fey & Endress (1983) reviewed the literature, in which it is implied that the cupule has arisen but once. Most workers interpret it as derived from pre-existing structures, not as a structure *de novo.* Whatever the origin of the cupule, it now has some qualities and functions unlike those of its ancestral parts. Fey & Endress (1983) found that ontogenetic observations in *Castanea, Fagus,* and *Quercus* revealed more orderly arrangement of cupular appendages than is evident at maturity. This is true for *Castanopsis* too, in which the mature cupule is often massively invested with rigid spines and other structures that obscure positional relationships. *Castanopsis* is largely unstudied developmentally, but floral development in *C. cuspidata* var. *sieboldii* of northeastern Asia and Japan has been shown in detail (Okamoto, 1983). *Castanea* has been the subject of several developmental studies, most recently by Fey & Endress (1983).

Many species of *Castanopsis* have spiny cupules, but in others spines are barely evident or absent, and the cupule is then smooth and figlike. Forman (1966a) interpreted the spines as emergences, not foliar homologues. Barnett (1940) noted that they do not appear to be the first cupular appendages to form, but develop later, often in the axils of the "scales." Fey & Endress (1983) interpreted spines of *Castanea* as axillary branch systems.

The patterns of distribution and elaboration of

TABLE 1. *Provenance and depositories of duplicate specimens of the species of* Castanopsis *illustrated.*

Species	Provenance	Collectors	Depositories of Voucher Herbarium Specimens	Depositories of Fruit Specimens	Figures in This Paper
acuminatissima (Bl.) Rehd.	Papua New Guinea	*Abbe et al. 10357*	A, BH, E, L	—	29–31, 77
acuminatissima	Papua New Guinea	*Abbe et al. 10310*	A, L, US	—	32
acuminatissima	Thailand	*Abbe et al. 9273*	—	BKF	33, 34
acuminatissima	Thailand	*Abbe et al. 9451*	A, BKF, E, L, US	—	76
argophylla King	Burma	*Bogle et al. 249*	A, E, L, MIN, US	A, E, L, US	78
armata Spach	Thailand	*Abbe et al. 9358*	A, BKF, SING	L	88
curtisii King	Malaya	*Abbe et al. 9721*	BKF, L, SING	—	55, 56
ferox Spach	Thailand	*Abbe et al. 9339*	A, BKF, E, L, MIN, SING, US	A, BKF, L, SING, US	44–46
formosana (Skan) Hayata	Taiwan	*Bogle et al. 656*	A, E, L, MIN, US	—	81
foxworthyi Schottky	Sarawak	*Abbe et al. 12064*	A, L	—	1–4
foxworthyi	Sarawak	*Abbe et al. 12091*	A, E, L, US	—	5–8, 75
foxworthyi	Sarawak	*Abbe et al. 12084*	—	—	74
guineri A. Camus	Viet Nam	*Abbe et al. 9537*	—	—	63, 64, 84
hypophoenicea (V. Seem.) Soep.	Brunei	*Abbe et al. 9917*	—	—	35–37
hystrix A. DC.	India	*Bogle et al. 225*	A, L	A, L	79
indica A. DC.	Thailand	*Abbe et al. 9332*	A, BKF, E, MIN, SING, US	A	71
inermis (Lindl.) Benth. & Hook. f.	Thailand	*Abbe et al. 9692*	A, BH, BKF, E, SING, US	—	47–51
inermis	Malaya	*Abbe et al. 9712*	A, L, MIN, SING, US	A, BKF, L, MIN, US	89
longipetiolata Hick. & A. Camus	Kampuchea	*Abbe et al. 9659*	A, BKF, E, MIN, SING, US	A	66–69, 91
lucida (Nees) Soep.	Singapore	*Abbe et al. 9816*	A, BKF, L, SING	A, BKF, L	85
motleyana King	Sarawak	*Abbe et al. 12036*	A, BKF, E, L, US	A, E, L, US	13, 17–19
motleyana	Sarawak	*Abbe et al. 12070*	A, E, L, US	L, US	9–12, 14–16
oviformis Soep.	Sabah	*Sandakan 31133*	SAN	—	27
oviformis	Sabah	*Sandakan 34687*	SAN	—	20–26, 28
pierrei Hance	Thailand	*Abbe et al. 9344*	A, BKF, L, MIN, SING, US	BKF	72
pierrei	Thailand	*Abbe et al. 9352*	—	—	65
piriformis Hick. & A. Camus	Viet Nam	*Abbe et al. 9534*	A, L, MIN, US	—	60–62
piriformis	Viet Nam	*Abbe et al. 9536*	—	—	90
psilophylla Soep.	Philippines	*Kaul et al. 2122*	A, L, MIN, US	A, L, MIN, US	52, 54
psilophylla	Sabah	*Sandakan 18830*	SAN	—	53

TABLE 1. *Continued.*

Species	Provenance	Collectors	Depositories of Voucher Herbarium Specimens	Depositories of Fruit Specimens	Figures in This Paper
purpurea Barn.	Thailand	*Abbe et al. 9689*	A, BKF, SING, US	US	83
schefferiana Hance	Malaya	*Abbe et al. 9011*	BKF, L, SING	—	73
schefferiana	Malaya	*Kaul et al. 1972*	—	—	82
tribuloides (Smith) A. DC.	Thailand	*Abbe et al. 9287*	BKF, SING	—	38, 39, 70
tribuloides	Burma	*Bogle et al. 241*	A, E, L, MIN, US	—	40–43
tribuloides	Burma	*Bogle et al. 260*	A, E, L, MIN, US	—	80

cupular scales, spines, and sutures vary among the species, and the functional and phylogenetic significance of the various patterns is not known. Forman (1966a) interpreted as primitive in *Castanopsis* the three- or more-flowered cymule; the four-valved cupule dehiscing between the valves; the spines branched, well developed, and in definite rows; and the cupule not adnate to the nut(s). Those characteristics are most common in paleotropical species. He saw derived conditions in the one-flowered cymule, the two-valved cupules, irregular dehiscence not along valve sutures, the spines absent or reduced and not in obvious rows, and the cupule fused to the nut(s). Those attributes occur in paleotropical and palearctic species. He also interpreted the American species as primitive because the valves are free, and some occur between the flowers of a cymule—characteristics used to distinguish *Chrysolepis* from *Castanopsis.* Hjelmqvist (1948) reported remnants of walls between the nuts in the cupules of *Castanopsis hullettii* and *C. fabri.*

Hjelmqvist (1948) interpreted one-flowered, three-parted cupules as originating by the union of three flower cupules, one middle and two lateral cupules. He suggested that in four-parted cupules the middle cupule is reduced and the remaining common (dichasium) cupule is four-parted, the parts corresponding to two bipartite, lateral cupules. Dehiscence then occurs along the longitudinal fissures through the middle of the part-cupules and at the border between the two anterior cupules.

MATERIALS AND METHODS

My colleagues and I collected *Castanopsis* and other Fagaceae from India to New Guinea and Japan, gathering developmental reproductive material wherever possible. We preserved specimens originally in various liquid fixatives and later transferred them to glycerine-alcohol for permanent storage. For three species from the lowlands of Borneo (*C. foxworthyi, C. motleyana,* and *C. oviformis*) we took samples at intervals from marked trees through most of a year. The species reported upon in this paper are listed in Table 1.

The study of reproductive structures of *Castanopsis* presents unusual technical difficulties. Sectioning and clearing, even of young flowers, do not produce photogenic results because of the hard spines and cupules, the numerous hairs, and the heavy sclerification of tissues. Specimens were examined with light and scanning electron microscopy (often following removal of obscuring structures), drawings were produced with the camera lucida, and photographs were taken with incident light.

The dense vestiture obscures many details, and so the line drawings are shown without hairs.

Various sets of herbarium voucher specimens were distributed to A, BH, BKF, E, L, MIN, SAN, SAR, SING, and US (Table 1). The fruits illustrated here are in my research collection, and not all the distributed vouchers have fruits at all stages illustrated in this paper.

Nomenclature for paleotropical species follows Soepadmo (1972), who identified most of my paleotropical specimens. I considered the *fissa*-group with *Lithocarpus* (Kaul, 1987), following Camus's system, but a good case can be made for including it in *Castanopsis* if the two genera are recognized as distinct (Forman, 1966a, b).

OBSERVATIONS

PISTILLATE CYMULES

The pistillate cymules (often called dichasia) are borne on androgynous, pistillate, or androgynecandrous spikes (Kaul & Abbe, 1984; Kaul, 1986). They contain one, two, three, or sometimes more flowers (Figs. 1, 4–6, 10, 11, 13, 14, 17, 20, 25, 29–31, 38–40, 47, 52, 55, 56, 66, 70–77). The number of flowers per cymule is more stable in some species than others. Often there are fewer flowers in more distal cymules, and in some species that ordinarily bear one-flowered cymules, occasional two-flowered cymules appear. When three or more flowers occur in a cymule, the central flower often develops slightly earlier than the others (Fig. 10).

Each cymule is subtended by a primary bract (shown in black in Figs. 1, 5, 14, 20, 25, 29, 30, 38, 47, 52, 55, 56, 60, and evident in Figs. 70, 72, 76) and secondary, tertiary, and sometimes quaternary or even higher-order bracteoles (Figs. 72–77). Distinctions between these bracteoles and those of the cupule (hereinafter called scales) are not always obvious. The pattern of bracteolation in *Castanopsis* is closely similar to that shown for *Lithocarpus* (Kaul, 1987 and in press).

The apparent pedicel of a flower in anthesis (Figs. 1–3, 12, 21, 22) is actually the very undeveloped inferior ovary, and the flower is thus sessile in the cupule.

All species examined at anthesis have prominent staminodia (e.g., Figs. 30, 31, 77), which are sometimes basally adnate to the perianth (Fig. 12).

FRUITS

The fagaceous nut develops from an inferior ovary, and the cupule is an accessory part. If all nuts of a cymule are abortive (probably due to lack of pollination or fertilization, or to competition for resources from other fruits on the rachis), cupular growth stops at about the stages shown in Figures 5, 7, 14, 18, 25, 31, 33, 35, 36, 39, 40, 48, and 53. But if one or more nuts mature, the cupule matures. The mature cupule is not fused to the nuts in some species; it is partially or completely fused in others. Some species have notably scaly and/or spiny cupules, others have rudimentary spines, and some are spineless or scaleless.

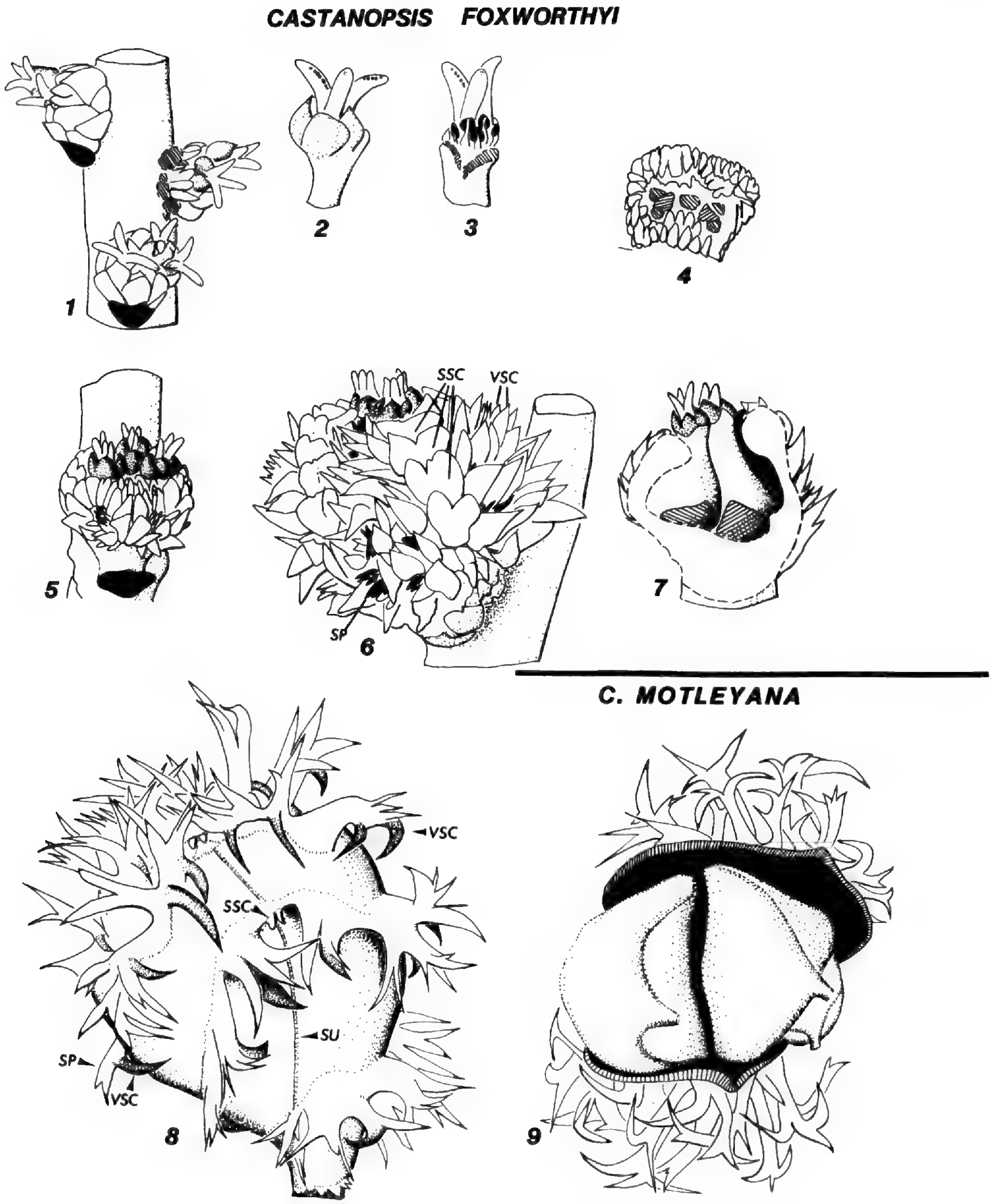
A cupule surrounds all flowers of a cymule, and there are no well-developed valves (segments of cupules) between the flowers except in the American species. Rudimentary interfloral valves were reported by Hjelmqvist (1948) in *C. hullettii* and *C. fabri*, but I have not studied those species and have not seen such valves in others.

Spiny cupules with one nut typically have two valves and dehisce along lines between them ("sutures" in the anatomical sense). In indehiscent fruits with one nut, the valves and sutures are evident at maturity in some species but not others. Fruits with three nuts typically have four valves, dehiscence occurring along the sutures between them (e.g., *C. hystrix*, Fig. 79; *C. schefferiana*, Fig. 82), but variations occur in both valve number and location of dehiscence lines. The mature cupule of *C. motleyana* shown in Figure 9, for example, has three fruits (one apparently abortive), but only two valves are evident. In *C. tribuloides* some cupules are one-flowered and have two valves (Figs. 41, 80), but other cupules, even on the same rachis, are three-flowered and have four valves (Figs. 42, 43). In the latter, some sutures between valves may not rupture.

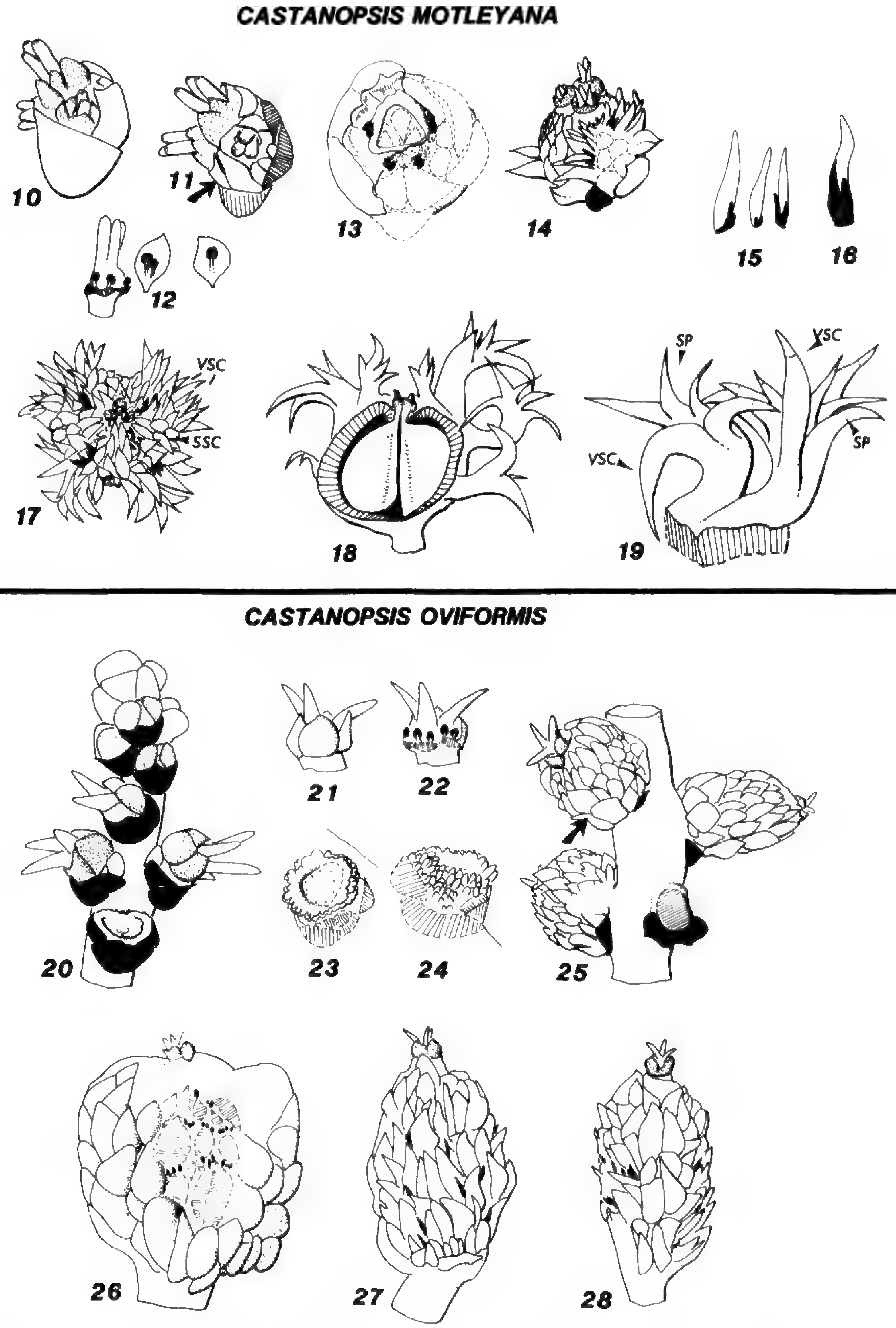
Species with one and three nuts per cupule occur at all elevations in southeastern Asia and southwestern Pacific islands, but in Taiwan they are only at middle and higher elevations. The size ranges (1–6 cm) and averages (ca. 4 cm) of maximum cupular diameters in all the species are about the same in the two areas, except that in southeastern Asia and southwestern Pacific islands there are two lower-elevation species with very large cupules (to 10 cm in diameter). Average maximum cupular diameter in the species with one-nut cupules is about that of those with three-nut cupules, again excepting the extremely large cupules of two southeastern Asiatic species, both of which have one nut per cupule.

SPECIES WITH SPINY CUPULES

In early anthesis the cupule is little developed and is hidden by the bracteoles (Figs. 10, 11, 29, 38, 47, 55, 72–76), but the cupular scales quickly



FIGURES 1–9. *1–8.* Castanopsis foxworthyi.—*1. Segment of pistillate portion of a spike showing three cymules in anthesis, the primary bract black. Primary bract and the bracteoles are removed in the middle cymule, revealing early cupular scales, 3.8×.—2, 3. Flower in anthesis; inferior ovary poorly developed, but staminodia well developed, 7.5×.—4. Polar view of cupule soon after anthesis, revealing scars of seven flowers, the outer four abortive, 3.8×.—5. Cymule after anthesis, with three functional flowers. Cupular scales are differentiating into sutural scales (center) and valvular scales, 3.8×.—6. Still later stage, the sutural scales (SSC) and valvular scales (VSC) now clearly differentiated, the axillary spines (black, SP) now showing, 3.8×.—7. Immature cupule longitudinally halved, with two nuts and their basal scar revealed, 3.8×.—8. Nearly mature cupule with the spines now in bands and somewhat confluent. The sutural scales (SSC) have not enlarged as much as the valvular scales (VSC), but the axillary spine clusters (SP) are now mostly much larger than the VSC. The future line of dehiscence between the two valves shown is indicated by SU, 1.9×.—9.* C. motleyana. *Mature, dehisced cupule in polar view, revealing one abortive and two functional nuts. The cupule has split on only two of its four sutures, 1.9×.*



FIGURES 10–28. *10–19.* Castanopsis motleyana.—*10, 11. Three-flowered cymule in anthesis, the primary bract and the bracteoles removed in Figure 11 to reveal early cupular scales, the lower two (arrow) being the first sutural scale pairs, 7.5×.—12. A single flower with perianth removed, revealing staminodia basally adnate to the tepals and showing the very undeveloped inferior ovary, 7.5×.—13. Three-flowered cupule in late anthesis, the primary bract (lowermost), the bracteoles on the right half, and some of the early cupular scales removed to reveal the four valvular primordia with their young scales (black). The second pair of abaxial sutural scales has formed between the lower two valvular primordia, 7.5×.—14. Lateral view of cymule in early postanthesis, the sutural scales (dashed lines) of the right lateral suture removed to reveal the valvular scales and their immature, axillary spines; primary bract black, 3.8×.—15, 16. Valvular scales (white) and early stages of the axillary spines (black), 15×.—17. Cupule about one-third mature, the sutural scales (SSC) and valvular scales (VSC) clearly differentiated, and the axillary spines (black) just emerging from among the scales, 7.5×.—18. Longitudinally halved immature cupule revealing two of the three nuts, 1.9×.—19. Two mature*

become evident and soon exceed the bracteoles (Figs. 5, 14, 25, 30, 39, 40, 52, 56, 77–83). In the species examined for preanthesis developmental detail (*Castanopsis foxworthyi, C. motleyana, C. oviformis*), the cupule primordium arises as an undulate ring at the base of the flowers, well within the bracteoles (Figs. 13, 23). In the three-flowered cymules of *C. motleyana*, four growth centers (valve primordia) of cupular scales are evident in the early stages (Fig. 13, scale primordia shown in black), but growth centers in *C. foxworthyi* and *C. oviformis* are less obvious, although there are differences in development among various parts of the early cupule (Figs. 4, 23, 24).

Distinctions develop among the cupular scales during and after anthesis, especially in cupules that will be spiny at maturity. Columns of shorter, broader, sometimes connate or paired scales alternate with masses of apparently random, pointed scales (Figs. 5, 6, 14, 17, 28, 31–33, 48, 49, 51, 58). The columns mark the sutures between valves and are potential sites of dehiscence, at which time sutural scales become separated onto adjacent valves (Figs. 34, 41–43, 54). In the three-flowered cupules of *Castanopsis foxworthyi, C. motleyana*, and *C. inermis* there are four such columns: one adaxial, one abaxial, and two lateral (Figs. 6, 13, 51). The columns define the four valves. The first pair of sutural scales is clearly evident in Figure 11, in which the primary bract has been removed to reveal them and the earliest valvular scales. Forman (1966a) found that dehiscence of the cupule of *C. inermis* (Figs. 48–51) does not occur along the sutures between the valves.

The valvular scales between the columns of sutural scales elongate, becoming indurate and spine-tipped with age. They do not comprise the majority of spines of the cupule; instead, most of the spines develop later, in groups axillary to the valvular scales; such spines are shown in black in Figures 6, 14–17, 26–28, 31, 32, 35, and 36, and are evident in Figures 72, 77–83. Figures 15 and 16 show that the spines in each group arise nonsynchronously and free, but they become basally connate and ultimately adnate with the subtending scale. By maturity, each subtending scale becomes spine-tipped, and the axillary spines are as large as or larger than it (Figs. 8, 19). Thus, in these spiny-cupuled species, the armament of the cupule is provided mostly by the axillary spines, with some contribution by the original valvular scales (Figs. 8, 37).

In some species with less cupular armament (e.g., *Castanopsis tribuloides*, Figs. 38–43, 80; *C. ferox*, Figs. 44–46; *C. psilophylla*, Figs. 52–54) the sutural scales are less obviously paired but instead occur in irregular groups. Such groups are evident in Figures 41–44 and 54, which show dehiscence of the cupule through them. In these species, the cupular scales become indurate and spine-tipped, forming much of the cupular armament; the mature axillary valvular spines are of similar size to the scales.

In *Castanopsis curtisii* (Figs. 55–59, 87) the asymmetric cupule is totally fused to the nut, the surface of which is therefore entirely scarred (Fig. 87) except for a tiny portion near the perianth. The flower and young cupule are rather symmetrical at anthesis (Fig. 55), but asymmetry is established soon thereafter (Fig. 56); massive abaxial growth of the cupule turns the fruit upward about 90°, and it becomes anatropous. Thus at maturity all the sutures appear to be on the adaxial side (Fig. 59). Sutural scales are evident only in the early stages of cupular development, when they can be seen to be entirely adnate to the body of the young cupule (Fig. 56, left cupule). The cupular scales in this species are also largely adnate, and are irregularly disposed at maturity (Fig. 59). In dry fruits, rupturing begins in the adaxial suture, but other ruptures radiate from the cupular pore (Fig. 59); those lines apparently do not represent

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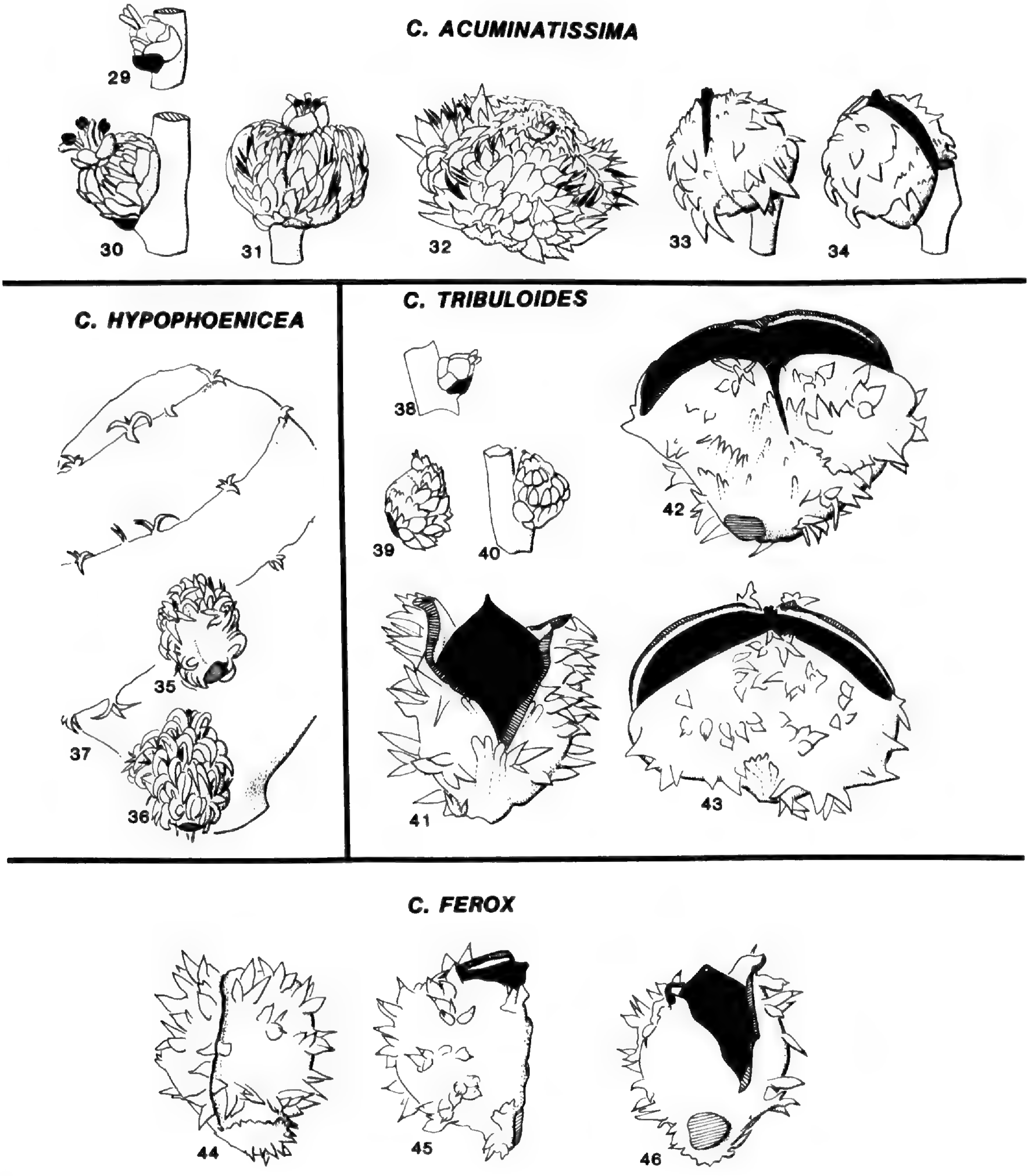
spine clusters, each consisting of one spine-tipped valvular scale (VSC) with its axillary cluster of spines (SP), 3.8×. 20–28. C. oviformis.—*20. Tip of spike in anthesis. Four one-flowered pistillate cymules are shown in anthesis, the lower with the flower removed to reveal the weakly developed cupule. Unopened distal flowers are staminate, 7.5×.—21, 22. Pistillate flower in anthesis, the tepals removed in Figure 22; inferior ovary very undeveloped, but staminodia prominent, 7.5×.—23, 24. Cymule in later anthesis, the primary bract and bracteoles removed to reveal the young cupule, 15×.—25. Segment of pistillate portion of spike well after anthesis, the cupule now emergent from the bracteoles; two pairs of large, sutural scales (arrow) are evident on the abaxial side of the uppermost cymule; cymule on lower right removed to reveal persistent bracteole (black), 3.8×.—26. Still older cupule with 12 valvular scales removed to reveal tiny primordia (black) of the axillary spines, 7.5×.—27, 28. Immature fruit in lateral (Fig. 27) and abaxial (Fig. 28) view, the axillary spines (black) now appearing among the valvular scales; Figure 28 also shows the abaxial column of large sutural scales, 2.8×.*



FIGURES 29–46. 29–34. Castanopsis acuminatissima.—*29. One-flowered cymule in anthesis, the primary bract in black and a few cupular scales evident, 2×.—30. Late anthesis, the cupular scales evident and overtopping the basal bracteoles; perianth and staminodia obvious, 4×.—31. Still later stage in abaxial view, the axillary spines (black) emerging from among the cupular scales, the abaxial suture indicated by the central, vertical depression abutted by sutural scales, 4×.—32. Still later stage of a specimen showing three sutures defined by appressed scales; between the sutures are groups of axillary spines (black) and valvular scales, 4×.—33, 34. Mature, dehiscing cupule showing few spines and dehiscence along two sutures, 2×. 35–37.* C. hypophoenicea.—*35. Adaxial view of one-flowered cupule soon after anthesis, the naked adaxial surface distinct, 2×.—36. Abaxial view of the same cupule showing the prominent recurved cupular scales and the emerging axillary spines (black), 2×.—37. Mature cupule, the scales and spines now widely separated and equally spiny, 0.4×. 38–43.* C. tribuloides.—*38. One-flowered cymule in early anthesis, the primary bract in black, 2×.—39, 40. Somewhat after anthesis, the relatively unadorned adaxial side evident in Figure 39, the neat rows of scales obvious in Figure 40, 2×.—41. Mature, dehiscing cupule in abaxial view, the rounded sutural scales evident adjacent to the suture, but the rows of valvular scales are no longer orderly, 2×.—42, 43. Adaxial (Fig. 42) and abaxial (Fig. 43) views of dehiscing cupule containing three nuts. Rounded scales of the partially opened adaxial*

intervalvular sutures, or at least such sutures are not evident in earlier stages (Figs. 57, 58). These fruits are possibly indehiscent in the wild, where they perhaps never dry, but my dry specimens show regular patterns of splitting.

Four related species reveal comparative details of reproductive structure: *Castanopsis armata, C. inermis, C. lucida,* and *C. pierrei.* The cupule is almost entirely fused to the nut in *C. pierrei* (Figs. 65, 86). Figure 65 shows the massive scar (hatched) and two small abortive nuts near the distal end of the single mature nut. The small free portion of each nut is indicated in black. The relationship of the mature and immature nuts to the cupule is evident in Figure 86, a polar view wherein the partially open cupule reveals two abortive nuts on the right. In this species the cupular scale–spine complexes are massively thickened (Figs. 65, 86). The spine-tips are not much elongated, but they are very sharp. The scale–spine complexes are arranged in slanting rows on the cupule, but that is not evident in Figures 65 and 86.

Castanopsis armata is similar to *C. pierrei* in that the cupule is entirely fused to the nut, but my specimens have no abortive nuts, and the single mature nut has about 20% of its distal end free (nonscarred) (Fig. 88). The mature cupule is massively thickened, and the cupule scale–spine complexes are not aligned in evident rows at maturity but are even more massive than those of *C. pierrei.* Each spine has a short, indurate, subulate tip, and the cupule is therefore formidably armed. Immature fruits display cupular sutures (cf. Fig. 51), along which dehiscence probably occurs eventually.

In *Castanopsis inermis* the cupule contains one to three nuts and is largely free from them (Fig. 89). Forman (1966a) noted a tendency toward reduction of the central flower of each cupule in this species, but I cannot confirm or deny that from observations of specimens from the Malay Peninsula, which show no regular pattern of reduction. The mature cupule displays horizontal rows of groups of low spines (Fig. 89, center). Such regular arrangement is more obvious on immature cupules, where the sutural scales are also readily distinguished (Figs. 48–51). The latter are permanently adnate to the cupule and do not become spiny. The cupular armament is largely made of spine-tipped cupular scales; axillary spines, if present, contribute little. Usually four sutures form on three-flowered cupules, and two form on one-flowered cupules. Variation occurs; some one-flowered cupules have four sutures (Fig. 51), for example. Dehiscence does not follow the sutures entirely and is therefore rather irregular.

The large fruits of *Castanopsis lucida* (Fig. 85) resemble those of *C. inermis,* but the cupular scale groups are proportionally larger and, at least in my specimens, the cupules seldom contain fewer than three nuts. The four sutures of a three-nut cupule are clearly evident in Figure 85 (upper photograph). Dehiscence usually begins with the opening of the adaxial and abaxial sutures, which are the shorter ones; later the longer lateral sutures open and reveal the free nuts within (Fig. 85). Mature spikes sometimes bear as many as ten fruits that collectively weigh 70 g when dry.

SPECIES WITH SMOOTH CUPULES

Some species of *Castanopsis* have nearly smooth, figlike cupules. Examples are shown of *C. piriformis, C. guineri,* and *C. longipetiolata* (Figs. 60–64, 66–69, 84, 89–91), all placed in section *Callaeocarpus* by Camus (1929). In these the indehiscent cupule is fused to the single nut and is unadorned except for low ridges and small, mostly adnate scales. No axillary spine complexes form.

The cupular scale-bearing ridges are widely separated and not concentric. In *Castanopsis piriformis* and *C. guineri* they converge distally on the cupule and there form a continuous spiral around the aperture (Figs. 62, 63, 84, 90). The ridges of *C. longipetiolata* are vertical in places (Figs. 67–69, 91) and converge near the aperture, but do not form a spiral (Fig. 67).

In adaxial view (Figs. 61, 64, 68), the adaxial suture is barely evidenced by a broad longitudinal depression. A few sutural scales show in Figures 61 and 64, but there are none in Figure 68. The cupular scales enlarge little as the cupule swells, and thus they become somewhat remote. In *Cas-*

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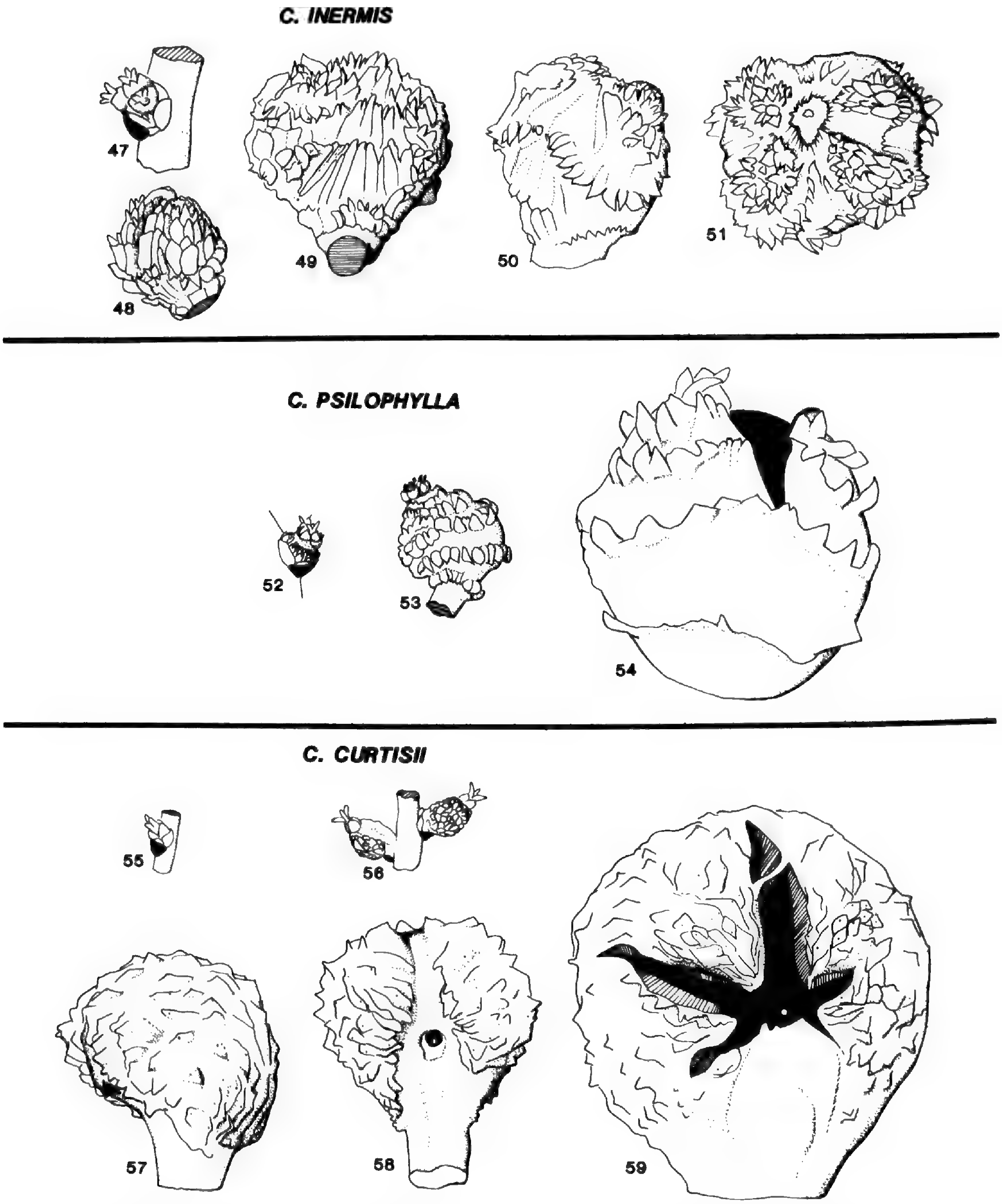
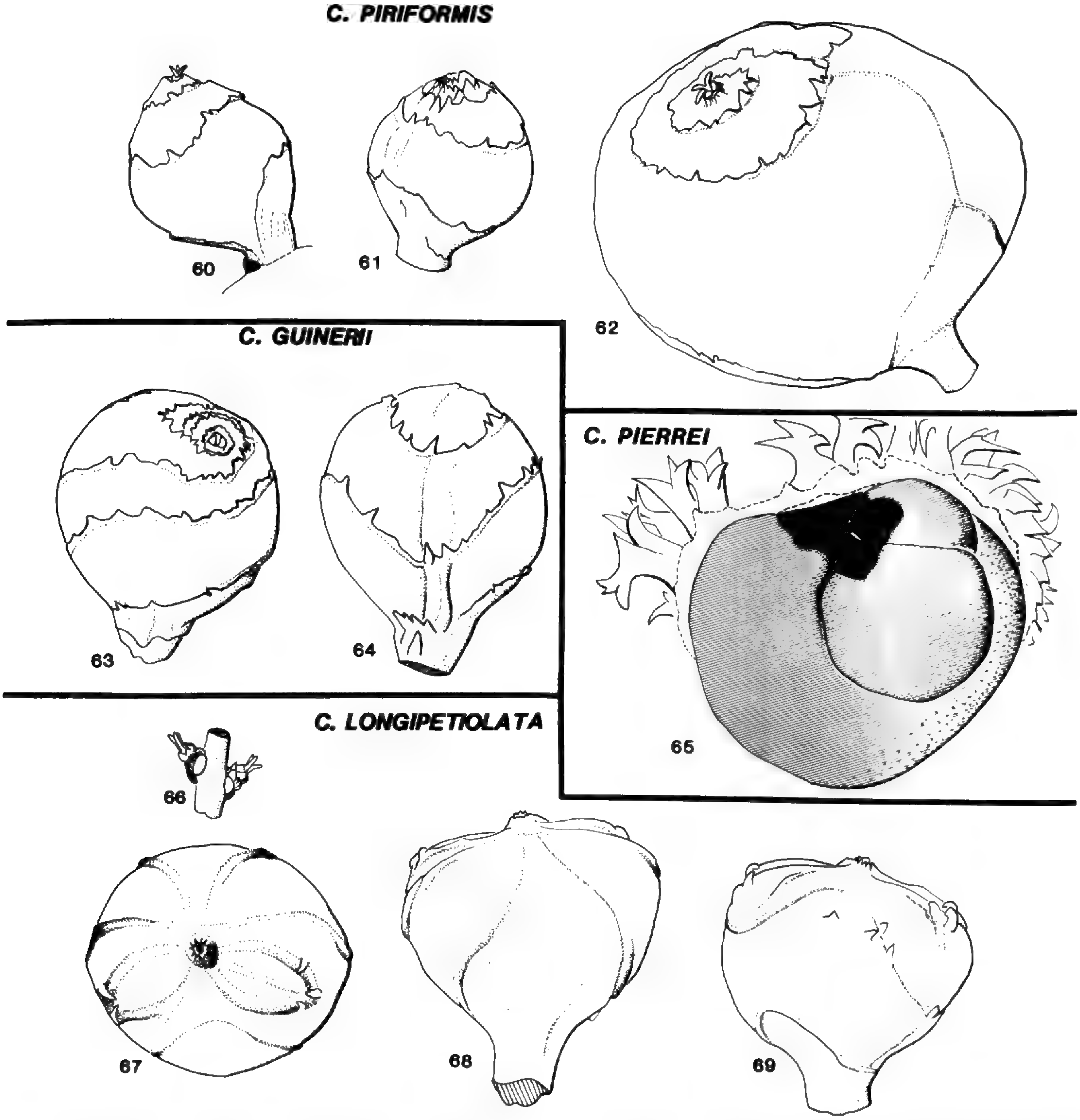
suture are seen to intergrade with the pointed valvular scales in Figure 42, but sutural scales on the abaxial side are confined to the base of the cupule (Fig. 43), 2×.—44–46. C. ferox *showing mature, dehiscing cupule in abaxial, lateral, and adaxial views, respectively. The adaxial side is essentially naked, and the suture there is without adjacent scales; the abaxial suture (Fig. 44) has a few scales, and the valvular scales are irregularly disposed at maturity, 2×.*



FIGURES 47–59. *47–51.* Castanopsis inermis.—*47. Three-flowered cymule in early anthesis, the primary bract shown in black, and only two cupular scales visible between the basal bracteoles, 2×.—48. Immature cupule in lateral view, the abaxial suture on the left shaded, the valvular scales still in rows, 2×.—49. Nearly mature cupule in adaxial view, the rounded sutural scales of the adaxial suture in tiers, the valvular scales less orderly than in Figure 48, 2×.—50. Lateral view of nearly mature cupule, showing rows of valvular scales, 2×.—51. Oblique polar view of nearly mature cupule, the four sutural areas evident and defined by appressed, more or less rounded sutural scales, and the valvular scales fully enlarged and pointed; there are no evident axillary spines, 2×. 52–54.* C. psilophylla.—*52. Three-flowered cymule in anthesis, the primary bract in black and the large basal bracteoles in white; numerous cupular scales are evident in rows above the bracteoles, 2×.—53. Postanthesis, the cupule and its scales enlarging, the latter yet in evident rows; perianths and staminodia of the three flowers persisting, 2×.—54. Mature, dehiscing cupule in abaxial view, showing a few elongate, appressed sutural scales to the left of the suture; valvular scales yet in rows but somewhat separated by diametric growth of the cupule, 2×. 55–59.* C. curtisii.—*55. One-flowered cupule in early anthesis, the primary bract shown in black, the cupular scales present under the basal bracteoles but not evident in this figure, 2×.—56. Two cymules soon after anthesis, the cupule already prominent above the primary bract and basal bracteoles,*



FIGURES 60–69. *60–62.* Castanopsis piriformis.—*60, 61. Half-mature one-flowered cupule in abaxial (Fig. 60) and semiadaxial (Fig. 61) views. The primary bract is shown in black in Figure 60. Cupular scales are already torn and widely spaced by this stage. The potential adaxial suture is seen on the left in Figure 61, although the fruit is probably indehiscent, 2×.—62. Mature cupule in oblique view, the adaxial side to the right. Upper rows of scales becoming spiral, 2×.—63, 64.* C. guineri, *nearly mature fruits in abaxial (Fig.63) and adaxial (Fig. 64) views. The strong spiral formation of cupular ridges is evident in Figure 63, and Figure 64 shows the adaxial vertical depression marking a potential suture, although the fruit is indehiscent, 2×.—65.* C. pierrei. *Mature fruit with foreground part of cupule removed to expose the massive scars (white) of the three nuts, two of which developed only partially; free portion of the nuts shown in black. The nuts are not fused to each other, 2×. 66–69.* C. longipetiolata.—*66. Two one-flowered cupules in anthesis, the primary bract of each shown in black; the first row of cupular scales is apparent above the basal bracteoles, 2×.—67–69. Nearly mature cupule in polar, adaxial, and lateral views, respectively. The few surviving cupular scales are mostly adjacent to the curving cupular ridges, and there is no obvious indication of potential sutures on this indehiscent cupule, 2×.*

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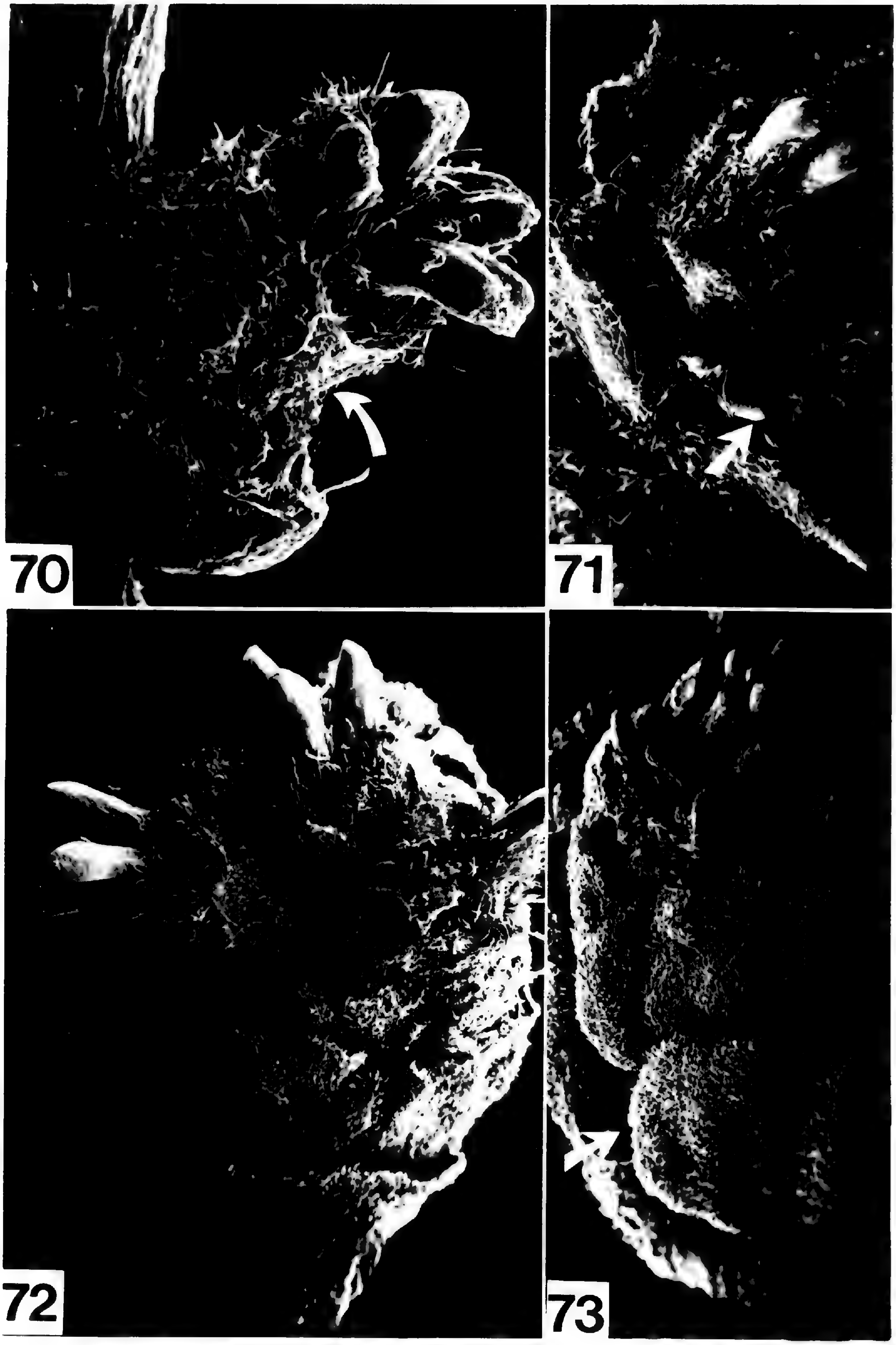
the scales more or less in orderly rows; the rather smooth, unadorned adaxial face of the left cupule is easily seen, 2×.—57, 58. Fruit about half grown, in lateral (Fig. 57) and adaxial (Fig. 58) views. Massive adaxial growth has produced strong asymmetry, and the pore through which the tip of the nut can be seen is now more than 90° from the vertical. Scales are no longer in rows, and some slight differentiation is beginning directly to the right and left of the pore, 2×.—59. Mature dehiscing cupule in adaxial view. Five lines of dehiscence are shown on this specimen, the vertical one through the upper, unadorned area visible in Figure 58 and the two upper, lateral ones between the barely differentiated scales, 2×.



FIGURES 70–73. 70. Castanopsis tribuloides, *lateral view of cymule in anthesis. The large primary bract is lowermost, but no cupular scales show between it and the prominent perianth (arrow),* 65×.—*71.* C. indica,

tanopsis longipetiolata there are few such scales from the beginning, so by maturity the cupule is nearly scaleless (Figs. 67–69, 91). No axillary spine complexes form.

DISCUSSION

Castanopsis shows primitive and advanced character states for the Fagaceae. If multiflowered cymules are primitive in the family, as suggested by Soepadmo (1970, 1972), Forman (1966a), and Kaul (1987), and by widely accepted interpretations of inflorescence evolution in the angiosperms, then it is likely that some associated character states are primitive too. Among the latter possibilities are four-valved cupules, dehiscence between the valves, the cupule free from the nut(s), and spines present on the cupule (Forman, 1966a). The general association of one-flowered cupules with spinelessness, adnation of the cupule to the nut, and irregular or no dehiscence thus suggests those states to be advanced. Forman (1966a) postulated such interpretations based upon other species, and they are supported by my observations. If the interpretations of Hjelmqvist (1948) and Forman (1966a) are correct, the dichasium cupule evolved by phylogenetic fusion of adjacent flower-cupules in the cymule and is thus highly derived. Strong cupular asymmetry approaching anatropy, as in *C. curtisii*, is certainly a derived state, although most species show at least some asymmetry.

There is some developmental evidence that adnation of cupule to nut is only apparent. Rather, it is possible that the basal scar enlarges enormously as the nut grows in species with apparently extensive adnation and that the basal part of the cupule expands simultaneously. The result is wide spacing of the lower cupular lamellae, but distally they remain rather crowded. With this interpretation the figlike, one-nut cupules can be viewed as the products of massive basal but little distal enlargement of the cupule. The distal part of the nut, which in other species enlarges more than the basal part, remains free, as it is in the species without apparent cupular adnation. Detailed developmental investigations, though technologically formidable, could provide further insights into this idea.

In some species, the scales and spines are arranged in concentric rows, but in others there is no apparent order in mature cupules. However, in the latter instances observed for this study, early developmental stages show rather regular rows of cupular scales, and I regard such rows as the primitive condition in the genus. In some species with figlike cupules (e.g., *Castanopsis guineri, C. piriformis*) the parallel rows of scales on the lower part of the mature cupule contrast with the distal, spiral rows, which are the last to form. The cupules of some species of *Quercus* subg. *Cyclobalanopsis* also show spiral lamellations, but most species of that subgenus, all of subg. *Quercus*, and nearly all of *Lithocarpus* have concentric lamellae (Kaul, 1985, 1987, and in press). Thus spiral lamellations are exceptional in the Fagaceae and are likely to have been derived by modification of the concentric pattern through alteration of later ontogenetic stages.

Forman (1966a) interpreted the sutural scales as derived from branched spines because he believed there are intermediates between scales and spines in some species. He thus considered the cupular scales of *Lithocarpus* and *Quercus* also to be modified spines. He saw the spines as single branched entities, but Barnett (1940) interpreted them as axillary to the first-formed cupular appendages. I also interpret the sutural and valvular scales to be homologous and synchronous, and the axillary spines to arise above the valvular but not the sutural scales. Thus intermediates between the two scale types are expected and, in fact, have been observed by Forman (1966a) as well.

Plant spines are sometimes emergences, not stem or leaf homologues, and that was Forman's (1966a) interpretation of the cupular appendages of *Castanopsis*. Evidence in favor of the spines of *Castanopsis* being modified stems are their branching capability (which sometimes occurs in other families in spines originating as emergences) and their position axillary to the scales. However, there are not even ephemeral subtending bracts at the nodes of branching on the spines, as could be expected in a reduced branching system. Furthermore, it is possible that the scales and spines, as defined here, are homologues and therefore not fundamentally different as suggested by the scale/axillary spine

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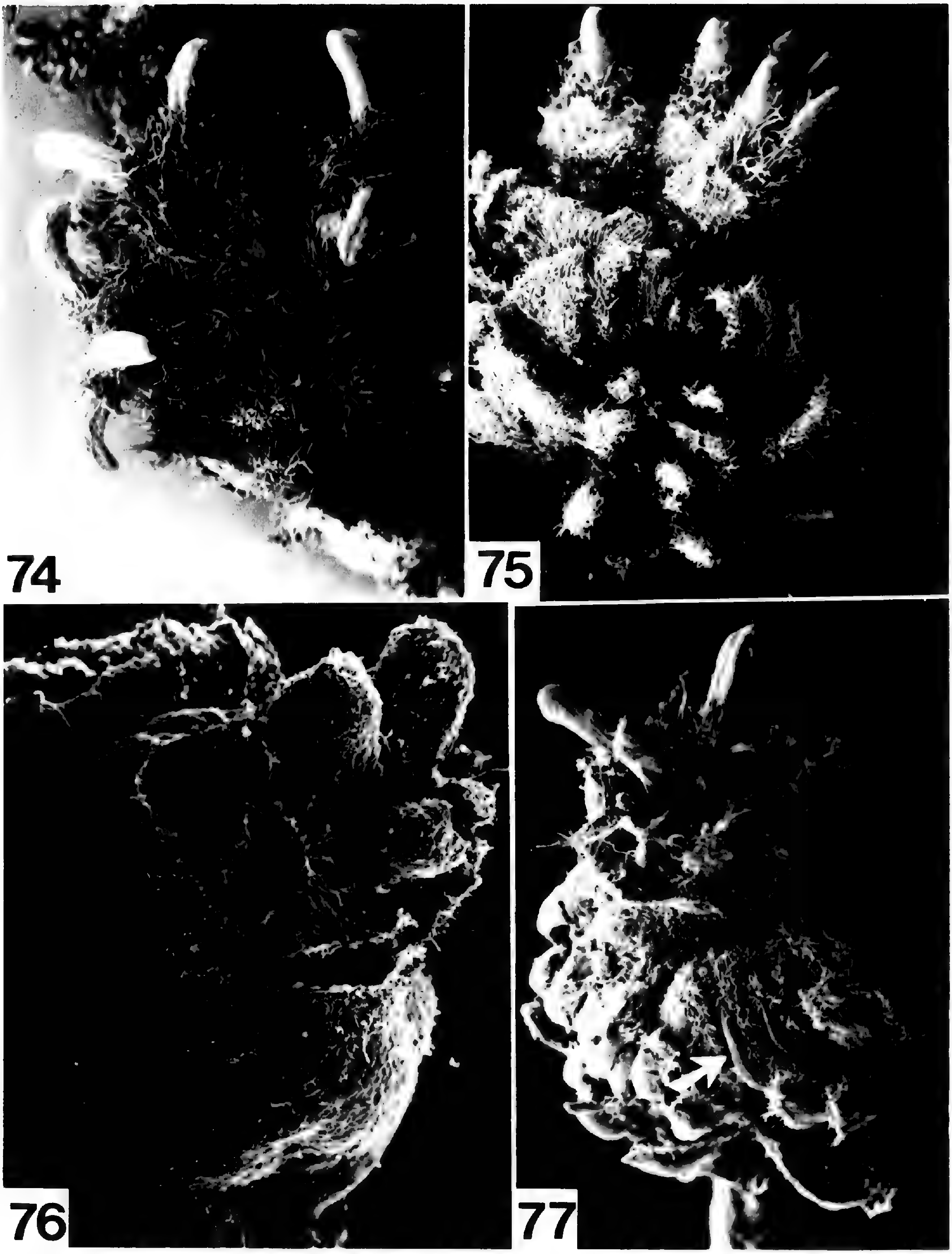
polar view of cymule soon after anthesis, five spines (arrow) appearing through the bracteoles and hairs, 28×.—72. C. pierrei, *abaxial view of three-flowered cymule in anthesis. A few cupular scales (arrow) are evident above the large basal bracteoles and below the perianths, 29×.—73.* C. schefferiana, *abaxial view of cymule soon after anthesis, the styles still showing. The cupular scales are now prominent above the basal bracteoles, 27×.*



FIGURES 74–77. 74, 75. Castanopsis foxworthyi.—74. *Abaxial view of three-flowered cymule in late anthesis. The subtending primary bract is seen in the lower right corner, but the bracteoles, emerging cupular scales, and much of the perianths are obscured by hairs, 32×.*—75. *Semiabaxial view of a cymule not long after anthesis, the abundant cupular scales having emerged from beneath the basal bracteoles. A few of the subulate structures are probably emerging spines, 24×.* 76, 77. C. acuminatissima.—76. *One-flowered cymule at anthesis, in nearly abaxial view. The prominent primary bract is below, and the equally large subtending bracteoles are just above it; only the perianth and styles emerge at this stage, 29×.*—77. *Cymule not long after anthesis, in nearly abaxial view. The subtending primary bract below is barely in focus, but the numerous cupular scales are plainly seen, as are a few emerging subulate spines (arrow), which are yet appressed to the young cupule. Some shriveled staminodia are seen below the styles, 24×.*

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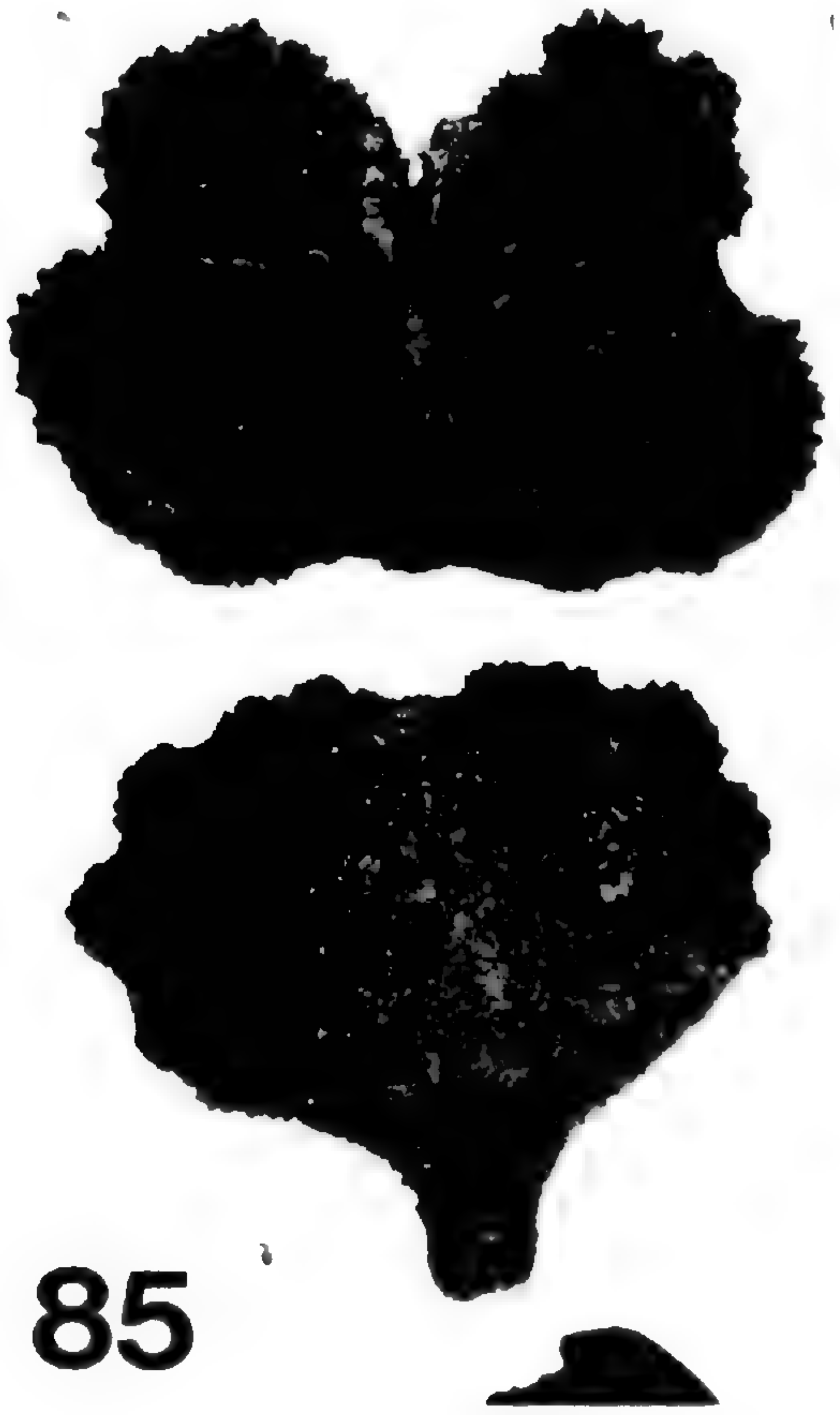
FIGURES 78–84. *Mature fruits of* Castanopsis.—*78.* C. argophylla. *Cupule dehiscing on two sutures, the nut free from it, 1.6×.*—*79.* C. hystrix. *Three-nut cupules dehiscing on four sutures, the nuts free, 0.8×.*—*80.* C. tribuloides. *One-nut cupules dehiscing on two sutures, the nut free, 1.2×.*—*81.* C. formosana. *Abaxial and adaxial views (upper and lower cupules, respectively). The unadorned adaxial surface is seen in the lower cupule, 1×.*—*82.* C. schefferiana. *Lateral and polar views (upper and central figures) of a three-nut cupule dehiscing on four sutures; the basal scar (arrow) of a nut shows in the lowest figure, 1.2×.*—*83.* C. purpurea. *Mature cupule armed with heavy, curved spines; the unadorned suture is evident in the center, 1.3×.*—*84.* C. guineri. *Mature, slightly asymmetric cupule in lateral views, showing the lamellae with the few persisting scales, 1× (cf. Figs. 63, 64).*



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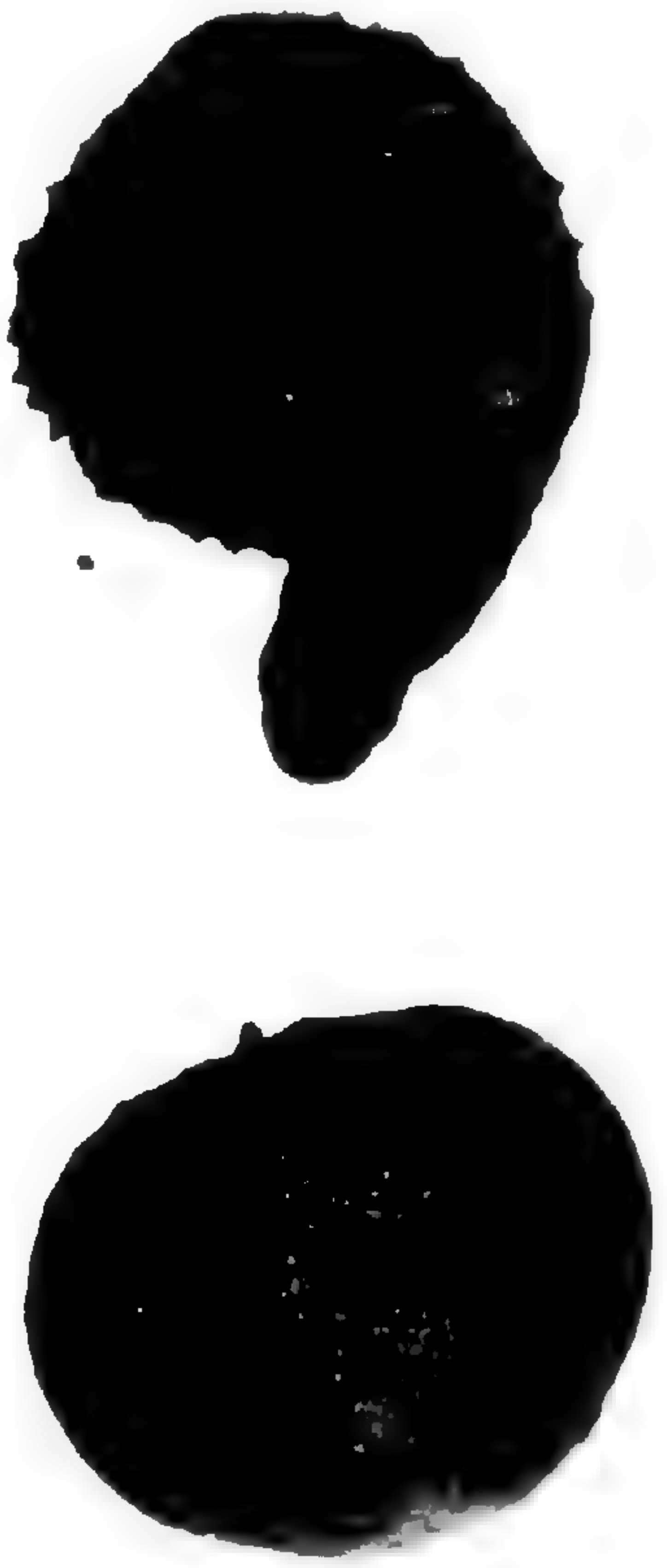

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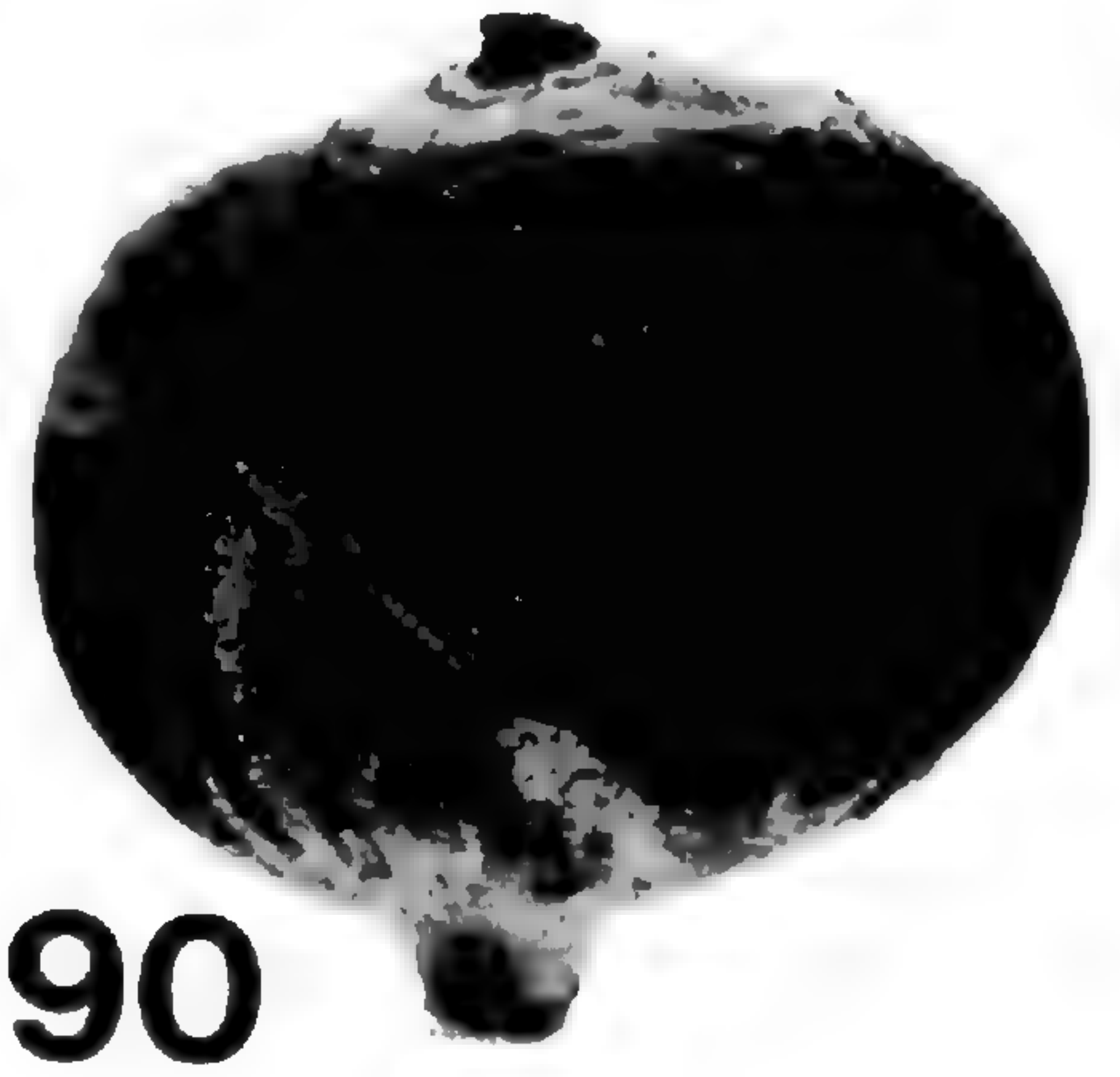

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FIGURES 85–91. *Mature fruits of* Castanopsis.—*85.* C. lucida. *Mature, dehiscing cupule in polar (upper) and abaxial (lower) views. This specimen has three nuts free from the cupule, the central one apparently abortive (upper figure), 1×.—86.* C. pierrei. *Mature fruit in lateral (upper figure) and polar (central figure) views. In the central figure, two abortive nuts are revealed to the right of the large, fertile nut (cf. Fig. 65). The fertile nut is shown removed from the cupule in the lowest figure; only the dark, upper part was free from the cupule, 0.8×.—87.* C. curtisii. *Upper figure: mature cupule in nearly adaxial view, the entire fruit anatropous, the apical pore visible left-central. Lower figure: mature nut removed from cupule and viewed laterally. The scar covers nearly the entire surface, 1×.—88.* C. armata. *Mature nut (upper figure) entirely scarred from fusion to the cupule, and lateral view (lower figure) of mature cupule with its massive but sparse armament, 1.3×.—89.* C. inermis. *More or less polar views (upper two figures) of mature cupule dehiscing along two sutures and showing only weak definition of sutural (unadorned) and valvular areas (cf. Figs. 47–51). Lowest figure is the mature nut, its basal scar (arrow) clearly evident, 1×.—90.* C. piriformis. *Lateral view of mature cupule (entirely fused* interpretation. For *Castanea*, Fey & Endress (1983) interpreted the valvular scales to be residual pherophylls of a condensed, cymose system and the spines to be axillary, cymose branches, based upon their comparative and developmental studies. I favor that interpretation for *Castanopsis* as well.

If the branched spines are relictual axillary branches—vestiges of a condensed, fused branching system that formed the cupule—then their presence is the primitive condition in the family. Their loss, both within *Castanopsis* and elsewhere in the family, would be the derived state. Spininess due to induration of cupular scales in a few species of *Quercus* and *Lithocarpus* would then be a secondary development.

Whatever interpretation is correct, there are unanswered questions about evolution of the various patterns of spine elaboration and distribution on the cupules. While protection of the immature nuts is a likely function of the spines, the fact that some nonspiniferous species of *Castanopsis* grow in the same forests with spiniferous species suggests that other protective measures are effective too. Detailed studies of life histories of *Castanopsis* and of its fruit predators and disseminators could reveal important information about cupular function.

It is likely that the solitary pistillate flowers of some species of *Lithocarpus* and *Castanopsis* and all species of *Quercus* are the results of phylogenetic elimination of all flowers but one (presumably the terminal one) of a cymule, as suggested by Forman (1966a). However, it is by no means evident that abortive flowers are always phylogenetically abortive—sometimes they are merely normal flowers that failed to produce fruit, probably for lack of pollination or fertilization, or due to competition from other fruits on the same rachis. Such failed flowers are frequent even among species with solitary flowers. In this paper and elsewhere (Kaul, 1987 and in press) examples are illustrated showing failed flowers of multiflowered cymules in every position in the cymules, varying greatly even on a single spike. If there are tendencies for lateral flowers in pistillate cymules of these genera to be phylogenetically abortive, I have seen little convincing evidence. However, such evidence appears in a few staminate spikes of *Lithocarpus* and possibly also of *Castanopsis*.

There are more differences in cupular structure within *Castanopsis* than between it and some species of *Lithocarpus*, and the distinctions between flower-cupules of the latter and dichasium-cupules of the former are not always convincing, especially in *Lithocarpus* species with cupules partially of both types. Thus, once again the generic and infrageneric taxonomy of Fagaceae is questioned: the long history of taxonomic doubt expressed in the literature is not eased by such observations. However, it is premature to propose new alignments because of the confusing levels of apparent parallelism and convergence in these large genera.

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to the nut), the weakly defined, remote lamellae essentially without scales; the distal lamellar spiral is seen more clearly in Figure 62, 1×.—91. C. longipetiolata. *Mature cupule in lateral view (entirely fused to the nut) showing the few naked lamellar ridges. The three dark spots are areas apparently damaged by chewing animals, 1.2×.*

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MALVACEAE OF JAMMU AND KASHMIR STATE, INDIA[1]

A. R. Naqshi, G. H. Dar, G. N. Javeid, and P. Kachroo[2]

ABSTRACT

The Malvaceae of the Jammu and Kashmir State are reviewed with a complete synopsis of the taxa recorded from this area. The state is situated on the northern fringe of India and comprises three distinct geographical regions: Jammu, Kashmir, and Ladakh. The family has a moderate representation here, but only a relatively few species are indigenous. Forty-one species in 15 genera are recorded in this treatment: 12 species cultivated (with at least half of them escaped from cultivation) and 29 wild species. A definite decline in the number of taxa of Malvaceae has been observed from the subtropical Jammu region through the temperate Kashmir to the cold, arid Ladakh. Malva bucharica *and* Althaea broussonetiifolia *are recorded for the first time from the Indian subcontinent;* Malva microcarpa, M. ambigua, *and* M. mohileviensis *for the first time from India; and* Hibiscus micranthus *is a new record for Jammu and Kashmir State. All the taxa are keyed, and the species are provided with descriptions and usually followed by brief notes on distribution and economic utility.*

In Hooker's *Flora of British India* (1874), Masters recognized 108 malvaceous species in 27 genera and sorted these into four tribes: Malveae, Ureneae, Hibisceae, and Bombaceae. As the tribe Bombaceae is now referred to family Bombacaceae, 97 species in 19 genera remain from Masters's listing. Of these, ten species in seven genera were cited from Jammu and Kashmir State. Many additional species have been described from this area since Hooker's publication, and the nomenclature of most of the species included there has changed.

Lambert (1933), in his list of trees and shrubs for the Jammu and Kashmir forest circles, listed the then-known arborescent taxa of the family. Stewart (1972) catalogued 70 species in 16 genera in West Pakistan and Kashmir. Of these, 30 species in 12 genera, including those based on literature, were listed from the Jammu and Kashmir State. Following Stewart, Abedin (1979) monographed the Malvaceae of West Pakistan, listing 94 specific and infraspecific taxa in 19 genera. However, Jammu and Kashmir materials are poorly represented in this work. Many of the collections referred by Stewart to our state are not mentioned by Abedin.

Lately, many local workers have included the family in floristic works (Javeid, 1970; Javeid & Naqshi, 1973; Singh & Kachroo, 1976; Sharma & Kachroo, 1981; Naqshi & Kachroo, 1982; Dar et al., 1983; Dhar & Kachroo, 1983), but none has given a descriptive account of all the taxa. Therefore, a complete synopsis of the family as it occurs in the Jammu and Kashmir State is given here.

The state is situated on the northern fringe of India between 32°10′ and 37°10′N latitudes and 72°30′ and 80°30′E longitudes. The eastern, northern, and western boundaries of the state comprise a segment of the border of India. To the east of the state lies Tibet, to the north lies China (with a very small portion of the border touching Afghanistan), to the west is Pakistan, and to its south is Himachal Pradesh and a very small part of the Punjab. It covers an area of about 222,000 km^2, which, except for a short belt in Jammu and the valley of Kashmir, is wholly mountainous, from ca. 270 m in Jammu and extending to the heights of the Himalaya in Kashmir and Ladakh (up to ca. 8,128 m at Nanga Parbat). The rock formations in the entire state belong to three broad groups: the Panjal, the Zanskar, and the Tertiary. The Panjal includes the outer hills, outer plains, and the middle mountains; the Zanskar includes the whole of the eastern region from Spiti to Lahul and to the lofty Karakoram in the north; and the Tertiary includes the valley of Kashmir and other river valleys (Wadia, 1953).

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[1] *Dr. Paul A. Fryxell, Research Botanist, Agronomy Field Laboratory, Texas A&M University, U.S.A., has been kind enough to read the manuscript and confirm identities of the representative taxa included in this treatment. He also supplied useful literature and made helpful suggestions. For all this generous help we are very grateful. Thanks are also due to Professors E. Nasir and S. I. Ali of Pakistan for providing literature.*

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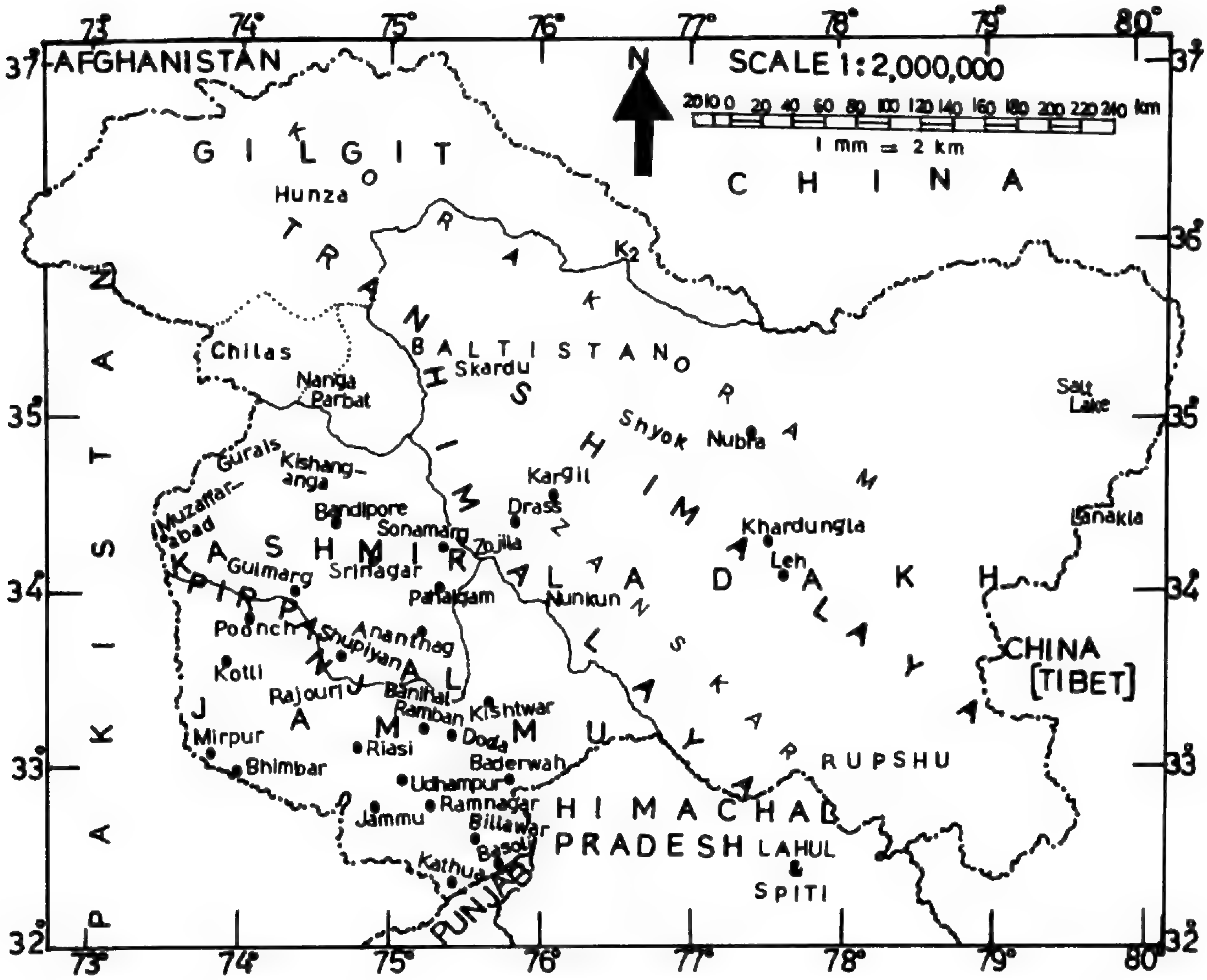

FIGURE 1. Map of Jammu and Kashmir State.

Geographically the state can be divided into three distinct regions, Jammu, Kashmir, and Ladakh (Fig. 1), embracing considerable variation in topography, physiography, and climate. Jammu has mostly a subtropical climate (moist temperate in higher reaches of Chenab Valley), with the southwest monsoons resulting in an average annual rainfall of over 1,100 mm. The mean maximum temperature during summer is as high as 40°C, and the mean minimum during winter as low as 6°C. Floristically the region is largely dominated by broad-leaved, deciduous and evergreen woody elements. Kashmir (separated from the Jammu region by the lofty Pir Panjal range, which also acts as a barrier to the southwest monsoons) is predominantly dry temperate, with an average annual rainfall of ca. 660 mm. The maximum temperature in summer reaches 35°C, and the minimum in winter (usually with heavy snowfalls) decreases to as low as −10°C. The fewer woody genera in Kashmir are evergreen—broad-leaved arborescent species are usually lacking. Ladakh, an extremely barren land with high elevations (above 3,000 m), has a cold, arid climate, approaching arctic cold in winter. The average annual rainfall varies between 80 mm (Leh) and 650 mm (Drass). The temperature in summer goes as high as 30°C and as low as −40°C in winter. The region harbors a desert flora largely dominated by xerophytic elements and, except for more humid valleys, almost lacks natural tree cover.

MATERIALS AND METHODS

Almost all the collections cited in this work were critically examined in the herbarium of the University of Kashmir (KASH) by the authors. The herbarium studies were supplemented by extensive observations in the field. Representative specimens of all our determinations were kindly seen by Dr. Paul A. Fryxell, U.S.A. However, a few collections, mostly made in the Pakistan-occupied part of Jammu and Kashmir State and deposited in various herbaria of Pakistan, were not accessible, and they

TABLE 1. *Distribution of the malvaceous species recorded from Jammu and Kashmir State.*

Genus	Total Number of Species Recorded	No. of Species Recorded from			Number of Species Common Between			
		Jammu	Kashmir	Ladakh	Jammu & Kashmir	Kashmir & Ladakh	Jammu & Ladakh	Jammu, Kashmir & Ladakh
Fioria	1 (—)[1]	1	—	—	—	—	—	—
Hibiscus	6 (2)	5	2	—	1	—	—	—
Abelmoschus	3 (1)	3	1	—	1	—	—	—
Kydia	1 (—)	1	—	—	—	—	—	—
Gossypium	2 (2)	—	2	—	—	—	—	—
Thespesia	1 (—)	1	—	—	—	—	—	—
Malva	9 (3)	4	8	6	3	6	3	3
Althaea	2 (—)	—	2	—	—	—	—	—
Alcea	3 (3)	1	3	—	1	—	—	—
Lavatera	1 (—)	1	1	—	1	—	—	—
Abutilon	4 (—)	3	1	—	—	—	—	—
Sida	5 (—)	5	—	—	—	—	—	—
Malvastrum	1 (—)	1	—	—	—	—	—	—
Urena	1 (—)	1	—	—	—	—	—	—
Sidalcea	1 (—)	—	1	—	—	—	—	—
Grand total	41 (12)	27	21	6	7	6	3	3

[1] Numbers within parentheses indicate the number of cultivated species and/or escapes from cultivation.

have been included with almost full citation of their collectors and places of collection and deposition.

RESULTS

The Malvaceae have a moderate representation in the Jammu and Kashmir State, but only a few species are indigenous. Altogether, 41 species in 15 genera are recorded in this study. Out of these, 12 species are cultivated, with at least half of them escaped from cultivation. Among the escaped cultivated species, *Sidalcea neomexicana*, *Alcea lavateriflora*, *A. pallida*, and *Malva verticillata* var. *rafiqii* are reported for the first time from India. Turning to wild species, *Malva bucharica* and *Althaea broussonetiifolia* are first recorded for the Indian subcontinent; *Malva microcarpa*, *M. ambigua*, and *M. mohileviensis* are new records for India; and *Hibiscus micranthus* is a first record for the Jammu and Kashmir State.

Twenty-seven of the 41 species occur in Jammu Province, 21 in Kashmir, and six in Ladakh. Twelve of the 15 genera occur in Jammu, nine in Kashmir, and only one (*Malva*) in Ladakh. It is evident that there is a marked decline in the number of genera and species as one proceeds from the sub-Himalayan Jammu through the Himalayan Kashmir to the trans-Himalayan Ladakh (Table 1). The number of species in common is highest between Jammu and Kashmir, while it is the lowest between Jammu and Ladakh. Almost all our arborescent species are restricted to Jammu, although *Hibiscus syriacus* is commonly grown ornamentally in Kashmir. None of our taxa except *Lavatera kashmiriana* and a few species of *Malva* reach subalpine and alpine ranges.

None of the taxa recorded here is endemic to the Jammu and Kashmir State. All our genera except *Sidalcea* (a North American plant, collected as an escape from cultivation only once in Kashmir) are shared with Pakistan. As for our other neighboring countries, *Fioria* does not occur in Afghanistan, U.S.S.R., China, and Iran; *Kydia* and *Thespesia* are absent from Afghanistan, U.S.S.R., and Iran; *Malva* and *Lavatera* are not found in Burma; *Sida* is unknown from Afghanistan; *Malvastrum* is unknown from Afghanistan, U.S.S.R., and Burma; and *Urena* does not occur in Afghanistan, U.S.S.R., and Iran. Almost all our species (38) are also in Pakistan, followed by 22 in Iran, 19 each in the U.S.S.R. and China, 11 in Burma, and 10 in Afghanistan. Both our new records for the Indian subcontinent (*Malva bucharica* and *Althaea broussonetiifolia*) grow in the U.S.S.R.

MALVACEAE A. L. DE JUSSIEU, GEN. PL. 271. 1789.

Plants annual, biennial, or perennial herbs, to small trees, mucilaginous, usually pubescent with stellate, furcate, and simple hairs, rarely with ferruginous peltate scales. Leaves alternate, simple, stipulate, petiolate, unlobed to deeply lobed. Flowers axillary, solitary, or fasciculate, or subracemose to paniculate, usually bracteate with an epicalyx of 3–13 free or basally connate segments, sometimes ebracteate, actinomorphic, usually perfect, sometimes polygamodioecious. Calyx usually campanulate or tubular, 5-lobed or -toothed, rarely spathaceous and 2- or 3-lobed, valvate, usually persistent. Corolla polypetalous, 5-merous, adnate basally to the staminal tube, contorted. Stamens numerous, monadelphous with filaments coherent to form a staminal tube, this wholly or partially antheriferous; anthers dorsifixed, monothecous, linear to horseshoe-shaped, solitary, rarely in clusters of 3–5. Carpels (3–)5–many, syncarpous in a single whorl (in ours) around the columella; ovary superior, with as many locules as carpels; placentation axile; style usually divided at the apex into as many (or twice as many) branches as carpels, or sometimes unbranched; stigmas sessile, linear or capitate or discoid. Fruit a dry, loculicidal (or indehiscent) capsule or a schizocarp separating into usually 1-seeded mericarps, rarely follicular and 2–3-seeded. Seeds reniform, ovoid or obovoid, glabrous or pubescent with short and long hairs.

Considerable embryological work has been done on this family (Schnarf, 1931; Venkata Rao, 1954, 1955; Winter, 1960; Ramchandani et al., 1966), and optimistic views are being held about the taxonomic significance of such studies. The structure and development of the seed and seed coat anatomy have also been shown to be of great taxonomic and phylogenetic value (Reeves, 1936; Wunderlich, 1967; Bouman, 1971; Mohana Rao, 1978; Kumar, 1981).

A family of 88 genera and ca. 2,300 species, most abundant in the tropics, common in subtropical and temperate regions, and usually absent from arctic regions. The Ureneae have style branches and stigmas twice as many as the carpels. The Malopeae have carpels irregularly arranged in two or more whorls around the carpophore and the style branches and stigmas are as many as carpels; the fruit is schizocarpic. In the Hibisceae the carpels are regularly arranged in a single whorl around the carpophore, the style branches and stigmas are as many as carpels or the style is unbranched, and the fruit is capsular. The Malopeae do not occur in our area. The Malveae are represented here by *Malva, Lavatera, Alcea, Althaea, Abutilon, Sida, Malvastrum,* and *Sidalcea*; the Hibisceae by *Fioria, Hibiscus, Abelmoschus, Kydia, Gossypium,* and *Thespesia*; and the Ureneae by *Urena*.

KEY TO THE GENERA OF MALVACEAE IN JAMMU AND KASHMIR STATE

1a. Flowers polygamous or polygamodioecious.
  2a. Plants trees; flowers white, polygamous; epicalyx present; anthers in globose head of 3–5; carpels not beaked .... 4. *Kydia*
  2b. Plants herbs; flowers rose-purple, polygamodioecious; epicalyx absent; anthers solitary; carpels beaked .... 15. *Sidalcea*
1b. Flowers bisexual.
  3a. Style branches and stigmas twice the number of carpels, always 10; mericarps glochidiate-spiny .... 14. *Urena*
  3b. Style branches and stigmas as many as carpels or style unbranched; mericarps never glochidiate-spiny.
    4a. Fruit a capsule, the carpels at maturity not separating from one another.
      5a. Style unbranched, ± clavate, or superficially divided into very short branches.
        6a. Plants herbaceous to suffrutescent, not covered with ferruginous peltate scales; leaves lobed; epicalyx segments cordate, foliaceous, persistent; calyx with oil glands; capsule fibrous, loculicidally dehiscent .... 5. *Gossypium*
        6b. Plants small trees, herbaceous portions covered with ferruginous peltate scales; leaves unlobed; epicalyx segments lanceolate, not foliaceous, caducous; calyx without oil glands; capsule ± woody, indehiscent .... 6. *Thespesia*
      5b. Style divided into 5 divergent branches.
        7a. Calyx spathaceous, irregularly 2- or 3-lobed, falling together with corolla and staminal tube .... 3. *Abelmoschus*
        7b. Calyx usually campanulate, regularly 5-lobed, persistent, not falling as a unit with corolla and staminal tube.
          8a. Capsule with 5 conspicuous, scarious, and strongly veined wings .... 1. *Fioria*
          8b. Capsule not winged .... 2. *Hibiscus*
    4b. Fruit a schizocarp, the carpels at maturity (mericarps) separating from one another leaving a distinct central columella.
      9a. Epicalyx present.
        10a. Epicalyx segments 3; staminal tube antheriferous only in the apical part.
          11a. Leaves ovate to lanceolate-oblong, unlobed; flowers yellow; stigmas capitate; mericarps tricuspidate (in ours) .... 13. *Malvastrum*

- 11b. Leaves orbicular-reniform or cordate, mostly lobed or angled; flowers pink-lilac (or white); stigmas linear, decurrent; mericarps awnless.
  - 12a. Stipules foliaceous; epicalyx segments ovate-orbicular, foliaceous, connate at base; mericarps 20–25; style base enlarged in fruit .... 10. *Lavatera*
  - 12b. Stipules not foliaceous; epicalyx segments linear or oblong-ovate, not foliaceous, free; mericarps 8–15; style base not enlarged in fruit .... 7. *Malva*
- 10b. Epicalyx segments 6–12; staminal tube antheriferous almost to the base.
  - 13a. Epicalyx segments 7–12; corolla 2–3 cm in diameter, 0.8–2.2 cm long; staminal tube cylindrical, the anthers brownish purple; mericarps 12–25, unilocular, wingless .... 8. *Althaea*
  - 13b. Epicalyx segments 6–7; corolla 5–8 cm in diameter, 3.5–7 cm long; staminal tube 5-angled, the anthers yellowish; mericarps 20–40, sub-bilocular, often winged .... 9. *Alcea*
- 9b. Epicalyx absent.
  - 14a. Calyx cupular; mericarps 10–20, follicular, 2–3-seeded .... 11. *Abutilon*
  - 14b. Calyx campanulate; mericarps 5–10, not follicular, 1-seeded .... 12. *Sida*

1. **FIORIA** Mattei, Boll. Reale Orto Bot. Giardino Color. Palermo 2: 71. 1916.

Four species, distributed in tropics and subtropics of the Old World; represented in our area by a single species.

Fioria vitifolia (L.) Mattei, Boll. Reale Orto Bot. Giardino Color. Palermo 2: 71. 1916. *Hibiscus vitifolius* L., Sp. Pl. 696. 1753; Masters in Hook. f., Fl. Brit. India 1: 333. 1874; Rakshit & Kundu, Bull. Bot. Surv. India 12: 166. 1970; Ngwe, Union Burma J. Life Sci. 4: 204. 1971; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 480. 1972; Sharma & Kachroo, Fl. Jammu 1: 112. 1981. *H. vitifolius* L. var. *genuinus* Hochr., in Annuaire Conserv. Jard. Bot. Genève 4: 169. 1900. TYPE: Herb. Hermann, Vol. IV, Fol. 39, *Linn. no. 265* (lectotype, BM); see Brenan & Exell, Bol. Soc. Brot. Ser. 2. 32: 72. 1958.

Hibiscus obtusifolius Willd., Sp. Pl. 3: 829. 1801.
H. truncatus Roxb., Hort. Bengal. 51. 1814; Fl. Ind. ed. 1832. 3: 200. 1832.
H. cuspidatus Edgew., J. Asiat. Soc. Bengal 21: 168. 1853.
Fioria vitifolia (L.) Mattei subsp. *vulgaris* (Brenan & Exell) Abedin, Pakistan J. Bot. 9: 59–66. 1977; Fl. W. Pak. 130: 5. 1979. *Hibiscus vitifolius* L. subsp. *vulgaris* Brenan & Exell, Bol. Soc. Brot. ser. 2. 32: 73. 1958.
H. heterotrichus DC., Prodr. 1: 450. 1824. *H. vitifolius* L. var. *heterotrichus* (DC.) Hochr., Annuaire Conserv. Jard. Bot. Genève 4: 170. 1900.

Annual, suffrutescent herbs. Stems and inflorescence axes usually densely tomentose with stellate and glandular hairs. Leaves ovate-cordate, entire or shallowly 3–5-lobed, coarsely serrate, stellately tomentose beneath or on both surfaces. Flowers axillary, solitary or clustered at the ends of branches, usually drooping; pedicels shorter than petioles, articulate at or below the middle. Epicalyx of 7–12 linear segments. Calyx campanulate, 5-lobed; lobes ovate, acute, 3–5-nerved, simple and 2-rayed pubescent within, stellate-tomentose outside. Corolla twisted, 3–5 cm diam., yellow with a purple center; petals obovate, glabrescent. Staminal tube truncate, shorter than corolla, antheriferous throughout. Capsule suborbicular, apiculate, 5-winged, hirsute. Seeds 2–4 in each cell, reniform, minutely tubercled.

Distribution. India, Pakistan, Burma, Sri Lanka, Australia, and tropical Africa. In our area it occurs in Jammu Province only. Sharma & Kachroo (1981: 113) wrongly reported it as a new record for Jammu and Kashmir.

Additional specimens examined. INDIA. JAMMU: Mandal, common along banks of irrigation channels, *B. M. Sharma 765* (KASH); Poonch Dist. Nawal Nadi, *A. Rashid s.n.* (RAW); Rajouri, *Jacquemont 1428* (fide Stewart, 1972: 480).

Abedin (1979) followed Brenan & Exell (Bol. Soc. Brot. Ser. 2. 32: 73. 1958) in placing the specimens of *Fioria vitifolia* from Pakistan and Kashmir under subsp. *vulgaris*, which is said to differ from subsp. *vitifolia* in the density of indumentum and leaf incision. However, the depth of leaf incision, the shape of the leaf lobes, and the density and rigidity of hairs have been found to be highly variable in the species, even within a single plant (Rakshit & Kindu, 1970). Subdivision of the species on the basis of the above-mentioned characters does not, therefore, seem to be satisfactory.

Most previous authors included *Fioria* in *Hibiscus*. This seems almost justified, especially when we consider their only superficial differentiating character of winged (*Fioria*) and nonwinged (*Hibiscus*) capsule. However, for a better understanding of these plants, it is now believed to recognize the two as distinct genera.

2. **HIBISCUS** L., Sp. Pl. 693. 1753; Gen. Pl. 5th Edition. 310. 1754.

Ketmia Miller, Gard. Dict. Abr. 4th Edition. 28. 1754.
Pariti Adans., Fam. Pl. 2: 401. 1763.
Paritium Adr. Juss. in St. Hilaire, Fl. Bras. Mered. 1(2): 255. 1827.

A genus of some 3,000 species distributed chiefly in the tropical and subtropical regions of both hemispheres. Six species occur in our area, of which two are cultivated.

KEY TO THE SPECIES OF *HIBISCUS* IN JAMMU AND KASHMIR STATE

1a. Flowers drooping; petals deeply laciniate; staminal tube much longer than corolla, exserted .... 2. *H. schizopetalus*
1b. Flowers not drooping; petals usually entire; staminal tube shorter than or equaling the corolla, included.
  2a. Epicalyx absent or rarely represented by minute teeth .... 5. *H. lobatus*
  2b. Epicalyx present, represented by conspicuous segments.
    3a. Epicalyx segments radiate; staminal tube antheriferous in the upper half only .... 6. *H. caesius*
    3b. Epicalyx segments not radiate; staminal tube antheriferous throughout.
      4a. Annual herbs; calyx inflated, more so in fruit; seeds glabrous .... 1. *H. trionum*
      4b. Shrubs; calyx not inflated; seeds villous or with a line of long white hairs.
        5a. Plants usually glabrous; leaves elliptic-rhombic, often 3-lobed; pedicels equal to or shorter than petioles; flowers 4–6 cm in diameter; seeds with a line of long white hairs .... 3. *H. syriacus*
        5b. Plants scabrous-bristly; leaves ± ovate, unlobed; pedicels longer than petioles; flowers 1–1.5 cm in diameter; seeds villous .... 4. *H. micranthus*

1. **Hibiscus trionum** L., Sp. Pl. 697. 1753; Masters in Hook. f., Fl. Brit. India 1: 334. 1874; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 159. 1949; Hu, Fl. China, Malvaceae. 57. 1955; Rakshit & Kundu, Bull. Bot. Surv. India. 168. 1970; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 480. 1972; Riedl in K. H. Rechinger, Fl. Iran. 120: 30. 1976; Singh & Kachroo, Forest Fl. Srinagar. 151. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 1300. 11. 1979. TYPE: *Linn. Herb. no. 875/39*, photo (LINN).

Hibiscus africanus et *H. hispidus* Miller, Gard. Dict. 8th Edition. HIB. 1768.
H. vesicarius Cav., Diss. 3: 171, tab. 64, f. 2. 1787.
H. dissectus Wallich, Cat. no. 3696. 1831, nom. nud.

Annual hispid herbs. Stems with simple and tuberculate-stellate hairs. Leaves orbicular-ovate, the lower leaves usually undivided, the upper leaves palmately 3–5-lobed, the lobes obovate or oblong, pinnatisect, punctate, nearly glabrous or sparsely stellate-pubescent, especially abaxially. Flowers solitary, axillary; pedicels longer than petioles, articulate above the middle. Epicalyx of 8–13 linear, long-hispid segments. Calyx campanulate, 5-lobed, inflated in fruit; lobes deltoid, acute, membranous; with many hispid, green-purplish, raised veins. Corolla 1.5–3 cm diam., pale yellow with a dark purple center; lobes glabrous. Staminal tube shorter than corolla, purplish, antheriferous throughout. Capsule oblong, obtuse, strigose-hispid, black, enclosed in the inflated persistent calyx. Seeds ± reniform, tuberculate-rugose when mature, glabrous.

Distribution. India, Pakistan, Afghanistan, southern U.S.S.R., Burma, China, Iraq, Iran, Turcomania, Transcaucasia, Mediterranean Region, southern Europe to southern Africa, Australia; naturalized in America. In our area it is common in Kashmir Province, often growing as a weed escaped from cultivation. Stewart (1972) gives Poonch, Jammu.

Specimens examined. INDIA. KASHMIR: university campus, *A. R. Naqshi 195* (KASH); Gulmarg, *A. R. Naqshi 514* (KASH); Kokernag, *I. M. Nahvi s.n.* (KASH); Anantnag, collector not known, *s.n.* (KASH); Srinagar, *G. N. Javeid 360* (KASH); Dachigam, *G. Singh 888* (KASH); Ganderbal, *G. H. Dar 3004* (KASH); Shuhama (Ganderbal), *G. H. Dar 2943–44* (KASH), *2942* (PF); Sarich (Ganderbal), *G. H. Dar 1767–68* (KASH); Narbal, *A. R. Naqshi & G. N. Dar 8173–75* (KASH).

This is a species of the eastern Mediterranean Region, now widespread in almost all the continents. Despite the extensive distribution, the species retains its essential morphological characters throughout. However, a number of species related to it have been described. Hochreutiner (1900) retained *H. trionum* s. str. and reduced to varieties some species described by earlier workers. We follow this conservative approach.

A diaphoretic syrup is prepared from its leaves, which contain 0.3% rubber substances. The seeds contain 23.8% oil. In South Africa the plant is said to be used for treatment of round worm, while in

China and Malaya the dried leaves are considered stomachic. An infusion of the flowers is used for itch, for painful skin diseases, and as a diuretic. It is reported to be poisonous to stock, particularly horses.

2. Hibiscus schizopetalus (Masters) Hook. f., Bot. Mag. 106, tab. 6524. 1880; Hu, Fl. China, Malvaceae. 46. 1955; Rakshit & Kundu, Bull. Bot. Surv. India 12: 166. 1970; Ngwe, Union Burma J. Life Sci. 4: 205. 1971; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 479. 1972; Abedin in Nasir & Ali, Fl. W. Pak. 130: 12. 1979. *Hibiscus rosa-sinensis* L. var. *schizopetalus* Masters, Gard. Chron. n.s. 12: 272, f. 45. 1879. TYPE: Gard. Chron. n.s. 12: 272, f. 45. 1879.

Glabrous shrubs with spreading-drooping branches. Leaves elliptic, glabrous, shining, palmately nerved, entire in basal half, serrate in apical half. Flowers solitary, axillary, pendulous; pedicels slender, longer than petioles, articulate at the middle. Epicalyx of 5–8 subulate, ciliate segments 1–2 mm long. Calyx spathaceous, tubular, irregularly 2–5-lobed. Corolla 4–9 cm diam., pinkish; petals deeply laciniate and recurved. Staminal tube much longer than corolla, filiform, pendulous, red, antheriferous in the upper half only. Capsule oblong-cylindrical. Seeds smooth, glabrous.

Distribution. Native of Kenya and Tanganyika (Exell, Fl. Zambes. 1: 470. 1960), cultivated elsewhere. It is commonly cultivated in gardens throughout India, Pakistan, Burma, and a few coastal cities in southern China. In our area it is rarely grown, collected only at Banihal in Jammu Province.

Specimen examined. INDIA. JAMMU: Banihal, *Sirajud-din s.n.* (KASH).

It is reported that the flowers in *H. schizopetalus* drop after anthesis and that fruits seldom form. According to Wilcox & Holf (Hawaii Agr. Exp. Sta. Bull. 29. 1913) it has been used as "male" parent in crosses with *H. rosa-sinensis* L. and its varieties. In 1984 Fryxell labeled the specimen cited above as "apparently a hybrid or a hybrid-derivative of *Hibiscus rosa-sinensis* L. and *H. schizopetalus* (Masters) Hooker."

3. Hibiscus syriacus L., Sp. Pl. 695. 1753; Masters in Hook. f., Fl. Brit. India 1: 344. 1874; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 152.1949; Hu, Fl. China, Malvaceae. 50. 1955; Kitamura, Fl. Afghan. 270. 1960; Rakshit & Kundu, Bull. Bot. Surv. India 12: 170. 1970; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 480. 1972; Riedl in K. H. Rechinger, Fl. Iran. 120: 29. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 13. 1979. TYPE: Syria: *Linn. Herb. no. 875/24* (LINN).

Ketmia syriaca Scop., Fl. Carniol. 2nd Edition. 2: 45. 1772.
K. syrorum Medikus, Malvaceae: 45. 1787.
K. arborea Moench, Suppl. Meth. 617. 1794.
Hibiscus floridus Salisb., Prodr. 383. 1796.
H. acerifolius Salisb., Parad. Londin. 1: tab. 33. 1805.
H. syriacus L. var. *sinensis* Lemaire, Jard. Fleur. 4: tab. 370. 1854.
H. chinensis sensu Forbes & Hemsley, J. Linn. Soc., Bot. 23: 88. 1886.

Glabrous, branched shrubs. Leaves elliptic-rhombic, acute at the apex, cuneate at the base, irregularly dentate, often 3-lobed. Flowers solitary, axillary, single or double; pedicels equaling or shorter than petioles. Epicalyx of 6–8 linear, single-nerved segments. Calyx campanulate, densely stellate-tomentose, shallowly 5-lobed; lobes triangular-lanceolate, acute. Corolla campanulate, 4–6 cm diam., usually lilac with a purple center; petals obovate, ciliate and stellately villose outside. Staminal tube shorter than corolla, antheriferous to the base. Capsule oblong-ellipsoid, yellowish, stellate-tomentose, shortly beaked at the apex. Seeds reniform, glabrous except for a line of long white hairs.

Distribution. China, cultivated elsewhere. Grown in gardens throughout India, Pakistan, Afghanistan, China, Iran, and other countries. In our area this species is extensively grown as an ornamental shrub or as a hedge plant in the Kashmir Valley.

Additional specimens examined. INDIA. KASHMIR: Beehama (Ganderbal), *G. H. Dar 2866* (KASH), *2866a* (PF); Srinagar University campus, *A. R. Naqshi 8176* (KASH); Nehru Bot. Garden (Cheshma Shahi), *A. R. Naqshi s.n.* (KASH).

A number of single and double horticultural varieties of this species have been described mainly on the basis of flower color, which ranges from purple-pink through pink to pure white. Hu (1955) recognized nine varieties mainly on the basis of floral size and color.

Although the plant is mainly used ornamentally, its stem is said to yield a strong fiber. The seeds contain 24.6% oil. In China, the flowers are reportedly eaten, and the tender leaves are used as a substitute for tea and as a shampoo.

4. **Hibiscus micranthus** L. f., Suppl. Pl. 308. 1781; Masters in Hook. f., Fl. Brit. India 1: 335. 1874; Rakshit & Kundu, Bull. Bot. Surv. India 12: 171. 1970; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 479. 1972. *Hibiscus micranthus* L. f. var. *genuinus* Hochr., Annuaire Conserv. Jard. Bot. Genève 4: 83. 1900. TYPE: *Linn. Herb. no. 875/2* (holotype, LINN).

H. gossypinus DC., Prodr. 1: 453. 1824, non Thunberg, 1800.

Erect shrubs with slender, terete branches, scabrid with scattered stellate bristles on almost all parts. Leaves ± ovate, 1.9–4.5 × 1.5–4 cm, acute or obtuse, serrate, eglandular. Flowers axillary, solitary; pedicels slender, longer than petioles, articulate above or below the middle. Epicalyx of 6–8 filiform, stiff, pubescent segments. Calyx 5-lobed; lobes triangular-lanceolate, pubescent. Corolla 1–1.5 cm diam., white or pink; petals often reflexed, stellately pubescent outside. Staminal tube to 5 mm long, shorter than corolla, antheriferous throughout. Capsule globose. Seeds reniform, black, villous.

Distribution. India, Sri Lanka, Pakistan, tropical Africa, South Africa, Madagascar, Arabia. In our area confined to Jammu Province.

Additional specimens examined. INDIA. JAMMU: Ram Nagar forest, common among hedges and on open roadside slopes; erect pubescent shrubs up to six feet tall with rosy-red flowers, *B. M. Sharma 249* (KASH).

Three varieties of *H. micranthus* are recognized from India and Pakistan (Abedin, 1979), but only var. *micranthus* occurs in our area.

The plant is reportedly valued as a febrifuge in Sri Lanka. This is the first record for Jammu and Kashmir State.

5. **Hibiscus lobatus** (Murray) Kuntze, Revis. Gen. Pl. 3rd Edition. 2: 19. 1898; Rakshit & Kundu, Bull. Bot. Surv. India 12: 169. 1970; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 479. 1972; Abedin in Nasir & Ali, Fl. W. Pak. 130: 18. 1979; Sharma & Kachroo, Fl. Jammu 1: 112. 1981. *Solandra lobata* Murray, Comment. Soc. Regiae. Sci. Gott. 6: 20, tab. 1. 1785. TYPE: Comment. Soc. Regiae. Sci. Gott. 6: 20, tab. 1.

Hibiscus solandra L'Hér., Stirp. Nov. 1: 103, tab. 49. 1789, nom. illeg.; Masters in Hook. f., Fl. Brit. India 1: 336. 1874. *H. solandra* var. *genuinus* Hochr., Annuaire Conserv. Jard. Bot. Genève 4: 128. 1900.
H. pumilis Roxb., Fl. Ind. 3: 203. 1832.
Lagunea lobata Willd., Sp. Pl. 4th Edition. 3: 733. 1800.
L. sinuata Hornem., Hort. Bot. Hafn. 2: 645. 1851.

Annual, erect, pubescent or somewhat hispid herbs. Leaves polymorphic, the lower leaves orbicular-ovate, the upper leaves deeply 3-lobed, the uppermost 3-fid, all cordate, crenate or coarsely serrate, pubescent with simple and stellate hairs on both surfaces. Flowers solitary and axillary, or in terminal racemes; pedicels equal to or longer than petioles, articulate near the apex. Epicalyx segments absent or rarely represented by minute teeth. Calyx 5-lobed, pubescent without; lobes lanceolate, prominently 3-nerved. Corolla 1–2 cm diam.; white to pale yellow; petals obliquely obcordate. Staminal tube shorter than or equaling corolla, pink, antheriferous throughout. Capsule ovoid, beaked, ± wrinkled and pubescent. Seeds ± reniform, black, usually granulated, minutely pubescent.

Distribution. India, Pakistan, Sri Lanka, Laccadive Islands, tropical Africa, Madagascar, and Java. In our area confined to Jammu Province.

Specimen examined. INDIA. JAMMU: Ram Nagar, common under shade on roadside slopes, often associated with *Triumfetta rhomboidea* Jacquem., *Bidens bipinnata* L., and other annuals; erect herbs up to 2 feet tall, flowers white with sticky calyx, *B. M. Sharma 204* (KASH).

6. **Hibiscus caesius** Garcke, Bot. Zeit. 7: 850. 1849; Rakshit & Kundu, Bull. Bot. Surv. India 12: 173. 1970; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 478. 1972; Abedin in Nasir & Ali, Fl. W. Pak. 130: 21. 1979. *H. caesius* Garcke var. *genuinus* Hochr., Annuaire Conserv. Jard. Bot. Genève 4: 160. 1900.

Hibiscus pentaphyllus F. Muell., Fragm. 2: 13. 1859, non Roxb., 1832.
H. gibsonii Stocks ex Harvey, Fl. Cap. 2: 587. 1859–1860; Masters in Hook. f., Fl. Brit. India 1: 339. 1874.
H. heptaphyllus Dalz. & A. Gibson, Bombay Fl. 20. 1861.

Erect, usually suffrutescent herbs; branches bristly or with minute bristle-pointed prickles. Leaves palmately 3–5-lobed, the lobes oblong-elliptic, sharply serrate, glabrous or stellately pubescent. Flowers solitary, axillary; pedicels longer than leaves, articulate near the apex. Epicalyx of usually 10 radiate, needlelike, subspiny segments. Calyx 5-lobed, the lobes lanceolate, acuminate, strongly

3-nerved, distantly ciliate. Corolla 3–5 cm diam., yellow with purple center or completely purple, rarely white with purple center; petals obovate, sparsely stellate-pubescent outside. Staminal tube shorter than corolla, purple, antheriferous in upper half only. Capsule ovoid, beaked; valves setose. Seeds dark brown, pilose.

Distribution. India, Pakistan, Afghanistan, south tropical Africa and north Australia. Rare in our area, reported from the Pakistan-occupied part of Poonch District in Jammu Province.

Specimen examined. INDIA. JAMMU: Poonch Mirpur, in bushes, *Stewart 27244* (RAW).

One more species, *Hibiscus hirtus* L. is reported from Kashmir by Stokoe (fide Stewart, 1972) and probably is based on misidentification and remains yet to be seen. The specimen *B. M. Sharma 249* (KASH) under this name turned out to be *H. micranthus*.

3. ABELMOSCHUS Medikus, Malvaceae 45. 1787; Schumann, Nat. Pflanzenfam. III. 6: 49. 1890; Hochr., Candollea 2: 83. 1924; Taxon 4: 188. 1955.

Laguna Cav., Diss. 3: 173. 1787.
Bamia R. Br. ex Wallich, Pl. Asiat. Rar. 1: 39. 1830.

Six species (Borssum-Waalkes, 1966), distributed in temperate and warm regions. Three species have been recorded form our state, one cultivated.

KEY TO THE SPECIES OF *ABELMOSCHUS* IN JAMMU AND KASHMIR STATE

- 1a. Epicalyx segments caducous before anthesis; corolla white (turning pinkish at maturity), with a dark purple center .... 2. *A. ficulneus*
- 1b. Epicalyx segments persisting until dehiscence of fruit; corolla yellow to yellowish white, with a purple center.
  - 2a. Epicalyx segments 7–12, linear to narrowly lanceolate, 1–2.5 mm wide; corolla 5–7 cm diam.; capsule cylindrical, 7–25 cm long; seeds glabrous .... 1. *A. esculentus*
  - 2b. Epicalyx segments 4–5, ovate-lanceolate, 5–10 mm wide; corolla 7–10 cm diam.; capsule ovate-ellipsoid, 3.5–6 cm long; seeds glabrescent .... 3. *A. pungens*

1. Abelmoschus esculentus (L.) Moench, Methodus 617. 1794; Hu, Fl. China, Malvaceae. 39. 1955; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 475. 1972; Abedin in Nasir & Ali, Fl. W. Pak. 130: 25. 1979. *Hibiscus esculentus* L., Sp. Pl. 696. 1753; Masters in Hook. f., Fl. Brit. India 1: 343. 1874; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 165. 1949; Ngwe, Union Burma J. Life Sci. 4: 203. 1971; Riedl in K. H. Rechinger, Fl. Iran. 120: 32. 1976. TYPE: "Habitat in Indiis," *Linn. Herb. no. 875/31* (LINN).

Hibiscus ficifolius Miller, Gard. Dict. 8th Edition. 15. 1768.
H. longifolius Willd., Sp. Pl. 4th Edition. 3: 827. 1800.

Annual, erect herbs, strigose-hirsute throughout. Leaves aceriform, wider than long, cordate, angular or palmately 3–7-lobed; lobes ovate to lanceolate, dentate. Flowers solitary and axillary. Epicalyx segments 7–12, linear to narrowly lanceolate, persisting until dehiscence of fruit. Calyx 5-toothed, spathaceous, bilabiate, caducous. Corolla 5–7 cm diam., yellow to yellowish white with a purple center; petals obovate. Staminal tube 2–2.5 cm long, included, antheriferous throughout. Capsule cylindrical, 7–25 cm long, 5-angled, acuminate, strigose-hirsute. Seeds ± globose, glabrous.

Distribution. Cultivated as vegetable in most tropical and many temperate countries; also in the Jammu and Kashmir provinces, known there as "Bhindi."

Additional specimen examined. INDIA. KASHMIR: Chatterhama (Srinagar), 1,700 m, *G. H. Dar 8963–66* (KASH).

According to Abedin (1979), the species is Asian in origin, as the whole genus is mainly of Asiatic distribution. On the basis of its close resemblance to *A. tuberculatus* Pal & Singh, a northern Indian species, Borssum-Waalkes (1966) considered the latter as one of the possible ancestors. This is taken to imply that *A. esculentus* originated in India (Hu, 1955 and Abedin, 1979). Babu (1977), however, thought it originated in Africa.

The species is primarily cultivated for the young fruits, which are eaten fresh or cooked as vegetables. Chopped capsules are used in making mucilaginous soups and sauces. Roasted seeds are also edible and are used as a substitute for coffee. The seeds contain 18% oil and ca. 15% water-soluble proteins. The plant is used in medicine for its diuretic and anticatarrhal effects. The stems furnish fiber and serve as raw material for paper production.

2. Abelmoschus ficulneus (L.) Wight & Arn. ex Wight, Cat. 14. 1833; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 475. 1972; Abedin in Nasir & Ali, Fl. W. Pak. 130: 26. 1979. *Hibiscus ficulneus* L., Sp. Pl. 695. 1753; Masters in Hook. f., Fl.

Brit. India 1: 340. 1874; Ngwe, Union Burma J. Life Sci. 4: 204. 1971. TYPE: Dillenius, Hort. Elth., tab. 157, f. 190.

Laguna aculeata Cav., Diss. 3: 173, tab. 71, f. 1. 1783.
Hibiscus sinuatus Cav., Diss. 3: 147, tab. 52, f. 2. 1787.
Abelmoschus alboruber F. Muell., Fragm. 1: 67. 1859.

Annual, sometimes prickly herbs. Leaves orbicular with cordate base and serrate margin, palmately 3–5-parted, scabrous on both surfaces; lobes obovate to spathulate. Flowers solitary, axillary or in terminal racemes. Epicalyx segments 5–6, lanceolate, falling before expansion of corolla. Calyx 5-toothed, spathaceous, rarely bilabiate, tomentose, caducous. Corolla 3–6 cm diam., white, turning pinkish at maturity, with a dark purple center; petals obovate. Staminal tube ca. 1.5 cm long, included, wholly antheriferous. Capsule pyramidal-ovoid, 3–4 cm long, 5-angled, hispid. Seeds ovoid to clavate-globose, black, striated with pilose stellate hairs.

Distribution. Northern Australia, southern Asia, Malaysia, eastern Africa, and Madagascar. Very rare in our area, this species has been collected from Jammu only (Stewart, 1972: 475).

3. **Abelmoschus pungens** (Roxb.) Voigt, Hort. Calc. 119. 1845; Abedin in Nasir & Ali, Fl. W. Pak. 130: 27. 1979. *Hibiscus pungens* Roxb., Hort. Bengal. 52. 1814, nom. nud., Fl. Ind. ed. 1832. 3: 213. 1832; Masters in Hook. f., Fl. Brit. India 1: 341. 1874. *Hibiscus manihot* L. var. *pungens* (Roxb.) Hochr., Annuaire Conserv. Jard. Bot. Genève 4: 155. 1900. *Abelmoschus manihot* (L.) Medicus, var. *pungens* (Roxb.) Hochr., Candollea 2: 87. 1924. *A. manihot* var. *pungens* (Roxb.) Hochr. sensu Hu, Fl. China, Malvaceae. 36. 1955. TYPE: Roxburgh's Icone *no. 1585* (K).

Annual or perennial herbs, densely covered with long, yellow, bristly hairs. Leaves orbicular to broadly ovate, cordate at base, palmately 3–7-lobed or -parted; lobes variable, ovate to lanceolate, oblong-lanceolate, obovate or elliptic, entire to coarsely serrate. Flowers solitary, axillary, sometimes subracemose towards the stem apex. Epicalyx segments 4–5, ovate-lanceolate, persisting until dehiscence of fruit. Calyx 5-toothed, spathaceous, caducous. Corolla 7–10 cm diam., yellow with a purple center; petals usually obovate. Staminal tube 1.5–3 cm long, included, antheriferous to base. Capsule ovate-ellipsoid, 3.5–6 cm long, 5-angular, short-beaked. Seeds globular or reniform, black, scabrid on the back, glabrescent.

Distribution. Northern India, Pakistan (rare), China, Malaysia, Philippines, and northern Australia. In our area this species has been collected only in the Pakistan-occupied part of Poonch District in Jammu Province and is no doubt very rare.

Specimen examined. INDIA. JAMMU: Poonch District, Nawal Nadi, 11-9-1953, *A. Rashid, E. Nasir & R. R. Stewart s.n.* (RAW).

According to Hu (1955), this species is found wild in China and northern India on grassy banks or along roadsides at altitudes of 1,500–1,600 m. She further reported that this plant (like her *Abelmoschus manihot* "typicus") is extensively cultivated in China for its flowers and roots. The flowers are said to be used in soup for the conservation of health during hot summer months. The root may be used fresh or dried. It is boiled with pork, and the preparation taken internally to cure abscesses. It is also soaked in rape seed oil and used for dressing boils.

The genus *Abelmoschus* was established by Medicus (1787) to accommodate species of *Hibiscus* with caducous calyces. The new genus was subsequently adopted by Gaertner (1791) and Moench (1794). Notwithstanding this, most workers on the Indian flora (Roxburgh, 1832; Masters, 1874; Prain, 1903; Duthie, 1903; Gamble, 1957; Cooke, 1958; and others) did not recognize the new genus but considered *Abelmoschus* as a section of *Hibiscus*. Hochreutiner (1924), however, stressed the need of placing *Abelmoschus* apart from *Hibiscus*, because in the former the calyx, corolla, and stamens are adnate basally and fall together after anthesis, although earlier (1900) he considered *Abelmoschus* only to be a section of *Hibiscus*. Most recent workers on Malvaceae (Hu, 1955; Borssum-Waalkes, 1966; Abedin, 1979) have treated *Abelmoschus* as a distinct genus. We also take this approach and agree with Paul A. Fryxell (1984, pers. comm.) in believing that the species of *Fioria*, *Abelmoschus*, and *Hibiscus* are better understood when separated into distinct genera.

4. **KYDIA** Roxb., Pl. Coromandel 3: 11, tab. 215–216. 1819.

Four or five species, distributed in India, Pakistan, Burma, and China; one species recorded from our area.

Kydia calycina Roxb., Pl. Coromandel 3: 11, tab. 215. 1819; Fl. Ind. ed. 1832. 3: 188. 1832; Masters in Hook. f., Fl. Brit. India 1: 348. 1874; Hu, Fl. China, Malvaceae. 71.

1955; Ngwe, Union Burma Life Sci. 4: 200. 1971; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 480. 1972; Abedin in Nasir & Ali, Fl. W. Pak. 130: 28. 1979; Sharma & Kachroo, Fl. Jammu 1: 110. 1981. TYPE: Roxb., Pl. Coromandel 3: 11, tab. 215. 1819.

Kydia fraterna Roxb., Pl. Coromandel 3: 12, tab. 216. 1819.

Medium-sized trees, the herbaceous portions with stellate pubescence. Leaves broadly cordate to suborbicular, entire or usually 3–5-angled, stellate-pubescent, the midrib (sometimes adjacent nerves also) with a basal gland abaxially. Flowers paniculate, polygamous. Epicalyx segments 4–6, oblong, in fruit obovate-spathulate, spreading stellately, densely stellate-villous, 5-parted; lobes triangular, incurved, persistent, ± enclosing fruit. Corolla rotate, connate at base, 1–2 cm diam., white; petals obovate-obcordate, barbate at the base. Staminal tube 3–5 mm long, included, divided in the apical half into 5 branches, each with a cluster of 3–5 sessile anthers, rudimentary in the carpellate flowers. Ovary globose, villous, 3-carpellate; style with 3 terminal branches, each with a peltate stigma, rudimentary in the staminate flowers. Capsule subglobose, loculicidally 3-valved, stellate-pubescent. Seeds reniform, glabrous.

Distribution. India, Pakistan, Burma, and China. In our area this species occurs, uncommonly, in Jammu Province.

Specimens examined. INDIA. JAMMU: Nandni, uncommon, collected from a slope opposite Brig. Atma Singh's Memorial, small tree, bark gray, young shoots and panicles grayish, leaves hoary, flowers white, *B. M. Sharma 728* (KASH); also reported from Mirpur and Billawar by Lambert (1933).

The wood of this species is straight-grained and good for house building. The liber yields fiber, and the leaves are said to be used as an embrocation.

5. GOSSYPIUM L., Sp. Pl. 693. 1753; Gen. Pl. 5th Edition. 309. 1754.

About 40 species distributed in tropical and subtropical regions; two cultivated species are recorded from our area.

KEY TO THE SPECIES OF *GOSSYPIUM* IN JAMMU AND KASHMIR STATE

1a. Perennial suffrutescent herbs; stipules linear; epicalyx segments connate at the base, ± entire, with 3 small teeth at the apex; filaments equal in length .... 1. *G. arboreum*
1b. Annual herbs; stipules ovate-falcate; epicalyx segments free, laciniate, with 7–9 long and acuminate teeth at the apex; filaments unequal in length, the upper ones longer .... 2. *G. hirsutum*

1. Gossypium arboreum L., Sp. Pl. 693. 1753; Masters in Hook. f., Fl. Brit. India 1: 347. 1874; Hu, Fl. China, Malvaceae. 62. 1955; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 477. 1972; Abedin in Nasir & Ali, Fl. W. Pak. 130: 30. 1979. TYPE: *Linn. Herb. no. 874/3* (holotype, LINN).

Gossypium rubrum Fôrskal, Fl. Aegypt.-Arab. 125. 1775.

Perennial, pubescent, suffrutescent herbs with purple branches. Leaves ovate to orbicular or subreniform, 5–7-parted; lobes oblong-lanceolate, acute, stellate-pilose adaxially, sparsely villous abaxially; stipules linear, caducous. Flowers solitary, axillary. Epicalyx segments 3, foliaceous, cordate, connate at the base, ± entire, with 3 small teeth at the apex, stellately hirsute and villose on the nerves. Calyx cupular, ± 5-dentate. Corolla pale yellow, usually with a maroon center, sometimes all purplish. Staminal tube included, antheriferous throughout; filaments equal in length. Capsule fibrous, ovoid, beaked, with persistent, accrescent epicalyx and calyx. Seeds densely covered with long and short hairs.

Distribution. Origin uncertain, possibly African; widely cultivated in tropical and subtropical regions of the Old World. According to Hu (1955), it has escaped from cultivation in Hainan and southwestern Sichuan in China. In our area it was occasionally grown in the Kashmir Valley until recently. Vernacular name: "Kapas."

Additional specimen examined. INDIA. KASHMIR: Pampore, 6 June 1970, *G. N. Javeid s.n.* (KASH).

2. Gossypium hirsutum L., Sp. Pl. 2nd Edition. 975. 1763; Prokhanov in Shishkin & Bobrov, Fl. U.R.S.S. 15: 178. 1949; Hu, Fl. China, Malvaceae. 66. 1955; Abedin in Nasir & Ali, Fl. W. Pak. 130: 31. 1979. *Gossypium herbaceum* L. var. *hirsutum* Schumann, Nat. Pflanzenf. III. 6: 51. 1890. TYPE: Miller's description (see Fryxell, 1968: 882).

G. religiosum L., Syst. Nat. 12th Edition. 2: 462. 1767.

Annual, erect, hirsute herbs with green or red-tinged branches. Leaves broadly cordate, ± orbicular, 3(–5)-lobed, upper ones sometimes entire and ovate; lobes triangularly ovate, abruptly acuminate, glabrescent with simple and stellate hairs on both surfaces; stipules ovate-falcate, caducous.

Flowers solitary, axillary. Epicalyx segments as in the preceding species but free and with 7–9 long and acuminate teeth at the apex. Calyx cupular, 5-toothed. Corolla pale yellow. Staminal tube as in the preceding species but filaments unequal in length, the upper ones longer. Capsule fibrous, ovoid, beaked. Seeds thickly covered with white pubescence.

Distribution. A native of Central America, acclimatized from Guatemala northwards to the cotton belt of the southern United States and cultivated in all cotton-growing countries. In our area it was grown in Kashmir Valley until recently. Vernacular name: "Kapas."

Specimen examined. INDIA. KASHMIR: exact locality not given, *M. Y. Khan s.n.* (KASH).

A third species, *Gossypium herbaceum* L., has been reported from the Kashmir Valley by Stewart (1972: 478), but we have not seen any specimens.

It is said that cotton thrives in Kashmir, but the practice of growing it here has now nearly ceased.

The various species of cotton are abundantly cultivated in many countries of the world for their seeds, which are densely covered with short and long hairs, forming the cotton of commerce.

6. THESPESIA Solander ex Correa, Ann. Mus. Natl. Hist. Nat. 9: 290, tab. 8, f. 2. 1807, nom. cons. *Azanza* Alef., Bot. Zeit. 19: 298. 1861.

About 15 species, distributed in tropics of both hemispheres; a single species has been reported from our area.

Thespesia populnea (L.) Solander ex Correa, Ann. Mus. Natl. Hist. Nat. 9: 290, tab. 8, f. 2. 1807; Masters in Hook. f., Fl. Brit. India 1: 345. 1874; Hu, Fl. China, Malvaceae. 69. 1955; Ngwe, Union Burma J. Life Sci. 4: 200. 1971; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 484. 1972; Abedin in Nasir & Ali, Fl. W. Pak. 130: 32. 1979. *Hibiscus populneus* L., Sp. Pl. 694. 1753. *Malvaviscus populneus* (L.) Gaertner, Fruct. Sem. Pl. 2: 253, tab. 135, f. 3. 1791. TYPE: Herb. Herm. Volume V, fol. 208, tab. 258 (lectotype, BM).

Hibiscus bacciferus Forster f., Fl. Ins. Austr. 48. 1786.
Thespesia macrophylla Blume, Bijdr. 2: 73. 1825.

Medium-sized bushy trees; herbaceous portions covered with ferruginous, peltate scales. Leaves ovate, cordate at base, shortly acuminate, entire; stipules linear-lanceolate, caducous. Flowers solitary, axillary; pedicels 1–5 cm long, articulate at base. Epicalyx segments 3, lanceolate, caducous. Calyx cupular, truncate, minutely 5-toothed, coriaceous, persistent. Corolla convolute, campanulate, pale yellow with a crimson center. Staminal tube cylindric, included, 5-dentate at the apex, antheriferous for most part; filaments paired, the anthers horseshoe-shaped. Ovary 5-loculate; style ± clavate, unbranched; stigma elongate, scabrous. Capsule ± globose, almost woody but easily compressed, indehiscent. Seeds obovoid, angular, pilose.

Distribution. A coastal plant, common in tropical countries. In Jammu and Kashmir State it has been reported only from Udhampur in the Jammu Province (Lambert, 1933: 3; Sharma & Kachroo, 1981: 113).

According to Ngwe (1971), the bark of this plant is used in treating piles, dysentery, and skin diseases.

7. MALVA L., Sp. Pl. 687. 1753; Gen. Pl. 5th Edition. 308. 1754.

Bismalva Medicus, Malvaceae. 39. 1787.

Over 100 species native to Europe, Asia, and Africa. Several species are naturalized in America, Australia, and New Zealand; represented in our area by nine species, three being cultivated or escapes from cultivation.

KEY TO THE SPECIES OF *MALVA* IN JAMMU AND KASHMIR STATE

1a. Epicalyx segments oblong, oblong-lanceolate, ovate, or ovate-lanceolate.
  2a. Leaves 5–7-lobed; staminal tube with simple or 2-rayed, retrorse hairs .... 4. *M. bucharica*
  2b. Leaves 3–5-lobed; staminal tube stellately pubescent.
    3a. Stipules ovate-lanceolate; flowers 5–15 (rarely fewer than 5) in fascicles; petals 1.5–2 cm wide at apex; mericarps 10–14, glabrous .... 3. *M. mauritiana*
    3b. Stipules lanceolate; flowers solitary or 2–4 in fascicles; petals 1 cm or less wide at apex; mericarps 9–12, glabrous or pubescent.
      4a. Petals oblong-obovate, 0.7–2 × 0.5 cm; mericarps pubescent .... 1. *M. ambigua*
      4b. Petals obovate, 2–3 × 1 cm; mericarps glabrous .... 2. *M. sylvestris*

1b. Epicalyx segments linear to linear-lanceolate.
  5a. Plants biennial or perennial; mericarps 12–15, pubescent, smooth throughout; seeds pubescent .... 5. *M. neglecta*
  5b. Plants mostly annual, rarely biennial; mericarps 9–12, glabrous, striate-rugose at least on sides and margins; seeds glabrous.
    6a. Calyx lobes ± rotate and spreading in fruit; corolla shorter than, equaling, or slightly exceeding calyx; staminal tube 1–2 mm long, glabrous; mericarps with raised reticulation on back, ± winged and acute along margins.
      7a. Flowers solitary or paired, rarely more than 2 but never compact; pedicels distinctly visible, 0.3–2 cm long; calyx 5–6 mm long, slightly enlarged in fruit; margins of mericarps slightly winged, ± entire .... 6. *M. microcarpa*
      7b. Flowers usually many, compactly fasciculate; pedicels generally not visible, 3–5 mm long; calyx 3–5 mm long, enlarged in fruit to ca. 1 cm; margins of mericarps distinctly winged, undulate-toothed .... 7. *M. parviflora*
    6b. Calyx lobes incurved and enclosing the fruit; corolla 1½–2 times as long as calyx; staminal tube 3–5 mm long, glabrous or pubescent; mericarps smooth on back, unwinged and rounded along margins.
      8a. Plants annual, pubescent; leaves suborbicular, 5–7-lobed; petioles 2–9 cm long; fruiting calyx less than 10 mm long; petals retuse, ca. 2 times the length of sepals, the claw ± pubescent; staminal tube retrorsely pubescent; fruit ca. 5 mm diam.; mericarps 12 .... 8. *M. mohileviensis*
      8b. Plants annual to biennial, glabrescent; leaves orbicular, usually 5-lobed; petioles (1.5–)4–20 (–24) cm long; fruiting calyx 10–15 mm long; petals scarcely notched, 1½ times or less the length of sepals, the claw glabrous; staminal tube glabrous or pubescent with simple hairs towards the apex; fruit 5–7 mm diam.; mericarps 10–12 .... 9. *M. verticillata*

1. Malva ambigua Guss., Fl. Sicul. Prodr. 2: 331. 1828; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 48. 1949. TYPE: described from Sicily (NAP).

Malva sylvestris L. var. *eriocarpa* Boiss., Fl. Orient. 1: 819. 1867.

Biennial to perennial herbs. Stems erect or ascending, usually weak, sparsely pubescent. Leaves ± semiorbicular, usually truncate (to cordate) at base, 3–5-lobed, serrate, glabrescent; stipules lanceolate, 2–4 mm long; petioles 2–8 cm long. Flowers axillary, solitary or in fascicles of 2–4; pedicels 1–3 cm long, with simple or stellate hairs. Epicalyx segments narrowly ovate or oblong. Calyx 3–6 mm long, stellately pubescent, slightly accrescent in fruit; lobes broadly triangular. Petals lilac, oblong-obovate, 0.7–2 × 0.5 mm, claw pubescent. Staminal tube 3–5 mm long, pilose with stellate hairs. Fruit 6 mm diam.; mericarps 9–12, pubescent, with raised reticulation on back. Seeds reticulate, glabrous.

Distribution. U.S.S.R., western and eastern Mediterranean, Iran, Afghanistan, and Pakistan. In our area infrequent in the Kashmir Valley, collected on house tops, waste places, moist sites, and sides of water courses.

Additional specimens examined. INDIA. KASHMIR: Ganderbal, *G. H. Dar 2499* (PF); Srinagar, *G. N. Javeid 590 A* (KASH); Srinagar, around graveyards in association with *Urtica dioica* L., *A. R. Naqshi 8165* (KASH).

First record for India.

2. Malva sylvestris L., Sp. Pl. 689. 1753; Masters in Hook. f., Fl. Brit. India 1: 320. 1874; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 41. 1949; Kitamura, Fl. Afghan. 171. 1960; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 481. 1972; Abedin in Nasir & Ali, Fl. W. Pak. 130: 37. 1979. TYPE: described from western Europe, *Linn. Herb. no. 870/22* (holotype, LINN).

Biennial to perennial herbs. Stems erect, pubescent to glabrescent with simple (or bifid) hairs. Leaves ± suborbicular, truncate to broadly cordate at base, usually 3-lobed, crenate-dentate, sparsely pilose; stipules lanceolate, scarious, ca. 5 mm long; petioles 2–7 cm long, pilose. Flowers axillary, solitary or in fascicles of 2–4; pedicels ca. 2 cm long. Epicalyx segments ovate-oblong. Calyx 3–6 mm long, glabrescent with stellate hairs; lobes broadly triangular. Petals pink-purple, obovate, emarginate, 2–3 × 1 cm, the claw ciliate. Staminal tube ca. 3 mm long, pilose with stellate hairs. Fruit 5–6 mm diam.; mericarps 10–12, glabrous, reticulate. Seeds sparsely punctate.

Distribution. Western Europe, northern Africa, and Asia. Occasionally cultivated for greens in the Kashmir Valley and at certain places evidently escaped from cultivation, also collected from Ladakh (Stewart, 1972: 481).

Additional specimen examined. INDIA. KASHMIR: Srinagar, *A. R. Naqshi 8153* (KASH).

The species resembles *M. ambigua* Guss. and

M. mauritiana L. but differs from the former in having glabrous fruits and from the latter in having narrower and emarginate petals, and fewer flowers in the fascicles. Riedl (1976) followed Boissier (1867) in treating all of the above three species as *M. sylvestris* varieties *sylvestris*, *eriocarpa* Boiss., and *mauritiana* (L.) Boiss.

Malva sylvestris is believed to have been cultivated by ancient Greeks and Romans as a medicinal and edible plant. An infusion of flowers and leaves is used internally and as a gargle. The infusion, mixed with honey, is taken in case of catarrhal ailments, inflammatory conditions of the digestive tract, and constipation. A paste of leaves and flowers is applied in case of external inflammatory conditions. Flowers are also used in coloring medicine, liquors, and wool. The coloring properties are said to be due to glucoside malvin and diglucoside malvidin in the petals.

3. **Malva mauritiana** L., Sp. Pl. 689. 1753; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 49. 1949; Abedin in Nasir & Ali, Fl. W. Pak. 130: 38. 1979. *Malva sylvestris* var. *mauritiana* (L.) Boiss., Fl. Orient. 1: 819. 1867; Masters in Hook. f., Fl. Brit. India 1: 320. 1874; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 481. 1972; Riedl in K. H. Rechinger, Fl. Iran. 120: 19. 1976. TYPE: *Linn. Herb. no. 870/24* (holotype, LINN).

Biennial to perennial herbs; stems mostly rigid, erect, rarely ascending, glabrescent with simple and bifid hairs. Leaves orbicular to suborbicular, truncate to shallowly cordate at base, 3–5-lobed, coarsely crenate, sparsely pilose with simple and bi- (tri-)fid hairs; stipules ovate-lanceolate, 3–6 mm long; petioles 4–12 cm long, with a line of dense hairs apically. Flowers axillary, in fascicles of 5–15, rarely fewer than 5; pedicels 1–4 cm long, unequal in length. Epicalyx segments ovate-lanceolate to ovate or oblong. Calyx 5–8 mm long, pilose with stellate hairs; lobes triangular, plicate at angles, accrescent in fruit. Petals dark pink to purple, 2–3 × 1.5–2 cm, obovate, retuse, claw pubescent at base. Staminal tube ca. 5 mm long, pilose with stellate hairs. Fruit 5–7 mm diam.; mericarps 10–14, glabrous, reticulate-wrinkled. Seeds finely punctate.

Distribution. Mediterranean region, western Europe, and U.S.S.R., elsewhere cultivated. In our area collected from Ladakh, where it grows, rare and handsome, along borders of cultivated fields, also reported from Kashmir by Stewart (1972: 481).

Additional specimen examined. INDIA. LADAKH: Nubra, along borders of cultivated fields, *A. R. Naqshi & G. N. Dar 7218* (KASH).

Most authors follow Boissier (1867) in treating this species as a variety of *Malva sylvestris* L. Whitmore (1979) considered *M. mauritiana* as synonymous with *M. sylvestris.*

The species is used for the same purpose as *M. sylvestris.* In the Iranian pharmacopoeia it is employed in a mixture with violets, *Nymphaea candida, Ziziphus jujuba, Alhagi camelorum,* and other species for preparation of the purgative infusion (Hooper, *Useful Plants and Drugs of Iran and Iraq,* 1937).

4. **Malva bucharica** Iljin, Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 5: 4. 1924; Shishkin & Bobrov, Fl. U.R.S.S. 15: 55. 1949; Riedl in K. H. Rechinger, Fl. Iran. 120: 19. 1976. TYPE: Kurgan-Tyube, *Roshewitz 175* (lectotype, LE).

Perennial herbs; stems erect or ascending, terete, glabrate or with simple to 2-branched hairs, sometimes completely glabrous. Leaves semiorbicular, truncate or ± cordate at base, 5–7-lobed, serrate-dentate, subglabrous, the nerves pilose with usually simple hairs; stipules ovate to broadly lanceolate; petioles 3–15 cm long. Flowers usually 3 in axils, crowded towards apices of branches; pedicels 1.5–5 cm long, much shorter than the subtending leaf; epicalyx segments oblong-lanceolate; calyx 3–7 mm long, glabrous or pubescent with simple and trifid hairs, the lobes accrescent and enclosing the fruit, triangular-ovate. Petals purplish, obovate or oblong-obovate, 0.8–2.2 × 0.4–1.2 cm, deeply notched, claw ± densely pilose. Staminal tube 4–6 mm long, with simple and 2-rayed, retrorse hairs. Fruit 6–7 mm diam.; mericarps (8–)10(–12), glabrous or pubescent, reticulate-rugose on back. Seeds puncticulate.

Distribution. U.S.S.R. and Kashmir. In our area it occurs frequently in the Kashmir Province but has not been collected in Jammu and Ladakh.

Additional specimens examined. INDIA. KASHMIR: Nagin, collector not known, *s.n.* (KASH); Srinagar, *G. N. Javeid 590 B* (KASH); Srinagar, Rambagh, *A. R. Naqshi 8152* (KASH); Srinagar, Hazratbal, roadsides near university gate, *G. H. Dar 7617* (KASH); Srinagar, Rainawari, in graveyards among *Urtica* bushes, *A. R. Naqshi 8178* (PF), *8179–81* (KASH).

In habit this species resembles *M. sylvestris* but differs from it mainly in having simple and two-rayed, retrorse hairs on the staminal tube. First record for Indian subcontinent.

5. Malva neglecta Wallr., Syll. Ratisb. 1: 140. 1824; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 56. 1949; Hu, Fl. China, Malvaceae. 6. 1955; Kitamura, Fl. Afghan. 271. 1960; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 481. 1972; Singh & Kachroo, Forest Fl. Srinagar. 151. 1976; Riedl in K. H. Rechinger, Fl. Iran 120: 24. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 38. 1979. TYPE: without exact locality, Germany, *Wallroth s.n.* (E).

Malva rotundifolia sensu Maxim., Acta Hort. Petrop. 11: 78. 1890, non L.; Masters in Hook. f., Fl. Brit. India 1: 320. 1874.
M. vulgaris Ten., Fl. Napol. Suppl. 1: 62. 1811–1815.
M. lignescens Iljin, Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 2: 173. 1921.

Biennial to perennial herbs with woody bases. Stems prostrate or decumbent, pubescent with stellate hairs, especially on younger parts. Leaves orbicular-reniform, cordate at base, crenate-denticulate, occasionally shallowly 5(–7)-lobed on elongated branches, sparsely pilose with simple and stellate hairs adaxially and densely so with stellate hairs abaxially; stipules ovate-lanceolate, ca. 5 mm long; petioles 3–15 cm long, stellately villous. Flowers axillary, 3–4 in a fascicle, those on the lower branches occasionally solitary; pedicels, 0.5–5 cm long, unequal in length, much longer than the flower but shorter than the subtending leaf; epicalyx segments linear to linear-lanceolate; calyx 5–8 mm long, stellately pilose; lobes triangular. Petals purplish to pinkish, sometimes white, 10–13 × 3–4 mm, oblong-obovate, retuse, claw pubescent on the margin. Staminal tube 4–5 mm long, pubescent with simple, ± retrorse hairs. Fruit 5–7 mm diam.; mericarps 12–15, pubescent, smooth. Seeds pubescent.

Distribution. Native to Old World, naturalized in America. In our area occurring widely in Kashmir Valley along wastelands, meadows, and cultivated fields from 1,600 m altitude to the alpine zone; also reported from the Jammu and Ladakh regions. It is commonly used as a wild vegetable under the local name "Sotsal."

Additional specimens examined. INDIA. KASHMIR: Srinagar, Habak, *G. N. Javeid 121* (KASH); Womens' College campus, *D. Sethi 101* (KASH); Harwan, *G. Singh 1986* (KASH); Tangmarg, *A. R. Naqshi 599* (KASH); Rainawari, *A. R. Naqshi 8159–60* (KASH); Ganderbal, exposed hill slopes, *G. H. Dar 2325–27* (KASH); Zakura, 1,630 m, *G. H. Dar 1053–57* (KASH), *1058* (PF); Srinagar (Lal Bazar), *A. R. Naqshi 8166* (KASH); Sonamarg, *G. H. Dar 7679–7682* (KASH); Gund-Haknar, *G. H. Dar 8644* (KASH); Hang (Sonamarg), *G. H. Dar 8643* (KASH); *Chatterhama* (Srinagar), *G. H. Dar 8841* (KASH); Manigam (Lar), *G. H. Dar 5328–31* (KASH).

A number of varieties and forms of this species can be distinguished in our area. However, their recognition is deferred until a satisfactory monographic work on the species within the area is available.

These plants are said to be used in medicine due to the high content of mucilage in the foliage and roots. The leaves contain vitamin C and provitamin A, while the seeds contain about 18% of a light green oil. A decoction of leaves and roots is used as a gargle for treatment of inflammatory conditions of the respiratory tract and as fomentations for external treatment of skin inflammations, ulcerations, and swellings. An infusion of leaves with milk is used for its diuretic effect. A decoction of the leaves is used as an enema to relieve constipation (Dar et al., 1984). The petioles are used for treating babies, instead of glycerine clysters.

6. Malva microcarpa Pers., Syn. Pl. 2: 251. 1806; Riedl in K. H. Rechinger, Fl. Iran. 120: 27. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 41. 1979. *Malva parviflora* var. *microcarpa* (Pers.) Loscos, Trat. Pl. Aragon 2: 203. 1877; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 481. 1972. TYPE: Herb. *Persoon s.n.* (holotype, L).

Annual herbs. Stems prostrate or ascending, stellately villous. Leaves orbicular-reniform, cordate at base, 3–7-angular, crenate to serrate, glabrescent; stipules ovate or lanceolate, 2–4 mm long; petioles 1–10(–25) cm long. Flowers axillary, solitary or paired, rarely more but then never compact; pedicels 0.3–2 cm long, distinctly visible; epicalyx segments linear; calyx 5–6 mm long, slightly enlarged and rotate in fruit; lobes triangular, acute to acuminate. Petals white (sometimes with pinkish tips), equaling or slightly exceeding the calyx. Staminal tube 1–2 mm long, glabrous. Fruit 3–6 mm diam.; mericarps 9–10, glabrous, reticulate, with slightly winged margins. Seeds glabrous.

Distribution. Native to the Mediterranean Region, Malaysia, Iran, Afghanistan, and Pakistan.

In our area it has been collected, infrequently, from Jammu.

Additional specimen examined. INDIA. JAMMU: Tilo Talab, common along drains; annual herbs, mucilaginous when bruised, flowers white, *B. M. Sharma 389* (KASH).

First record for India.

7. **Malva parviflora** L., Demonstr. Pl. 18. 1758; Sp. Pl. 2nd Edition. 269. 1763; Masters in Hook. f., Fl. Brit. India 1: 321. 1874; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 63. 1949; Kitamura, Fl. Afghan. 271. 1960; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 481. 1972; Riedl in K. H. Rechinger, Fl. Iran. 120: 23. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 42. 1979. TYPE: described from Barbary (north Africa), *Linn. Herb. no. 870/17* (holotype, LINN).

Annual herbs; stems erect or prostrate-ascending, sparsely pubescent with stellate hairs to glabrescent. Leaves orbicular-reniform, cordate at base, crenate-serrate, often shallowly 3–7-lobed, sparsely pubescent with simple or 2-fid hairs on the adaxial surface, usually stellately pilose abaxially; stipules lanceolate to ovate, 2–5 mm long; petioles 3–17 cm long, longer than blade, simple and stellately pubescent, especially apically. Flowers usually in compact axillary fascicles; pedicels 3–5 mm long, generally not visible, subglabrous. Epicalyx segment linear. Calyx 3–5 mm long, pilose with stellate hairs, accrescent in fruit to ca. 1 cm; lobes triangular, mucronate. Petals white, sometimes pinkish at the tips, usually shorter than or equaling the calyx, oblong, slightly narrowed at base, scarcely notched at apex, claw glabrous. Staminal tube ca. 2 mm long, glabrous. Fruit 5–6 mm diam.; mericarps 9–10, glabrous, with raised reticulation and toothed, winglike margins. Seeds glabrous.

Distribution. Mediterranean Region, Anatolia, Iran, Iraq, Afghanistan, Pakistan, India, and Arabia. Many workers (Javeid, 1970; Stewart, 1972; Sharma & Kachroo, 1981) have reported this species from our area, but there is no authentic specimen, because all the specimens under this name turned out to be either *Malva neglecta* or *M. microcarpa*.

8. **Malva mohileviensis** Downar, Bull. Soc. Mosc. 1: 177. 1861; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 64, pl. 3, f. 1. 1949; Abedin in Nasir & Ali, Fl. W. Pak. 130: 43. 1979. TYPE: vicinity of Mogilev (LE).

Annual herbs; stems erect, ± purplish, pubescent with simple and 2-fid hairs, especially towards the apex. Leaves suborbicular, cordate at base, 5–7-lobed, serrulate to crenulate-dentate, sparsely pubescent with simple or 2-fid hairs on the upper surface, more pubescent and with mixed stellate hairs beneath; stipules lanceolate-ovate, 3–5 mm long; petioles 2–9 cm long. Flowers axillary, in fascicles of 4–7(–many); pedicels 5–10 mm long. Epicalyx segments linear, green to purple. Calyx ca. 5 mm long, green to purple, glabrescent, accrescent and scarious in fruit, the lobes triangular. Petals pinkish, about twice the length of calyx, obovate, retuse, claw slightly pubescent. Staminal tube ca. 4 mm long, retrorsely pubescent. Fruit ca. 5 mm diam.; mericarps 12, glabrous, smooth on the back, transversely rugose along the rounded margins, radially wrinkled on the sides. Seeds minutely puncticulate.

Distribution. Japan, China, U.S.S.R., Pakistan. In our area it occurs infrequently in Kashmir and Ladakh.

Additional specimens examined. INDIA. KASHMIR: Sonamarg, along roadsides just near the Shutkar Bridge, *G. H. Dar 8483* (PF), *8484* (KASH). LADAKH: Leh, *A. R. Naqshi & G. N. Dar 7217* (KASH).

In Tibetan medicine the flowers of this species are used as a diuretic. The leaves and young shoots can be used as a salad or as a vegetable. It is a valuable forage plant due to a high protein content and tender consistency. It has been estimated that this species contains twice as much protein as any other forage plant, so it increases the yield and quality of milk when fed to cows. First record for India.

9. **Malva verticillata** L., Sp. Pl. 689. 1753; Masters in Hook. f., Fl. Brit. India 1: 320. 1874; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 68. 1949; Hu, Fl. China, Malvaceae. 5. 1955; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 481. 1972; Riedl in K. H. Rechinger, Fl. Iran. 120: 22. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 43. 1979. LECTOTYPE: *Linn. Herb. no. 870/26* (LINN).

9a. **Malva verticillata** var. **verticillata** [see Abedin in Nasir & Ali, Fl. W. Pak. 130: 45. 1979].

M. chinensis Miller, Gard. Dict. 8th Edition. 670. 1768.

Annual or biennial herbs; stems erect, green to purplish, sparsely stellately pubescent. Leaves usually orbicular, cordate to subtruncate at base, usually 5-lobed, coarsely crenate-dentate, glabrescent on the adaxial surface with simple, or 2-fid hairs, more pubescent abaxially with stellate, simple, or 2-fid hairs; stipules lanceolate, 5 mm long; petioles 4–20(–24) cm long, glabrescent, with villous grooves. Flowers axillary, subsessile, in dense and compact fascicles of 5–many; pedicels 5–8 mm long, ± of equal length, all hidden by flowers or fruits. Epicalyx segments linear or linear-lanceolate, acute. Calyx 5–6 mm long, sparsely hirsute with stellate hairs, prominently reticulate-veined, accrescent in fruit to 10–15 mm, the lobes triangular, with long-ciliate margins. Petals purplish, 7–9 mm long, scarcely notched, the claws glabrous. Staminal tube 3–5 mm long, glabrous or pubescent with simple hairs towards the apex. Fruit 5–7 mm diam., enclosed in accrescent calyx, the mericarps 10–12, glabrous, smooth on the back, rugose along the rounded margins, radially striate on the sides. Seeds glabrous.

Distribution. China, Europe, Asia, Ethiopia, Egypt. In our area commonly cultivated in the Kashmir Valley for its leaves which are used as a vegetable, also collected from Jammu and Ladakh. Vernacular names: "Parim sotsal", "Bagh sotsal."

Additional specimens examined. INDIA. KASHMIR: university campus, *A. R. Naqshi 107* (KASH); Chatterhama (Srinagar), *G. H. Dar 7562* (KASH, PF); Beehama, *G. H. Dar 7563–65* (KASH); Hirpur (Pir Panjal), *G. A. Gammie s.n.* (K, fide Abedin, 1979). JAMMU: Poonch Dist., *A. Rashid, E. Nasir & RRS 25586* (RAW).

9b. Malva verticillata var. **rafiqii** S. Abedin in Nasir & Ali, Fl. W. Pak. 130: 45. 1979. TYPE: Hazara District, Pakistan, *S. Abedin & M. Qaiser 9109* (holotype, KUH).

Malva verticillata var. *chinensis* sensu Hu, Fl. China, Malvaceae. 6, tab. 15, f. 5. 1955. Not *M. chinensis* Miller.

Differs from the preceding variety in having smaller habit, comparatively thinner stems, smaller and shallowly 3–5-lobed leaves with shorter (1.5–10 cm) petioles, flowers in looser fascicles of 2–6, pedicels of unequal length, 10–20(–25) mm long, the longer ones not hidden by the clusters of flowers or fruits.

Distribution. China and Pakistan and in the Kashmir Valley.

Additional specimens examined. INDIA. KASHMIR: Ganderbal, *G. H. Dar 1762–66* (KASH); Haknar (Gund), 2,050 m, *G. H. Dar 8640* (PF), *8641–8642* (KASH).

8. ALTHAEA L., Sp. Pl. 686. 1753; Gen. Pl. 5th Edition. 307. 1754.

About 12 species, distributed in Africa, Asia, and Europe; two species are recorded from our area.

1a. Leaves entire to shallowly 3-lobed; corolla almost twice the length of calyx; staminal tube pubescent; mericarps 15–25, pubescent throughout; seeds smooth, not verrucose .... 1. *A. officinalis*
1b. Leaves deeply 3–5-fid or parted; corolla usually less than twice the length of calyx; staminal tube almost glabrous; mericarps 12–18, pubescent towards apex, glabrous at base; seeds minutely whitish-verrucose on back .... 2. *A. broussonetiifolia*

1. Althaea officinalis L., Sp. Pl. 686. 1753; Masters in Hook. f., Fl. Brit. India 1: 319. 1874; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 131. 1949; Kitamura, Fl. Afghan. 270. 1960; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 417. 1972; Riedl in K. H. Rechinger, Fl. Iran. 120: 39. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 46. 1979. LECTOTYPE: *Linn. Herb. no. 863/1* (LINN).

Perennial herbs, stems erect, with densely tomentose branches. Leaves triangular to broadly ovate, acute, base rounded or truncate, the margin irregularly serrate-dentate, sometimes superficially 3-lobed, densely pubescent on both surfaces, especially beneath; stipules linear-lanceolate, caducous. Flowers axillary, borne on many-flowered peduncle; pedicels 2–10 mm long. Epicalyx segments 8–12, linear. Calyx with the lobes connate below the middle, 5-lobed, 6–12 mm long, persistent. Corolla pinkish to white, 2–3 cm diam.; petals broadly obovate to oblong-obovate, 1.2–2.2 cm long, slightly notched at apex, the claw with ciliate margin. Staminal tube cylindric, with short-papillose hairs. Mericarps 15–25, minutely stellate-pubescent throughout. Seeds smooth, glabrous.

Distribution. Europe, Palestine, Syria, Turkey, Iran, Afghanistan, Pakistan, India. Though the species has been collected in the Kashmir Valley, it appears to be rare in our area now. A report from Baramulla, Kashmir is in Stewart (1972).

Additional specimens examined. INDIA. KASHMIR: Bandipur, *Jacquemont 1082*; Pampore, *Drum 15029.*

Abedin (1979) described the fruit of this species as glabrous in his key, perhaps an error.

2. Althaea broussonetiifolia Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 678. 1949. TYPE: Stalingrad (Olim Zarizyn), *Wunderlich 1839* (LE).

Perennial herbs; stems ± erect, densely stellate-pubescent on almost all parts. Leaves deeply 3–5-fid or -parted with irregularly dentate, oblong-lanceolate lobes, densely pubescent on both surfaces, especially beneath; stipules linear, caducous. Flowers on axillary and terminal racemose-paniculate peduncles; pedicels much shorter than calyx. Epicalyx segments 7–9, lanceolate. Calyx lobes 5, connate below the middle, 6–10 mm long, persistent. Corolla pink, 2–2.5 cm diam.; petals obovate to oblong-obovate, 8–15 mm long, slightly notched at apex, the claw fringed-pubescent. Staminal tube cylindric, almost glabrous. Mericarps 12–18, stellate-pubescent except at base. Seeds sparsely and minutely whitish-verrucose, especially in the lower part.

Distribution. U.S.S.R. The taxon, hitherto considered endemic to the U.S.S.R., has been collected in the Kashmir Valley. Apparently it is rare in our area.

Additional specimens examined. INDIA. KASHMIR: Narbal-Suzeath, on the borders of vegetable gardens, *A. R. Naqshi 8167* (PF), *8168* (KASH); Shalteng (Srinagar), *G. N. Javeid 596* (KASH).

First record for Indian subcontinent.

9. **ALCEA** L., Sp. Pl. 687. 1753; Gen. Pl. 5th Edition. 307. 1754.

About 60 species distributed chiefly in eastern Mediterranean Region; represented in our area by three species, all cultivated or escapes from cultivation.

KEY TO THE SPECIES OF *ALCEA* IN KASHMIR AND JAMMU STATE

1a. Upper leaves undivided or shallowly lobed.
  2a. Stem and branches sparsely setose with stellate hairs when young, ± glabrous at maturity .... 1. *A. rosea*
  2b. Stem and branches densely bristly with persistent stellate hairs .... 3. *A. pallida*
1b. Upper leaves palmately lobed almost to the base .... 2. *A. lavateriflora*

1. Alcea rosea L., Sp. Pl. 687. 1753; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 126. 1949; Zohary, Israel J. Bot. 12: 12. 1963; Abedin in Nasir & Ali, Fl. W. Pak. 130: 49. 1979. TYPE: *Linn Herb. no. 869/1* (LINN).

Biennial (or perennial) herbs; stem erect, sparsely setose with stellate hairs when young, ± glabrous at maturity. Leaves orbicular-ovate, cordate at base, obtuse at apex, the lower ones shallowly 5–7-lobed, the upper leaves undivided or shallowly 3-lobed, crenate-dentate, scabrous with stellate pubescence on both surfaces; stipules ovate, tricuspidate. Flowers axillary, solitary or subfasciculate, the inflorescences spikelike towards the apices due to shorter pedicels and gradual diminution of the subtending leaves into leaflike bracts. Epicalyx 6–7-lobed, the lobes ovate-lanceolate. Calyx campanulate, 5-lobed, densely stellate-pubescent like the epicalyx. Corolla 5–8 cm diam., of various colors but usually red; petals obovate-cuneate, notched at apex, the claw barbate. Staminal tube 5-angled, glabrous. Fruit depressed, covered by persistent calyx; mericarps 20–40, stellate-pubescent, channeled and winged dorsally. Seeds reniform, pubescent.

Distribution. According to Zohary (1963), "Wild *A. rosea* L. seems to be indigenous almost exclusively on the Aegean islands and the adjacent Balkan Peninsula. The areas of its origin are no doubt the northeastern Mediterranean countries, but not China which is beyond the natural range of the genus." *Alcea rosea* is cultivated as an ornamental almost everywhere. In the Kashmir Valley it often grows as an escape from cultivation, together with the two following species. Sharma & Kachroo (1981) reported this species from Batote, Jammu.

Additional specimens examined. INDIA. KASHMIR: Srinagar, *G. N. Javeid 33* (KASH); Sind Valley, Prang, *G. H. Dar 6217* (KASH); Ganderbal, *G. H. Dar 6619* (KASH, PF); university campus, *A. R. Naqshi & G. N. Dar 8169* (KASH); women's college campus, *D. Sethi 30* (KASH).

The flowers and seeds of this species are said to have diuretic properties, and the roots and seeds are used as demulcents. According to Dar et al. (1984), a decoction of the roots boiled with water and milk is applied externally for treating dermatitis and goiter; it is also given to pregnant women to ease delivery. A decoction of flowers with milk and "gud" is reportedly applied for boils.

2. Alcea lavateriflora (DC.) Boiss., Fl. Orient. 1: 828. 1867; Riedl in K. H. Rechinger, Fl. Iran. 120: 65. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 50. 1979. *Althaea lavateriflora* DC., Prodr. 1: 437. 1824; Kitamura, Fl. Afghan. 270. 1960. TYPE: Prope Seydeol rodius Lipain, *Meryon.*

Alcea persarum Bornm. sensu Zohary, Israel. J. Bot. 12: 15. 1963.

This species resembles *A. rosea* L. in habit and flowers but differs chiefly in having deeply palmate-lobed leaves, especially towards the apices of branches, and in having narrower calyx lobes.

Distribution. Turkey, Greece, and Bulgaria; occasionally cultivated in Iraq, Iran, Pakistan, and elsewhere.

Additional specimens examined. INDIA. KASHMIR: university campus, *A. R. Naqshi & G. N. Dar 8170* (KASH); Ganderbal, Power House, *G. H. Dar 6620–6621* (KASH); Prang, *G. H. Dar 6216* (KASH, PF).

3. Alcea pallida (Waldst. & Kit.) Besser, Enum. Pl. 2: 872. 1822; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 118. 1949; Zohary, Israel J. Bot. 12: 11. 1963; Abedin in Nasir & Ali, Fl. W. Pak. 130: 50. 1979. *Althaea pallida* Waldst. & Kit. in Willd., Sp. Pl. 3: 773. 1800; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 477. 1972. TYPE: described from Hungary (Prague).

This species also resembles *A. rosea* L. in general habit, leaves, and flowers but differs in having dense, persistent, stellate hairs on the stem and branches and in having transversely rugose wings on the mericarps.

Distribution. Central Europe, Balkan Peninsula, and Asia Minor; cultivated elsewhere.

Additional specimens examined. INDIA. KASHMIR: Sind Valley, Ganderbal, *G. H. Dar 6618* (KASH, PF).

All species of *Alcea* L. are raised as ornamentals in the Kashmir Valley under the local name of "Saz Posh." They are often grown in close associations. The three species were, until now, referred to *Althaea rosea* (L.) Cav. However, the genera *Alcea* and *Althaea* differ so markedly, particularly in the structures of the staminal column and carpels, that they are no longer considered a single genus. In fact *Alcea* approaches more closely *Lavatera* than *Althaea*.The species of *Alcea* contain 12–14% fiber in the stem and are suitable for paper production. The flowers contain mucilage and are used for gargling. They are also taken internally as an emollient for treatment of catarrhal gastric complaints. A dye extracted from the petals is used for coloring wines, vinegar, liquors, food products, silk, and wool.

10. LAVATERA L., Sp. Pl. 690. 1753; Gen. Pl. 5th Edition. 308. 1754.

Some 45 species, chiefly Mediterranean, but extending to the Canaries, northwest Himalaya, central Asia, eastern Siberia, Australia, and the U.S.A. (California); represented in Jammu and Kashmir by a single species.

Lavatera kashmiriana Cambess. in Jacquem., Voy. Inde 4: 29, tab. 32. 1844; Masters in Hook. f., Fl. Brit. India 1: 319. 1874; Iljin in Shishkin & Bobrov, Fl. U.R.S.S. 15: 78. 1949; Riedl in K. H. Rechinger, Fl. Iran. 120: 14. 1976; Singh & Kachroo, Forest Fl. Srinagar. 151. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 51. 1979. TYPE: India. Kashmir: *Jacquemont s.n.* (K).

Malva cachemiriana (Cambess.) Alef., Osterr. Bot. Z. 12: 258. 1862.

Lavatera cachemiriana var. *haroonii* sensu Abedin in Nasir & Ali, Fl. W. Pak. 130: 52. 1979.

Lavatera thuringiaca L. var. *macromera* Litw., Russk. Bot. Zurn. 7: 117. 1922. *L. thuringiaca* subsp. *macromera* (Litw.) Iljin, Bot. Syst. Leningrad 5: 7. 1924.

Perennial, densely stellate-pubescent herbs with erect terete stems. Leaves orbicular, the base truncate to slightly cordate, margin crenate-serrate, 3–7-angled or palmatifid to parted; stipules foliaceous, persistent. Flowers solitary, axillary; pedicels 3–6 cm long, articulate near the apex. Epicalyx segments 3, foliaceous, connate in the lower half, ovate-orbicular, mucronate, accrescent in fruit. Calyx 5-lobed, longer than epicalyx, the lobes triangular to deltoid, accrescent in fruit. Corolla 4–7.5 cm diam., pink-lilac; petals obovate, deeply notched. Staminal tube densely pubescent at base, antheriferous in the upper half. Fruit discoid; mericarps 20–25, glabrous, ± rugose. Seeds glabrous.

Distribution. India (Himalayan Mountains), Pakistan, Afghanistan, U.S.S.R., Iran. Stewart (1972) reported it for Poonch, Jammu.

Additional specimens examined. INDIA. KASHMIR: Sonamarg, *A. R. Naqshi 3975* (KASH); Aharbal, *A. R. Naqshi 7523* (KASH); Baltal, *A. R. Naqshi 4010–12* (KASH); Harwan, *G. Singh 1984* (KASH); Hadurah (Ganderbal), *G. H. Dar 2176* (KASH); Naranag, *G. H. Dar 4142–43, 45* (KASH), *4144* (PF); Soraphraw (Sind Valley), *G. H. Dar 8594* (PF), *8595–96* (KASH); Najwan (Kangan), *G. H. Dar 6827* (KASH); Sonamarg, *G. H. Dar 7787* (KASH), *7788* (PF); Harwan, *G. N. Javeid 361* (KASH); Ferozpur Nullah (Gulmarg), *U. Dhar 1258* (KASH).

In Kashmir, this species serves as a vegetable to hill tribes under the name of "Wan Sotsal." It can be raised as an ornamental. Its seeds contain about 12% oil, and a small amount of vitamin C is present in the stem and leaves. The plant has the capacity of yielding a good quality of fiber for binder twine, string, and ropes.

Based on leaf pubescence Abedin (1979) recognized two varieties as follows: adaxial surface of leaf with dense stellate hairs (var. *cachemiriana*) and adaxial surface of leaf except veins with simple and fascicled hairs (var. *haroonii*). Close scrutiny of a number of collections from different parts of our state, however, revealed that the varietal distinction does not hold up. The difference in the pubescence of upper leaf surface does not seem to be constant, and intermediate conditions are not uncommon.

11. **ABUTILON** Miller, Gard. Dict. Abr. 4th Edition. 1: AB. 1754; 8th Edition. 1768.

Over 150 species distributed in the tropics and subtropics of both hemispheres; represented in our area by four species.

KEY TO THE SPECIES OF *ABUTILON* IN JAMMU AND KASHMIR STATE

- 1a. Corolla 2.5–3.5 cm diam.; staminal tube 5–8 mm long; mericarps (14–)15–20 ..... 4. *A. indicum*
- 1b. Corolla 1–2 cm diam.; staminal tube 1–4 mm long; mericarps 10–16.
  - 2a. Annual herbs; staminal tube glabrous ..... 2. *A. theophrastii*
  - 2b. Perennial suffruticose herbs; staminal tube stellate-pubescent to puberulent.
    - 3a. Calyx lobes deltoid-ovate, erect in fruit; petals 10–12 mm long; fruit cylindrical; mericarps usually 10; seeds furfuraceous-dotted ..... 1. *A. ramosum*
    - 3b. Calyx lobes lanceolate, reflexed in fruit; petals 7–9 mm long; fruit ovoid; mericarps 13–16; seeds stellately pilose ..... 3. *A. bidentatum*

1. **Abutilon ramosum** (Cav.) Guill. & Perr. in Guill. et al., Fl. Seneg. Tent. 1: 68. 1831; Masters in Hook. f., Fl. Brit. India 1: 328. 1874; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 477. 1972; Abedin in Nasir & Ali, Fl. W. Pak. 130: 55. 1979; Sharma & Kachroo, Fl. Jammu 1: 111. 1981. *Sida ramosa* Cav., Diss. 1. 28, tab. 6, f. 1. 1785. TYPE: Senegal, *Adanson* (holotype, MA, photo; isotype, P).

Abutilon sparmanoides Guill. & Perr. in Guill. et al., Fl. Seneg. Tent. 1: 70. 1831.
A. elaeocarpoides Webb, Fragm. Fl. Aethiop. 53. 1854.
A. sidoides A. Gibson, Bombay Fl. 18. 1861.

Perennial, suffruticose herbs, tomentose with stellate and long, spreading hairs. Leaves broadly ovate, the base cordate, the apex acuminate, the margin coarsely crenate-serrate, often 3-lobate; stipules filiform to linear. Flowers axillary or terminal, solitary or paired or divided above dichotomously as in a cyme; pedicels shorter than petioles. Calyx cupular, 5-lobed; lobes deltoid-ovate, acuminate-cuspidate. Corolla yellow, ca. 1.5 cm diam.; petals 10–12 mm long. Staminal tube very short, puberulous. Fruit cylindrical; mericarps usually 10, biaristate with awns ca. 2 mm long. Seeds 2–3 per mericarp, furfuraceous-dotted.

Distribution. Tropical Africa, Arabia, Pakistan, and India. Confined in our area to the Jammu Province. For a Billawar report see Lambert (1933).

Additional specimen examined. INDIA. JAMMU: Ram Nagar, among *Carissa spinarum* L., tomentose green shrub with yellow flowers, *B. M. Sharma 674* (KASH).

2. **Abutilon theophrastii** Medicus, Malvenfam. 28. 1787; Hu, Fl. China, Malvaceae. 31. 1955; Kitamura, Fl. Afghan. 269. 1960; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 477. 1972; Riedl in K. H. Rechinger, Fl. Iran. 120: 7. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 61. 1979. LECTOTYPE: India: Herb. Cliff. (BM).

Sida abutilon L., Sp. Pl. 685. 1753.
Abutilon avicennae Gaertner, Fruct. Sem. Pl. 2: 251, tab. 135, f. 1. 1791; Masters in Hook. f., Fl. Brit. India 1: 327. 1874.
A. behrianum F. Muell. in Trans. & Proc. Philos. Inst. Victoria 1: 13. 1855.

Annual, velutinous herbs. Leaves orbicular or broadly ovate, the base deeply cordate, the apex acuminate, the margin crenulate or undulate; stipules caducous. Flowers axillary, solitary or in few-flowered terminal racemes; pedicels shorter than petioles. Calyx 5-lobed; lobes ovate or lanceolate, acute. Corolla yellow, 1–2 cm diam.; petals 1–1.2 cm long, obovate. Staminal tube 2–4 mm long, glabrous. Fruit hemispherical; mericarps 12–16, strongly birostrate with awns 3–5 mm long. Seeds 3 per mericarp, stellate-pilose.

Distribution. Native to India, introduced and naturalized in northern America, northern Asia, and westward to southern Europe. Confined in our area to the Kashmir Valley, where this is the only *Abutilon* growing now, although some other species have been reported by earlier workers. Vernacular name: "Yachkad."

Additional specimens examined. INDIA. KASHMIR: university campus, *A. R. Naqshi 189* (KASH); Srinagar, *A. R. Naqshi 3981* (KASH); Narbal, *A. R. Naqshi & G. N. Dar 8171* (PF), *8172* (KASH); Shalteng, *G. N. Javeid s.n.* (Sind Valley) (KASH); *G. H. Dar 8820* (KASH); Jhelum River, cultivated fields, *R. R. & I. D. Stewart 4980* (RAW).

Abutilon, especially *A. theophrastii*, has been long cultivated for its coarse fiber suitable for making ropes, sackcloth, binder twine, string, and fishing nets. Its fiber is fairly tough, water resistant, and brittle. In America this is said to be preferred over jute and Manila hemp. The stem is used for paper manufacture and as fuel. The seeds yield up to 30% of a yellow, tasteless, and odorless oil, which approaches cotton oil, sesame oil, and peanut oil in its chemical composition. The oil is suitable for use in food and for hydrogenation. Inferior grades may be used as varnish oil and in soap manufacture. The flowers are used for coloring wines and, in China, for making ink. A decoction of roots and infusion of flowers is used internally and externally against inflammatory conditions.

3. Abutilon bidentatum Hochst. ex A. Rich., Tent. Fl. Abyss. 1: 68. 1847; Masters in Hook. f., Fl. Brit. India 1: 326. 1874; Kitamura, Fl. Afghan. 269. 1960; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 475. 1972; Riedl in K. H. Rechinger, Fl. Iran. 120: 5. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 63. 1979. TYPE: Abyssinia, prope Aguar, prov. Modat, *Schimper 1003* (K).

Abutilon cornutum Dalz. ex T. Cooke, Fl. Bombay 1: 98. 1901.
A. pakistanicum Jafri et Ali in Jafri, Fl. Karachi. 220. 1966.

Perennial, suffruticose herbs, canescent-tomentose with stellate, weak, spreading hairs. Leaves broadly ovate, the base deeply cordate, the apex acute-acuminate, the margin crenate-dentate, rarely 3-angular; stipules filiform. Flowers solitary, axillary; pedicels longer or shorter than petioles. Calyx 5-lobed, slightly accrescent; lobes lanceolate, ultimately reflexed. Corolla pale yellow to yellow, 1–1.5 cm diam.; petals 7–9 mm long, obovate. Staminal tube 2–3 mm long, stellate-pubescent. Fruit ovoid; mericarps 13–16, acute-acuminate, awn 1–2 mm long. Seeds 3 per mericarp, sparsely pilose with stellate hairs.

Distribution. India, Pakistan, Iran, tropical Africa, and Arabia. Apparently confined to the Jammu region in our area. Stewart (1972) reported it from the Kashmir Valley, but we have not seen any specimens. Also note: Jammu: Billawar (Lambert, 1933: 3; Sharma & Kachroo, 1981: 111); Poonch, Mirpur. Kashmir: Jhelum Valley road; Barsala (Stewart, 1972: 476).

4. Abutilon indicum (L.) Sweet, Hort. Brit. 1st Edition. 54. 1826; Masters in Hook. f., Fl. Brit. India 1: 326. 1874; Hu, Fl. China, Malvaceae. 32. 1955; Ngwe, Union Burma J. Life Sci. 4: 207. 1971; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 476. 1972; Riedl in K. H. Rechinger, Fl. Iran. 120: 6. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 69. 1979; Sharma & Kachroo, Fl. Jammu 1: 111. 1981. *Sida indica* L. in Torner, Cent. Pl. 2: 26. 1756. LECTOTYPE: *Linn. Herb. no. 866/29* (LINN).

Sida populifolia Lam., Encycl. 1: 7. 1783. *Abutilon populifolium* (Lam.) Sweet, Hort. Brit. 1st Edition. 53. 1826. *A. indicum* var. *populifolium* (Lam.) Wight & Arn. ex Masters in Hook. f., Fl. Brit. India 1: 326. 1874.
A. indicum var. *microphyllum* Hochr., Annuaire Conserv. Jard. Bot. Genève 6: 20. 1902.
A. badium Husain & Baquar, Phyton 15: 229. 1974.

Perennial, suffruticose herbs to subshrubs, canescent with stellate hairs; branches and petioles generally purple on one side. Leaves broadly ovate, the base cordate, the apex acute or acuminate, the margin coarsely dentate, sometimes 3-angular; stipules linear. Flowers solitary, axillary; pedicels longer than petioles. Calyx 5-lobed, not or slightly accrescent in fruit; lobes lanceolate to ovate, mucronate, ultimately reflexed. Corolla orange-yellow to yellow, 2.5–3.5 cm diam.; petals 1–1.5 cm long, obovate. Staminal tube 5–8 mm long, stellate-hirsute. Fruit ovoid-truncate; mericarps (14–)15–20, very short-awned, erect at maturity. Seeds 3 per mericarp, minutely stellate-pilose.

Distribution. Tropics and subtropics of the New and Old worlds. Confined to the Jammu region in our area.

Additional specimens examined. INDIA. JAMMU: Ram Nagar forest, common along hedges; erect shrubs, profusely branched, flowers orange-yellow, *B. M. Sharma 110* (KASH). KASHMIR: *Falconer 273* (fide Stewart, 1972: 476).

According to Ngwe (1971), the bark of this plant is used as an anthelmintic and the roots as a diuretic. The seeds are utilized in the treatment of piles and coughs, and as emollients and demulcents. The leaves are also said to be medicinal.

12. SIDA L., Sp. Pl. 683. 1753; Gen. Pl. 5th Edition. 306. 1754.

About 150 species distributed in the tropics and subtropics of both hemispheres; represented in our area by five species.

Key to the Species of *Sida* in Jammu and Kashmir State

- 1a. Branches, petioles, pedicels, and calyx pubescent with stellate hairs mixed with simple, spreading hairs up to 3 mm long.
  - 2a. Leaves cordate, palmately nerved; calyx 4–5 mm long; fruit 3–4 mm diam.; mericarps 5, muticous with pilose mucro .... 1. *S. cordata*
  - 2b. Leaves usually ovate, suborbicular-subcordate, or lanceolate, penninerved; calyx 5–10 mm long; fruit 5–8 mm diam.; mericarps 9–10, birostrate with apical awns 3–5 mm long covered with stiff reflexed hairs .... 4. *S. cordifolia*
- 1b. Branches, petioles, pedicels, and calyx pubescent with stellate hairs only.
  - 3a. Leaves ovate-oblong; calyx tube subangular; corolla white, 1–1.5 cm diam.; mericarps 7–8, coriaceous; awns connivent, ± inflexed; seeds farinose .... 5. *S. ovata*
  - 3b. Leaves elliptic, obovate, oblong or rhomboid; calyx tube not angular; corolla yellow, up to 1 cm diam.; mericarps 5, membranous; awns not connivent, erect; seeds not farinose.
    - 4a. Leaves 1–6.5 × 0.6–5 cm; flowers subfasciculate; pedicels in fruit up to 1 cm long; mericarps densely stellate-pilose all over .... 2. *S. yunnanensis*
    - 4b. Leaves 1–2 × 0.5–1.2 cm; flowers solitary (–paired); pedicels in fruit 1–2 cm long; mericarps pubescent at apex only .... 3. *S. alba*

1. Sida cordata (Burm. f.) Borssum Waalkes, Blumea 14: 182. 1966; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 483. 1972; Abedin in Nasir & Ali, Fl. W. Pak. 130: 77. 1979; Sharma & Kachroo, Fl. Jammu 1: 109. 1981. *Melochia cordata* Burm. f., Fl. Indica 143. 1768. TYPE: (G).

Sida veronicifolia Lam., Encyl. 1: 5. 1783; Hu, Fl. China, Malvaceae. 23. 1955. *S. humilis* var. *veronicifolia* (Lam.) Masters in Hook. f., Fl. Brit. India 1: 322. 1874.
S. radicans Cav., Diss. 1: 8, tab. 9, f. 3. 1785.
S. morifolia Cav., Diss. 1: 9, tab. 10, f. 2. 1785.
S. humilis Cav., Diss. 5: 277, tab. 134, f. 2. 1788. *S. veronicifolia* Lam. var. *humilis* (Cav.) K. Schum., Fl. Bras. 12(3): 320. 1891.
S. humilocularis L' Hér., Stirp. Nov. 1: 117. bis 56. 1789.

Perennial, prostrate to procumbent herbs. Branches, petioles, pedicels, and calyx stellate-pubescent and villose with long, spreading hairs. Leaves cordate, palmately nerved, stellate-hispid on both surfaces, the hairs adaxially often simple, the apex acuminate, the margin evenly crenate to serrate. Flowers axillary, solitary, fasciculate or subpaniculate; pedicels 1.5–2.5 cm long, in fruit up to 3.5 cm. Calyx 4–5 mm long; lobes deltoid, acuminate. Corolla yellow, 7–10 mm diam., slightly exceeding the calyx. Staminal tube 2–3 mm long, hirsute with simple hairs. Fruit depressed-globose, 3–4 mm diam.; mericarps 5, muticous, membranous, truncate and pilose at apex. Seeds glabrous.

Distribution. Tropical and subtropical regions of the world. Confined in our area to the Jammu region.

Additional specimens examined. INDIA. JAMMU: Gajansu, common; herbs with long trailing branches among hedges, *B. M. Sharma 569* (KASH); Jammu & Kashmir road, *R. R. Stewart s.n.* (RAW).

A distinctive species distinguishable from all other local species by its cordate leaves with palmate venation and by its mucronate mericarps. The species shows great variation in its indumentum and inflorescence. At least two taxa, *Sida veronicifolia* and *S. humilis*, are occasionally recognized on the basis of variation in the inflorescence. In the former the flowers are described as fasciculate or subpaniculate, whereas in the latter they are solitary. However, a close study of herbarium specimens has shown variation in the inflorescence to be continuous, so any division on this basis is not justified. Similarly Cavanilles (Class. Diss. Dec. 5: 277. 1788) distinguished *Sida multicaulis* Cav. and *S. humilis* on the basis of stem pubescence. The former has tomentose-canescent stems, while the latter has scabrous ones. However, Masters (1874) did not see this difference in the Indian material and, accordingly, interpreted *S. multicaulis* as synonymous with *S. humilis*.

2. Sida yunnanensis Hu, Fl. China, Malvaceae. 16, tab. 16, f. 7. 1955; Abedin in Nasir & Ali, Fl. W. Pak. 130: 79. 1979. TYPE: China. Yunnan: *Forrest 11088* (K, BM).

Sida obovata Wallich, Cat. no. 1864. 1828, nom. nud. *S. rhombifolia* var. *obovata* Wallich ex Masters in Hook. f., Fl. Brit. India 1: 324. 1874.

Perennial, suffruticose herbs or undershrubs; almost all parts stellate-pubescent. Leaves variable; elliptic, oblong, oblong-elliptic, rhomboid or obovate, 1–6.5 × 0.6–5 cm, penninerved, the base obtuse or cuneate, the apex obtuse or acutish, margin serrate-crenate, the abaxial surface velutinous, adaxially green and glabrescent. Flowers subfasciculate, axillary and terminating the upper branches; pedicels 3–6 mm long, in fruit up to 1 cm. Calyx 4–6 mm long; lobes triangular, acuminate, carinate at base. Corolla yellow, ± 1 cm diam., slightly longer than calyx. Staminal tube ca.

3 mm long, sparsely hirsute or subglabrous. Fruit depressed-globose, 4–5 mm diam.; mericarps 5, membranous, densely stellate-pilose, birostrate with convergent apical awns less than 1 mm long. Seeds glabrous.

Distribution. Burma, China, India, and Pakistan. In our area confined to the Jammu region, where it is common along roadsides in the Nagrota-Salora area, in orchards at Tilo Talab, Udhowalla, and elsewhere.

Additional specimen examined. INDIA. JAMMU: Nandni, common on roadsides; erect shrubby perennial with yellow flowers, leaves whitish-gray beneath, *B. M. Sharma 688* (KASH).

In having subfasciculate flowers and pubescent birostrate mericarps, this species is close to *Sida spinosa* L. However, the broad elliptic or obovate leaves with very short petioles of the former can easily be differentiated from the ovate-lanceolate, long-petiolate leaves of the latter species.

The plants are said to yield good bast fiber. The roots are used to relieve rheumatism.

3. Sida alba L., Sp. Pl. 2nd Edition. 960. 1753; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 483. 1972; Abedin in Nasir & Ali, Fl. W. Pak. 130: 81. 1979. TYPE: *Linn. Herb. no. 866/2* (LINN).

Perennial, suffruticose, stellate-pubescent herbs. Leaves small, elliptic to obovate, 1–2 × 0.5–1.2 cm, penninerved, evenly crenulate-serrate. Flowers mostly solitary, sometimes paired; pedicels 5–6 mm long, in fruit 1–2 cm. Calyx 4–6 mm long; lobes triangular, acute to acuminate. Corolla yellow, 6–10 mm diam., slightly longer than calyx. Staminal tube 2–3 mm long, hirsute. Fruit depressed-globose, 4–6 mm diam.; mericarps 5, membranous, pubescent at apex, birostrate with convergent apical awns less than 1 mm long. Seeds glabrous.

Distribution. India, Pakistan, and China. In our area apparently confined to Pakistan-occupied area in Jammu Province. Stewart (1972: 483) reported *Sida alba* from Mirpur, Poonch, in Jammu. The *S. alba* of Sharma & Kachroo (1981: 110) has turned out to be *S. yunnanensis*.

The differences between *Sida alba*, *S. spinosa*, and *S. alnifolia* L. seem to be few. In fact, Riedl (1976) cited *S. alba* and *S. alnifolia* as synonyms of *S. spinosa*. However, a thorough study of the type specimens of these three species, together with field observations and analysis of enough herbarium material from different geographical regions is needed to gain an insight into their ranges of variation and to ascertain their relationships.

4. Sida cordifolia L., Sp. Pl. 684. 1753; Masters in Hook. f., Fl. Brit. India 1: 324. 1874; Hu, Fl. China, Malvaceae. 25. 1955; Ngwe, Union Burma J. Life Sci. 4: 207. 1971; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 483. 1972; Riedl in K. H. Rechinger, Fl. Iran. 120: 3. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 83. 1979. TYPE: *Linn. Herb. no. 866/12* (LINN).

Sida herbacea Cav., Diss. 1: 19, tab. 13, f. 1. 1785.
S. holosericea Willd. ex Sprengel, Syst. Veg. 3: 112. 1826.

Perennial, suffruticose herbs; branches, petioles, pedicels, and calyx stellate-hispid and long-villose with simple, spreading hairs ca. 3 mm long. Leaves usually ovate, suborbicular-subcordate or lanceolate, penninerved, the base subcordate or rounded, the apex obtuse or acute, the margin irregularly crenate, uniformly stellate-hirsute on both surfaces, the hairs longer beneath. Flowers axillary, solitary or paired or fasciculate; pedicels 4–7 mm long, in fruit up to 2 cm. Calyx 5–10 mm long; lobes triangular or deltoid, acute to acuminate. Corolla yellow, 1–1.3 cm diam., slightly longer than calyx. Staminal tube 3–5 mm long, hirsute. Fruit subdiscoid, 5–8 mm diam.; mericarps 9–10, stellate-strigose at apex, birostrate with divergent apical awns 3–5 mm long covered with stiff reflexed hairs. Seeds glabrous except hilum.

Distribution. Common in tropical and subtropical countries. Confined to the Jammu region in our area. Jammu: Rajouri (Stewart, 1972: 483); Jammu (Sharma & Kachroo, 1981: 110; Lambert, 1933: 3).

The plant is said to be used as a tonic, emollient, and astringent. The bark is considered useful in urinary troubles.

5. Sida ovata Fôrskal, Fl. Aegypt.-Arab. 124. 1775; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 483. 1972; Riedl in K. H. Rechinger, Fl. Iran. 120: 4. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 86. 1979. TYPE: Arabia, Surdud, *Fôrskal* (C).

Sida grewioides Guill. & Perr. in Guill. et al., Fl. Seneg. Tent. 1: 71. 1830; Masters in Hook. f., Fl. Brit. India 1: 323. 1874.

Perennial, suffruticose herbs with all parts stellate-pubescent. Leaves ovate-oblong, penninerved, the base cuneate or rounded, the apex obtuse, the margin ± entire towards base, obtusely crenate or crenate-serrate elsewhere, stellate-pubescent on both surfaces. Flowers axillary, solitary or paired; pedicels 5–8 mm long, in fruit 1(–1.5) cm. Calyx 4–6 mm long, the tube slightly angular; lobes triangular-deltoid, acuminate. Corolla white, 1–1.5 cm diam., slightly longer than calyx. Staminal tube to 3 mm long, pubescent. Fruit depressed-globose, 3–5 mm diam.; mericarps 7–8, coriaceous, reticulate toward the margins, glabrous except awns; awns 2, connivent, ca. 0.5 mm long, ± inflexed. Seeds farinose.

Distribution. In drier parts of Africa, Arabia, India, and Pakistan. In our area reported from Mirpur (Pakistan-occupied area) in Jammu Province. Note the following reports: Jammu: Poonch, Mirpur (Lambert, 1933: 3; Stewart, 1972: 483; Sharma & Kachroo, 1981: 110).

Sida spinosa L., Sp. Pl. 683. 1753, has been reported from Jammu by Lambert (1933). This is probably based on misidentification, because *Sharma 688* (KASH) under this name turned out to be *Sida yunnanensis.*

13. MALVASTRUM A. Gray, Mem. Am. Acad. Arts n.s. 3: 21. 1849, nom. conserv.

Fourteen species (Hill, 1982), distributed in tropical and subtropical America and in Australia; one species is known from our area.

Malvastrum coromandelianum (L.) Garcke, Bonplandia 5: 297. 1857; Hu, Fl. China, Malvaceae. 11. 1955; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 481. 1972; Riedl in K. H. Rechinger, Fl. Iran. 120: 36. 1976; Abedin in Nasir & Ali, Fl. W. Pak. 130: 89. 1979; Sharma & Kachroo, Fl. Jammu 1: 109. 1981. *Malva coromandeliana* L., Sp. Pl. 687. 1753. LECTOTYPE: *Linn. Herb. no. 870/3* (LINN).

Malva carpinifolia Desr. in Lam., Encycl. 3: 754. 1789.
Malva tricuspidata Aiton, Hort. Kew. 2nd Edition. 4: 210. 1811. *Malvastrum tricuspidatum* (Aiton) A. Gray, Plantae Wright. 1: 16. 1852; Masters in Hook. f., Fl. Brit. India 1: 321. 1874.

Erect to suberect, herbaceous or suffruticose, sparsely pubescent plants with simple and 4-fid, appressed hairs. Leaves ovate to lanceolate-oblong, coarsely serrate, acute or obtuse; stipules linear-lanceolate, acuminate. Flowers axillary, solitary or fascicled, sessile or with pedicels to 5 mm long. Epicalyx segments 3, linear, persistent. Calyx 5-lobed; lobes ovate, acuminate. Corolla yellow, 1.5–2 cm diam.; petals obliquely obovate, pubescent at base. Staminal tube 2–4 mm long, glabrous, antheriferous only at the apical end. Fruit discoid, ca. 6 mm diam.; mericarps 8–14, reniform, sparsely stellate-pilose, tricuspidate with an apical and 2 dorsal awns at the middle, 1-seeded. Seeds reniform, glabrous.

Distribution. Native to North America, distributed in tropical regions of both New and Old worlds. In our area it occurs in the Jammu region only. Lambert (1933: 3) reported the species from Billawar, Jammu, Mirpur.

Additional specimens examined. INDIA. JAMMU: Rihari, common in waste places; semierect gregarious herbs with yellow flowers, *B. M. Sharma 453* (KASH); Poonch, Bufliaz, 2,000 m, *G. Singh & H. Kiran 775.*

14. URENA L., Sp. Pl. 692. 1753; Gen. Pl. 5th Edition. 309. 1754.

About six species distributed in the warmer regions of both hemispheres; represented in our area by a single species.

Urena lobata L., Sp. Pl. 692. 1753; Masters in Hook. f., Fl. Brit. India 1: 329. 1874; Hu, Fl. China, Malvaceae. 73. 1955; Ngwe, Union Burma J. Life Sci. 4: 206. 1971; Stewart in Nasir & Ali, Ann. Cat. Vasc. Pl. W. Pak. & Kashm. 484. 1972; Abedin in Nasir & Ali, Fl. W. Pak. 130: 92. 1979; Sharma & Kachroo, Fl. Jammu 1: 111. 1981. LECTOTYPE: *Linn. Herb. no. 873/1* (LINN).

Urena monopetala Lour., Fl. Cochinch. 418. 1790.
U. diversifolia Schum., Danske Vidensk.-Selsk. Nat.-Math. Afd. 4. 4: 82. 1829.

Erect, herbaceous to suffruticose, ± stellate-tomentose plants. Leaves stellate-pubescent on both surfaces, densely so and ± tomentose abaxially, evenly serrate, with a basal nectary on 1–3 middle nerves beneath, variable in shape and size: the lower leaves usually subcordate or suborbicular, angled or shallowly 3-lobed at the apex; the middle leaves ovate; the upper leaves ovate to ovate-elliptic; stipules linear, caducous. Flowers axillary, usually solitary or in fascicles of 2–3; pedicels 2–3 mm long, in fruit up to 5 mm. Epicalyx segments 5, connate basally, linear-lanceolate. Calyx 5-parted, almost as long as the epicalyx; lobes ovate or ovate-lanceolate, keeled. Corolla pink with a darker center, ca. 2 cm diam.; petals obovate, 1–1.5 cm long. Staminal tube ca. 1.5 cm long, antheriferous in the apical part; anthers subsessile. Carpels 5, style branches and stigmas 10. Fruit subglobose, 1 cm or less diam.; mericarps 5, triangularly obovoid, coriaceous, stellate-pubescent and glochidiate-spiny, shortly awned. Seeds pubescent to glabrescent.

Distribution. Tropical regions of both hemispheres. Confined to the Jammu region in our area. Udhampur (Stewart, 1972: 484).

Additional specimen examined. INDIA. JAMMU: Udhowala Ashram, common in orchards; erect shrubs, 1.2 m high, with pink flowers, leaves variable, *B. M. Sharma 111* (KASH).

A variable species sometimes divided into a number of varieties. Hu (1955), mainly on the basis of leaf shape and the nature and density of hairs, recognized five varieties from China. As we have very little material at hand, no attempt is made to segregate the various varieties at present.

An important fiber-yielding plant. The bast-fiber from the stems is said to be more lasting than jute. In Cuba, Madagascar, Nigeria, and Brazil it is cultivated for making coffee sacks. The roots are used in rheumatism, and the twigs are chewed for relieving toothache.

15. SIDALCEA A. Gray, in Benth. Pl. Hartw. 300. 1848.

About 35 species distributed in western North America, chiefly in California and Oregon; one species has been recorded from our area.

Sidalcea neomexicana A. Gray subsp. **thurberi** (Robinson ex A. Gray) Hitchcock, in Univ. Wash. Publ. Bot. 18. 1957. *S. parviflora* Greene var. *thurberi* Robinson ex A. Gray, Syn. Fl. N. Amer. 11: 305. 1897. TYPE: described from Santa Monica, Los Angeles County, California, U.S.A.

Perennial, erect, glabrescent-glabrous herbs, glaucous throughout. Leaves orbicular, palmately lobed or divided; stipules small, deciduous. Inflorescence terminal, racemose; bracts mostly bifid. Flowers usually polygamodioecious, the pistillate flowers smaller than the perfect or staminate ones. Epicalyx absent; pedicels and calyces stellate-pubescent. Calyx 4–7 mm long; lobes triangular-ovate, acuminate. Corolla rose-purple, 10–16 mm long. Staminal tube biseriate, glabrous except for a few retrorse hairs on the apical portion. Mericarps beaked, reticulate on angles, smooth on back, indehiscent, 1-seeded.

Distribution. From southern Monterey County (Jolon) to eastern San Bernardino County, California, U.S.A.

Additional specimen examined. INDIA. KASHMIR: Srinagar, Emporium Garden, in grassy lands, an escape from cultivation, 4/5/1967, *G. N. Javeid 6* (KASH).

The species is restricted to America, and its occurrence in Kashmir is interesting. It is probable that seeds were brought and raised ornamentally in our area in the 1960s. We have a single specimen identified as "*S. malvaeflora* A. Gray." The specimen comprises a single upper leaf and inflorescence and has been determined by Paul A. Fryxell, as *S. neomexicana* subsp. *thurberi.*

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THREE NEW SPECIES OF *NECTANDRA* FROM THE VENEZUELAN GUAYANA[1]

Jens G. Rohwer[2]

ABSTRACT

Three new species of Nectandra *from the Venezuelan Guayana are described in advance of a complete monograph of the genus.*

During work towards a monograph of the genus *Nectandra*, several undescribed species were found. Three of these occur within the area of the *Flora of the Venezuelan Guayana*, currently in preparation at the Missouri Botanical Garden. Since the treatment of the Lauraceae for this flora is scheduled to appear before the monograph of *Nectandra* will be completed, the new species are published here in anticipation of the more complete work.

All three new species are somewhat similar to *Nectandra globosa* (Aubl.) Mez, and two of them seem to be closely related to it. They differ from *N. globosa* and from each other mainly by striking characters of the indumentum in addition to less conspicuous differences in venation, leaf shape, flowers, and fruits. While any one of these characters alone would hardly warrant recognition on the specific level, their combination makes the entities described below quite distinct.

Nectandra aurea Rohwer, sp. nov. TYPE: Venezuela. Apure: Dtto. San Fernando, mouth of the Río Arauca at its intersection with the Río Orinoco, 66°36′W, 7°24′N, 35 m, 14–15 May 1977 (fl, immature fr), *Davidse & González 13215* (holotype, MO). Figure 1.

Arbor, ad 15 m alta. Ramuli novelli ± angulati vel longitudinaliter exarati, dense rufo- vel aurantio-tomentosi, vetustiores teretes, dense griseo-tomentelli, demum tarde glabrescentes. Folia alterna, lanceolata vel raro lanceolato-elliptica, (7–)9–17(–19) cm longa, 2.8–5(–6) cm lata, nervis lateralibus utroque costae latere 5–7(–9) sub angulo 35–50° prodeuntibus, in sicco rigide chartacea vel subcoriacea, laevia, apice in acumen angustata, basi acuta margine (sub)plano, folia novella supra ± dense et molliter (sed plerumque inconspicue) flavido-tomentella, subtus dense et ± adpresse aureo-sericeo-tomentella, raro axillis nervorum rufo-tomentosa, vetustiora supra praeter costam leviter pubescentem glabrescentia, subtus indumento fere persistente vel tarde deminuente sed demum sparso. Inflorescentiae axillares, breviter thyrsoideae, 2–5(–9) cm longae, pedunculo 1–2(–3) cm longo, dense rufo- vel aurantio-tomentosae, cymis lateralibus 2–4, 1–3(–4)-furcatis. Pedicelli 0.5–2.5 mm longi. Flores 5–8(–9.5) mm diametro. Tepala elliptica, intus papillosa, exteriora interioribus paulo majora, ad 4 mm longa. Stamina papillosa, subsessilia, 0.7–0.9 mm longa, exteriores 6 late pentagona vel quadrato-rhombica, apice paulo producto, obtuso vel late subrotundato, serie prima secunda plerumque paulo latiora, interiores 3 apice late rotundata vel paene truncata. Staminodia parva sed crassiuscula, apice papillosa, inter stamina seriei tertiae ± celata et basi eis connata. Pistillum ± gracile, glabrum, 1.5–2 mm longum, stylo crasso ovarium ± aequante. Receptaculum profunde urceolatum, intus (interdum parce modo et inaequaliter) adpresse pubescens. Fructus (non nisi immaturus notus) ovato-ellipticus. Cupula profunda, campanulata, iam ca. 11 mm diametro et 9 mm profunda, margine integro.

Tree to 15 m. Twigs at first ± angular or longitudinally furrowed, densely covered with curled reddish longer hairs (0.5–1.5 mm long) over an extremely dense layer of very short yellowish hairs, older twigs roundish with the short hairs persistent for a long time and becoming grayish. Leaves alternate, lanceolate or rarely lanceolate-elliptic, (7–)9–17(–19) cm long, 2.8–5(–6) cm wide, with 5–7(–9) pairs of lateral veins diverging at 35–50°, dried laminae stiffly chartaceous to subcoriaceous, smooth (secondaries slightly prominent below), the apex tapering towards a narrow acumen, the base acute, flat or nearly so, young leaves above ±

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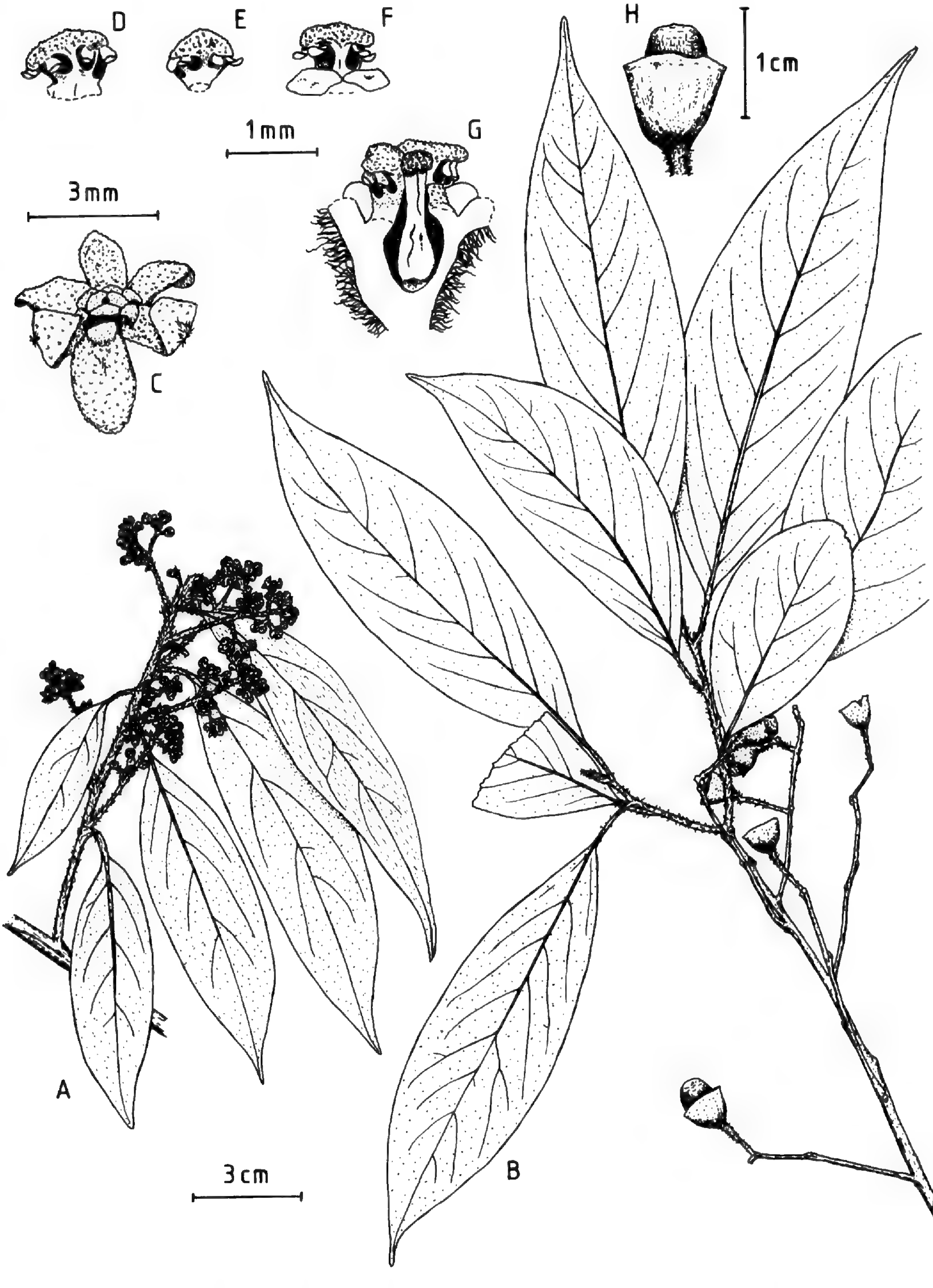

FIGURE 1. Nectandra aurea.—*A. Habit, flowering branch.—B. Habit, fruiting branch.—C. Flower, seen obliquely from above.—D. Stamen of the first whorl, seen from inside.—E. Stamen of the second whorl, seen from inside.—F. Stamen of the third whorl, seen from outside.—G. Receptacle with ovary, staminode, and two inner stamens, cut open, tepals and outer stamens removed.—H. Fruit. Vouchers: A,* Davidse & González 14492; *B–H,* Davidse & González 13215.

densely yellowish pubescent (often inconspicuous but soft to the touch), below densely and often shining golden-pubescent, hairs predominantly appressed but with a few ± erect reddish hairs, these rarely forming indistinct tufts in the vein axils, older leaves above glabrescent except for some hairs on midrib, below with an almost persistent indumentum, or very slowly subglabrescent. Inflorescences short thyrsoids, axillary to distal leaves or occasionally some of them axillary to cataphylls below the terminal bud, covered with the same kind of indumentum as the young twigs, 2–5(–9) cm long with a peduncle of 1–2(–3) cm, with 2–4 lateral cymules below a terminal cluster of cymules, the cymules branched 1–3(–4) times. Pedicels 0.5–2.5 mm long. Flowers 5–8(–9.5) mm diam. Tepals elliptic, up to 4 mm long, papillose on the inside, the outer ones slightly larger than the inner ones. Stamens papillose, subsessile, 0.7–0.9 mm long, the outer 6 broadly pentagonal to broadly rhombic, with a slightly prolonged, broadly triangular, obtuse to almost rounded apex, those of the first whorl (opposite the outer tepals) usually slightly wider than those of the second whorl, the 3 inner stamens broadly rounded to almost truncate at the apex. Staminodes small but thickish, papillose at the tip, hidden between the stamens of the third whorl and united with them at the very base. Pistil ± slender, glabrous, 1.5–2 mm long, the style relatively thick and about as long as the ovary. Receptacle deeply urceolate, on the inside covered with tightly appressed hairs (sometimes only in patches). Fruit (known only immature) ovoid-elliptic, its cupule deep, campanulate, already about 11 mm diam. and 9 mm deep, with an entire margin.

Additional specimens examined. VENEZUELA. APURE: Dtto. San Fernando, banks of the Río Arauca, 5 km directly (in a straight line) SW of El Faro, 7°19′N, 66°54′W, 35 m, 18–19 May 1977 (fl), *Davidse & González 13412* (MO); Dtto. Pedro Camejo, banks of the Río Orinoco, opposite Isla Pantallo, 48 airline km NE of Puerto Páez, 6°13′N, 67°09′W, 40 m, 24–25 Feb. 1978 (fl), *Davidse & González 14492* (MO). BOLÍVAR: Dtto. Cedeño, ± 20 km al E de Túriba, 6–11 Dec. 1970 (fl), *Marcano-Berti 2595* (MER); margen del Caura, Temblador, 100 m, 28 Mar. 1939 (fl), *Ll. Williams 11612* (F, US); Las Trincheras, 80 m, 11 June 1984 (fl, immature fr), *S. López P. et al. 4598* (NY); same data, (fl), *S. López P. et al. 4664* (NY).

Nectandra aurea is a small to medium-sized tree of gallery forest formations on the banks of the Orinoco River and its tributaries. It is easily recognized by the characteristic pubescence on young leaves, young twigs, and inflorescences. The tertiary venation is rather inconspicuous above and below, and the young leaves tend to dry with a much lighter and more yellowish color than the mature leaves, which dry medium brown above. The deep campanulate cupule is also quite unusual, but it seems to become wider towards maturity and therefore may not be a reliable specific character.

Allen (1964) cited the collection *Williams 11612* under *N. pisi* Miq. (= *N. globosa* (Aubl.) Mez). With only this specimen at hand, one might indeed think of it as an unusually hairy variant of *N. globosa*. In that species, however, the leaves are generally more elliptic and much wider when mature, the veins are more distinct, and the immature cupules are constricted, not expanded towards the margin.

Nectandra fulva Rohwer, sp. nov. TYPE: Venezuela. Amazonas: Dep. Río Negro, 0–1 km E of Cerro de Neblina Base Camp on Río Mawarinuma, 140 m, 0°50′N, 66°10′W, 27 Nov. 1984 (fl, fr), *Liesner & Kral 17338* (holotype, MO). Figure 2.

Arbor, ad 20 m alta (raro frutex). Ramuli novelli ± angulati, apice ipso ± dense cupreo-subtomentosi, celeriter autem densitate indumenti deminuente, nigricantes. Folia alterna, (ob)lanceolato-oblonga vel (ob)lanceolato-elliptica, raro elliptica, 12–26 cm longa, 3.3–8.5 cm lata, nervis lateralibus utroque costae latere (6–)7–9(–10) sub angulo 50–55(–65)° prodeuntibus, in sicco rigide chartacea, supra plerumque nervis paulo impressis venulis parum elevatis, subtus costa nervisque prominentibus venulis paulo elevatis, apice acuminata, basi acuta vel subcuneata, basi ipsa autem plerumque paulo producta, margine plano, folia novella (si circa anthesin pullulantia) supra dense et molliter flavido- vel fulvo-tomentella, subtus parce et inconspicue puberula sed costa nervisque pilis aliquantum majoribus rufescentibus praedita, vetustiora utrinque (supra primum interveniis) subglabrescentia. Inflorescentiae axillares, laxe thyrsoideae, 7–12(–15) cm longae, pedunculo 3.5–6(–7.5) cm longo, pedunculo modice cupreo- et floribus dense flavido-tomentellae, cymis lateralibus (2–)4(–6), 2–4-furcatis. Pedicelli 3.5–7 mm longi. Flores (7–)9–10 mm diametro. Tepala elliptica vel anguste-elliptica, intus papillosa, aequalia vel exteriora interioribus aliquantum majora, ad 4.5 mm longa. Stamina papillosa, 0.9–1.4 mm longa, filamentis brevissimis, serie prima suborbicularia vel late rhomboidea apice rotundato vel obtuso, serie secunda paulo angustiora, ± ovata vel trullata apice acuto vel parabolico, serie tertia ± rectangularia, apice truncata vel late rotundata. Staminodia parvula sed crassiuscula, apice papillosa, inter stamina seriei tertiae ± celata et basi eis connata. Pistillum elongatum, 1.7–2.7 mm longum, stylo papilloso ovarium glabrum ± aequante. Receptaculum profunde urceolatum, intus glabrum. Fructus (non nisi immaturus notus) oblongus vel ovato-oblongus, ca. 14 mm longus et 8 mm diametro. Cupula ± hemispherica, ca. 10 mm diametro et 5 mm profunda, margine paulo 6-dentato.

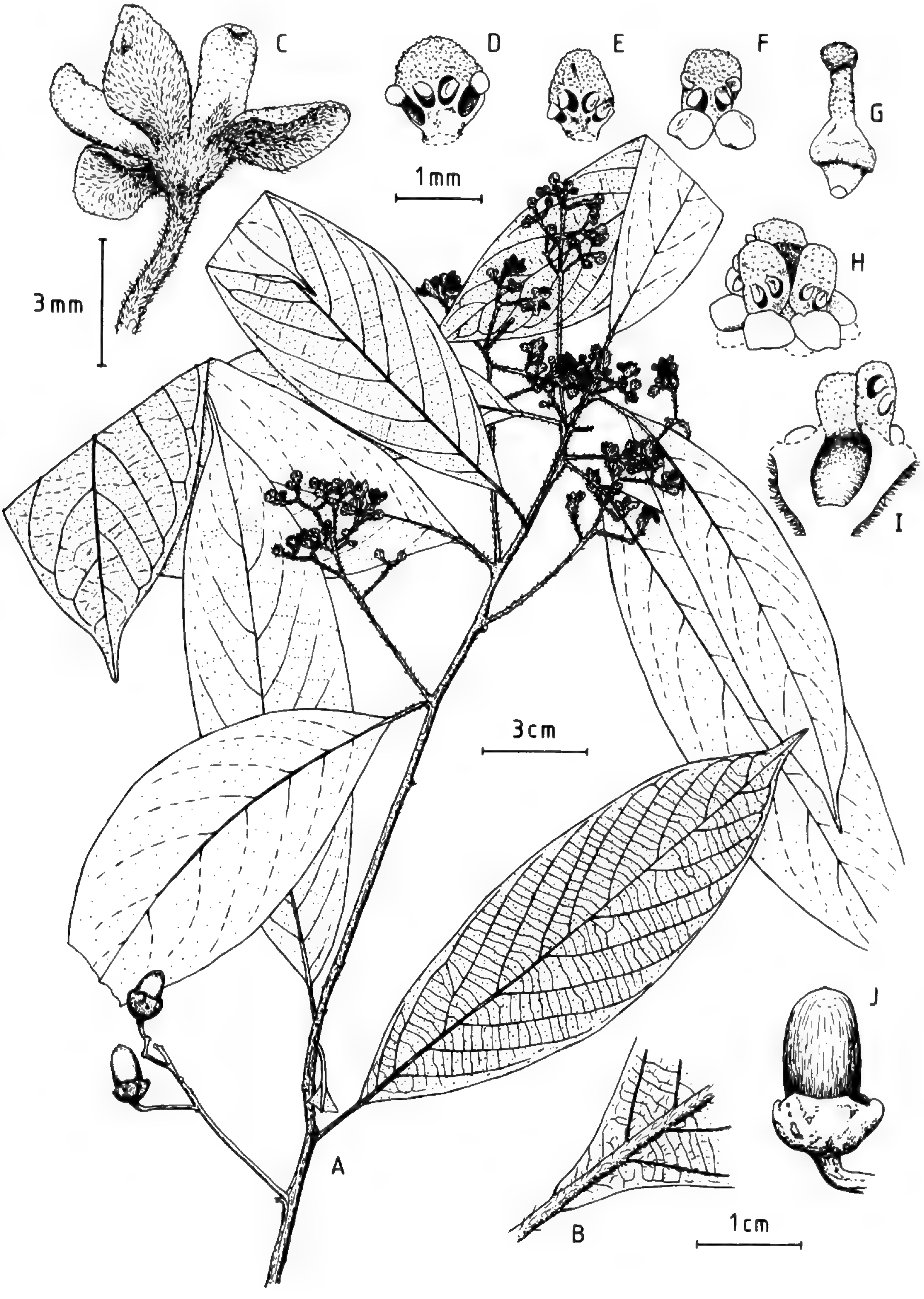

FIGURE 2. Nectandra fulva.—*A. Habit.*—*B. Leaf base.*—*C. Flower, seen from side.*—*D. Stamen of the first whorl, seen from inside.*—*E. Stamen of the second whorl, seen from inside.*—*F. Stamen of the third whorl, seen from outside.*—*G. Ovary.*—*H. Stamens of the third whorl, with stigma and staminode between them, glands and scars of outer stamens at the periphery.*—*I. Receptacle with two inner stamens, cut open; tepals, outer stamens, and ovary removed; semischematic.*—*J. Fruit. Vouchers: A, C–J,* Liesner & Kral 17338; *B,* Gentry & Stein 46954.

Tree (rarely shrub) to 20 m. Twigs at first ± angular, immediately below the terminal bud with a relatively dense copper-colored indumentum of very short to moderately long (ca. 1 mm) curled to almost straight hairs, these quickly becoming sparser below the tip and revealing the blackish epidermis. Leaves alternate, (ob)lanceolate-oblong to (ob)lanceolate-elliptic, rarely elliptic, 12–26 cm long, 3.3–8.5 cm wide, with (6–)7–9(–10) pairs of lateral veins diverging at 50–55(–65)°, dried laminae stiffly chartaceous, above usually with the secondary veins slightly impressed and the tertiary veins very slightly raised, below with midrib and secondaries prominent and the tertiary veins noticeably raised, ± at right angles to the secondary veins, the apex acuminate, the base acute or almost cuneate, at the very base often extended into a short projection along the petiole, margin flat; young leaves (only those developed around flowering time, see below) very densely covered above with predominantly short strongly curled yellowish hairs, soft to the touch, below with a (moderately) sparse indumentum of short appressed hairs between the secondary veins and slightly longer more reddish curled hairs on the veins, the indumentum of older leaves first worn off between the secondary veins above, later slowly subglabrescent. Inflorescences ± lax thyrsoids, axillary to distal leaves, 7–12 (–15) cm long with a peduncle of 3.5–6(–7.5) cm, this with a moderately dense to sparse indumentum similar to that of the twigs, becoming shorter, denser and more yellowish towards the flowers, with (2–)4(–6) lateral cymules below the terminal cymule or cluster of cymules, the cymules branched 2–4 times. Pedicels 3.5–7 mm long. Flowers (7–)9–10 mm diam. Tepals elliptic to elongate-elliptic, up to 4.5 mm long, papillose on the inside, ± equal or the outer ones somewhat larger than the inner ones. Stamens papillose, 0.9–1.4 mm long, with very short filaments, these in the outer whorls sometimes adnate to the tepals, the stamens of the first whorl suborbicular to broadly rhomboid, with a rounded or obtuse tip, those of the second whorl slightly narrower, ± ovate to slightly angular, with an acute to parabolic tip, the third whorl almost rectangular, truncate to broadly rounded at the apex. Staminodes very small but thickish, papillose at the tip, hidden between the stamens of the third whorl and basally united with them. Pistil elongate, 1.7–2.7 mm long, the style papillose and about as long as the glabrous ovary. Receptacle deeply urceolate, glabrous on the inside. Fruit (known only immature) elongate to ovoid-elongate, its cupule nearly hemispherical, ca. 10 mm diam. and 5 mm deep, with a tendency to develop 6 thick teeth on the margin, each corresponding to the midvein of a tepal.

Additional specimens examined. VENEZUELA. AMAZONAS: Dep. Río Negro, Neblina Base Camp on the Río Mawarinuma, 0°50′N, 66°10′W, 140 m, 17 July 1984 (fl), *Davidse & Miller 27417* (MO); same data, 120 m, 17 July 1984 (fl), *Davidse 27520* (MO); Cerro Neblina, between base camp and Puerto Chimo along Río Mawarinuma, 150–180 m, 0°50′N, ca. 66°08′W, 26 Apr. 1984 (fl), *Gentry & Stein 46954* (MO); upstream end of large island in Río Mawarinuma just upstream from Neblina Base Camp, 0°50′N, 66°10′W, 160 m, 27 Nov. 1984 (fl, immature fr), *Kral 71844* (MO); 1–3 km E of Cerro de Neblina Base Camp on Río Mawarinuma, 140 m, 0°50′N, 66°10′W, 8 Feb. 1984 (immature fr), *Liesner 15739* (MO); same data (post fl), *Liesner 15755* (MO); along Río Mawarinuma, 0–5 km E of Cerro de La Neblina Base Camp, 140 m, 0°50′N, 66°10′W, 10 Mar. 1984 (immature fr), *Liesner & Funk 16521* (MO); along Río Mawarinuma, 2–6 km E of Base Camp, between Base Camp and "Puerto Chimo" camp, 160 m, 0°50′N, 66°08′W, 26 Apr. 1985 (fl), *Thomas 3189* (MO, NY, US).

Nectandra fulva is known from only one population near the Neblina Base Camp on the Río Mawarinuma. The tendency to develop dentate or even thickly lobed cupules is a very rare character in *Nectandra*, and it suggests a close relationship with the group around *N. acutifolia* (Ruiz & Pavón) Mez. The structure of the indumentum and the presence of often distinct gland dots in the leaves further support this conclusion. *Nectandra fulva* differs, however, from the other species in this group (among other characters) by less elongate anthers and the lack of an inrolled leaf base.

Nectandra fulva shows an interesting dimorphism in the indumentum of leaves developed during the flowering and fruiting periods. Only those from the flowering period show the dense indumentum on the upper surface described above. In those from the fruiting period there are only somewhat curled reddish hairs, moderately dense on the major veins and sparse from the beginning between them. While these sparsely hairy new leaves are developed, some of the older ones may still show remnants of the dense indumentum developed during flowering time.

Nectandra ruforamula Rohwer, sp. nov. TYPE: Venezuela. Amazonas: 0.5 to 2 km N of San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro & Brazo Casiquiare, 1°56′N, 67°03′W, 120 m, 10 May 1979 (fl), *Liesner 7318* (holotype, MO). Figure 3.

Arbor, ad 10 m alta. Ramuli novelli ± angulati, dense rufo-tomentelli, vetustiores plerumque ± teretes et pilis coactis inconspicuis fumosi, demum glabrescentes (in typo autem ramuli permanifeste angulati et pubescentia persistente). Folia alterna, elliptica vel lanceolato-elliptica, 8.5–20(–26) cm longa, 2.7–8(–10) cm lata, nervis lateralibus utroque costae latere 5–7(–9) sub angulo 35–50(–55)° prodeuntibus, in sicco subcoriacea, supra griseo-virentia vel raro olivacea, costa nervisque impressis venulis paulo impressis, subtus ± fusca, costa nervisque prominentibus venulis elevatis, apice anguste acuminata, basi acuta vel raro obtusa, basi ipsa autem plerumque angustata vel quidem paulo producta, margine subplano vel recurvulo, folia novella utrinque costa nervisque rufo-tomentella, supra interveniis glabra vel paulo pallido-tomentella, subtus indumento densiore, interveniis plerumque pilis brevibus adpressis pallidis modice sparsis et pilis crispatis ± erectis rufescentibus (ut in venis) sparsis, ventustiora supra (interdum praeter basin costae) glabrescentia, subtus subglabrescentia, pilis brevibus adpressis pallidis valde inconspicuis persistentibus. Inflorescentiae axillares, breviter et ± dense thyrsoideae, 2–7 cm longae, pedunculo 1–2.5 (–3.5) cm longo, dense rufo- vel fusco-tomentellae, cymis lateralibus (0–)2–4, 1–2(–3)-furcatis. Pedicelli 1–3 mm longi. Flores 5.5–7.5 mm diametro. Tepala elliptica, intus papillosa, aequalia vel exteriora interioribus paulo majora, ad 3.5 mm longa. Stamina papillosa, 0.7–0.9 mm longa, filamento evidente sed anthera breviore, exteriores 6 depresse obtrullata vel fere transverse elliptica, apice paulo producto obtuso, serie prima secunda plerumque paulo latiora, interiores 3 apice late rotundata vel paene truncata. Staminodia parva sed crassiuscula et paulo capitata, intrinsecus paulo glandulosa, extrinsecus papillosa, inter stamina seriei tertiae ± celata. Pistillum crassiusculum, glabrum vel stylo aliquantum papillosum, 1.4–1.8 mm longum, stylo crasso ovario breviore. Receptaculum late urceolatum (hemisphericum sed supra staminibus staminodiisque fere praeclusum), intus glabrum vel pilis sparsis adpressis. Fructus (immaturus, ex *Maguire & Politi 28001*) ellipticus. Cupula profunda, subhemispherica, iam ca. 11 mm diametro et 6 mm profunda, margine integro.

Tree to 10 m. Twigs at first ± angular, densely covered with a rusty red indumentum of erect and somewhat curled longer hairs (0.3–0.8 mm) over an extremely dense layer of very short hairs, older twigs usually roundish and with much of the indumentum persistent for a long time as a matted gray layer over the epidermis, finally glabrescent (in the type collection all twigs strongly angular and covered with a dense reddish indumentum). Leaves alternate, elliptic to lanceolate-elliptic, 8.5–20(–26) cm long, 2.7–8(–10) cm wide, with 5–7(–9) pairs of lateral veins diverging at 35–50 (–55)°, dried laminae subcoriaceous, above grayish green (older leaves rarely olive), with impressed midrib and secondaries, the tertiary veins usually slightly impressed, below yellowish brown to reddish brown, midrib and secondaries prominent, the tertiary veins noticeably to distinctly raised, ± at right angles to the secondary veins, the apex narrowly acuminate, the base acute or rarely obtuse but at the very base attenuate or at least extended into a short projection along the petiole, almost flat or slightly curved downwards; young leaves on both sides with erect curled reddish hairs on midrib and secondaries, the intercostal fields glabrous or with some paler hairs above, below indumentum denser both on veins and in the intercostal fields, the latter usually with pale, short, appressed hairs and with longer reddish hairs similar to those on the veins; older leaves glabrescent above (some hairs on base of midrib often persistent), subglabrescent below, with the inconspicuous, pale, short, appressed hairs persistent for a long time. Inflorescences short and ± dense thyrsoids, axillary to distal leaves, covered with an indumentum similar to that of the young twigs (but becoming shorter and more grayish brown towards the flowers), 2–7 cm long with a peduncle of 1–2.5(–3.5) cm, with (0–)2–4 lateral cymules below a terminal cluster of cymules, the cymules branched 1–2(–3) times. Pedicels 1–3 mm long. Flowers 5.5–7.5 mm diam. Tepals elliptic, up to 3.5 mm long, papillose on the inside, equal or the outer ones slightly larger than the inner ones. Stamens papillose, 0.7–0.9 mm long, the outer 6 with short but distinct filaments; anthers broadly obtrullate to almost transversely elliptic, with a slightly prolonged obtuse apex, those of the first whorl (opposite the outer tepals) usually slightly wider than those of the second whorl, the 3 inner stamens broadly rounded to almost truncate at the apex. Staminodes small but thickish with a small heart-shaped head, slightly glandular on the adaxial side, papillose on the abaxial side, hidden between the stamens of the third whorl. Pistil relatively stout, glabrous or somewhat papillose at the style, 1.4–1.8 mm long, the style relatively thick, reaching about ½–⅔ the length of the ovary. Receptacle broadly urceolate (hemispherical but above closed by stamens and staminodia), on the inside glabrous or with a few tightly appressed hairs. Fruit (immature, after *Maguire & Politi 28001*, see below) elliptic, its cupule deep, roughly hemispherical but slightly contracted at the margin, already about 11 mm diam. and 6 mm deep, with an entire margin.

Additional specimens examined. VENEZUELA. AMAZONAS: Dep. Atabapo, Cucurital de Caname, southern bank of the middle part of Caño Caname, 3°40′N, 67°22′W, 100 m, 30 Apr.–1 May 1979 (fl), *Davidse et al. 17008* (MO); Río Orinoco 1–10 km below San Fernando de Atabapo, 150 m, 11 May 1954 (fl), *Level 65* (F, NY, US); 4–7 km NE of San Carlos de Río Negro along road, ca. 20 km S of confluence of Río Negro & Brazo Casiquiare, 1°56′N, 67°03′W, 120 m, 19 May 1979 (fl), *Liesner 7550* (MO); Río Atabapo, along Yavita–Pimichin trail near Yavita, 125–140 m, 10 June 1959 (fl), *Wurdack & Adderley 42902* (MO, NY); Cerro Sipapo (Paráque), near base camp, 125 m, 28 Dec. 1948 (fr), *Maguire & Politi 28001* (US).

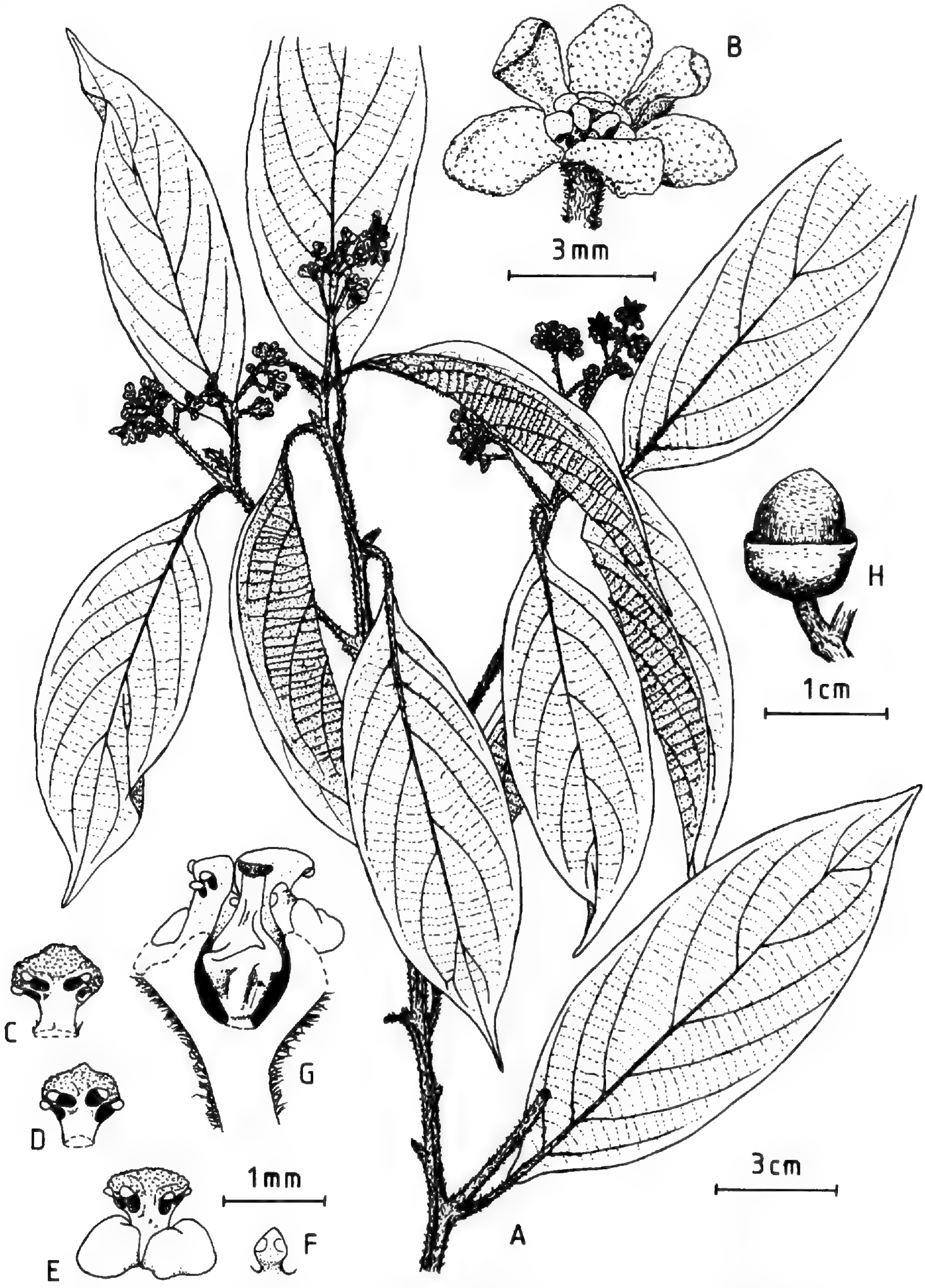

FIGURE 3. Nectandra ruforamula.—*A. Habit.—B. Flower, seen from side.—C. Stamen of the first whorl, seen from inside.—D. Stamen of the second whorl, seen from inside.—E. Stamen of the third whorl, seen from outside.—F. Staminode with glandular patches, seen from inside.—G. Receptacle with ovary, staminode, and two inner stamens, cut open; tepals and outer stamens removed.—H. Fruit. Vouchers: A–G,* Liesner 7318; *H,* Maguire & Politi 28001.

Nectandra ruforamula occurs in the lowland region that connects the basins of the Orinoco and the Amazon. At present it is only known from the Venezuelan side, but it is likely to occur in Colombia as well. *Nectandra ruforamula* is recognized mainly by its dense reddish indumentum on the young twigs, but the leaves have a characteristic appearance, too. They usually show a marked difference between a grayish green upper surface with impressed reticulation and a reddish brown lower surface with raised reticulation.

Despite these rather obvious characters, there is a problem with the delimitation of *N. ruforamula* against *N. globosa* (Aubl.) Mez. The type collection of *N. ruforamula* is not fully representative of the species but has been selected because it is so strikingly unlike any other species of *Nectandra*, including *N. globosa*. In the other collections, however, the reddish indumentum (which in the type collection covers the entire twigs) is restricted to the apical part of the branchlets. Further from the tip it quickly turns into a gray matted mass in which individual hairs can hardly be resolved, and which imperceptibly intergrades with the grayish bark still further down. Where this gray indumentum prevails over the reddish hairs, the specimens may become similar to *N. globosa*, and three of the collections included here (*Level 65, Maguire & Politi 28001, Wurdack & Adderley 42902*) have been cited under its synonym *N. pisi* Miq. by Allen (1964). *Nectandra ruforamula* is treated as a separate entity here because in *N. globosa* the tertiary reticulation is less distinct, even the youngest leaves never show erect curled reddish hairs, and the dry leaves are usually medium to dark brown on both sides.

The fruiting collection, *Maguire & Politi 28001*, is placed here with some doubt. It shows the characteristic color of the leaves, but it altogether lacks the reddish hairs, and the tertiary venation is somewhat less conspicuous than should be expected in leaves of this size. The indumentum, however, is lost or significantly altered with age in most species of *Nectandra*.

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A SYNOPSIS OF *MATELEA* SUBG. *DICTYANTHUS* (APOCYNACEAE: ASCLEPIADOIDEAE)[1]

Warren Douglas Stevens[2]

ABSTRACT

Matelea *subg.* Dictyanthus *comprises thirteen currently known species ranging from northwestern Mexico to southern Nicaragua. One of the species is provided with a new combination,* M. aenea, *and five are described as new,* M. eximia, M. hamata, M. lauta, M. macvaughiana, *and* M. suffruticosa. *The synopsis provides descriptions and a key.*

The genus *Dictyanthus* was described by Decaisne in de Candolle's *Prodromus* in 1844. The description was based on a Sessé & Mociño collection which had been distributed by Pavón. A few years later, sometime in the late 1840s, *Dictyanthus pavonii* was introduced into European botanical gardens and became relatively well known. During this period the species was illustrated in horticultural journals and was provided with several new names. The next treatment of the genus was that of Bentham & Hooker in their *Genera Plantarum* (1876). They considered the genus to comprise three or four Mexican species. Six years later, Hemsley (1882) treated the genus in *Biologia Centrali-Americana, Botany* and recognized four species, one of which was described as new. In Engler & Prantl's *Die natürlichen Pflanzenfamilien*, Schumann (1895) again considered *Dictyanthus* to be a Mexican genus of three or four species. Next, Standley in his *Trees and Shrubs of Mexico* (1924) included six species, one of which was described as new. Woodson (1941), in providing a generic revision of the North and Central American Asclepiadaceae, reduced *Dictyanthus* to a subgenus of *Matelea* and made new combinations for the ten species he recognized. These were listed with partial synonymy to document the subgenus. In the present treatment there are recognized seven of the species Woodson listed, two are reduced to synonymy, and one is excluded from the subgenus. To these are added five new species and one species resurrected from Woodson's synonymy. Finally, Standley & Williams (1969) included the two Guatemalan species of the subgenus in their treatment of Asclepiadaceae in *Flora of Guatemala*. This summarizes the taxonomic history of *Dictyanthus*, except for the description of individual species. Since Woodson's generic revision, no species have been added to or removed from the subgenus, and no species belonging to the group have been described since 1930.

Matelea belongs to the New World tribe Gonolobeae, which can be distinguished within the subfamily by having the pollinia partially sterile and excavated on one or both faces and oriented more or less horizontally along the margin of the style apex. Woodson (1941) recognized three genera in the tribe, *Matelea*, *Gonolobus*, and *Fischeria*, reducing many previously recognized genera to synonymy. While the larger generic concepts offer significant advantages, it seems clear that reinstating some segregates would improve all the circumscriptions. *Matelea* is the least satisfactory of the concepts but, although certain small segregates, notably *Macroscepis* and *Pherotrichis*, can easily be recognized, the bulk of the species require more careful consideration than has yet been possible. Most of Woodson's subgenera of *Matelea* are ill-conceived, but *Dictyanthus* is such a distinctive group that Woodson expressed some misgivings about submerging it. He correctly noted, however, that *Matelea altatensis* (Brandegee)

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Woodson, which he included in subgenus *Dictyanthus*, is intermediate with the larger group of *Matelea*. To *M. altatensis*, which is here excluded from the subgenus, can be added the additional intermediate species *M. aspera* (Miller) W. D. Stevens and *M. sepicola* W. D. Stevens. Subgenus *Dictyanthus* is separated from the rest of *Matelea* by having the corona deeply five-lobed with the axis of each lobe entirely adnate to the corolla; also partially diagnostic are 1) simple inflorescences, 2) a mixed indumentum with at least some of the trichomes glandular and at least some of the long trichomes uncinate, and 3) narrowly fusiform follicles with thickish projections. Thus, while adequate generic and subgeneric circumscriptions within the Gonolobeae are yet to be established, *Dictyanthus* is an easily defined but not entirely discrete group within the current concept of *Matelea* and is here treated as such.

To interpret properly the following key and descriptions, the following should be considered. 1) The description of the indumentum has been simplified and, to a certain extent, generalized by the convention of referring to all trichomes as either short, glandular, or long and by modifying these terms as appropriate. These trichomes are, unless otherwise indicated, uniseriate and multicellular and have straight or uncinate tips. Short trichomes are less than 0.1 mm long, typically about 0.05 mm. Short trichomes on the inner surface of the corolla, when present, are somewhat different in form and have a glassy appearance when dried. Glandular trichomes are the same length to slightly shorter than the short trichomes, with which they are almost always mixed, and have a short stalk, an inflated middle, and a short apiculum. The glandular trichomes are probably not secretory, but the inflated part frequently collapses on drying, giving these the appearance of normal capitate glandular trichomes. Long trichomes are typically much longer than 0.1 mm. The maximum length of long trichomes is given only for the stem. Trichomes on other structures tend to be shorter. When only long trichomes are present on a structure, as is often the case on the leaf blade, they often occur in two discrete lengths, giving much the same appearance as mixed long and short trichomes. 2) The terminology used for describing the surfaces of the leaves and seeds is according to Stearn (1966). 3) The leaves are described essentially according to Hickey (1973). The same terminology is employed to describe the shape of the bracts, calyx lobes, and corolla lobe apices. *The leaf length has been considered to be the length of the midrib.* In all cases the leaves are described on the basis of the largest leaf of each specimen examined. The largest leaves, especially on specimens of the erect species, tend to be near the middle of the stems; the lower leaves tend to be broader and the upper leaves tend to be narrower. 4) The inflorescence and floral characters are described only on the basis of examples in anthesis. The bracts are described on the basis of the largest bract of each inflorescence. The first bract (opposite the first flower) tends to be the largest, and the subsequent bracts are gradually reduced in size. 5) The corolla lobes are considered to be distinct from the limb; thus the corolla is composed of the tube, limb, and lobes. The descriptions of flower colors have been much simplified. In general, only the basic color pattern of the corolla has been described. This color pattern applies only to the inner surface of the corolla, and considerable care should be exercised in attempting to discern the pattern by examining the outside of pressed flowers. 6) Measurements of bipollinia are taken in lateral view and in the normal orientation they assume when removed; the depth or thickness is ignored. The length of the pollinium is measured from the point of attachment of the corpusculum to the tip, including the caudicles of most other asclepiad bipollinia; in most species of the Gonolobeae there is no sharp demarcation of the caudicles from the pollinia.

In the preparation of this synopsis, 694 specimens of 302 collections from 41 herbaria were examined. A list of the specimens examined is available on request. Ten of the thirteen species were studied in the field and nine were cultivated.

TAXONOMIC TREATMENT

Matelea subgenus **Dictyanthus** (Decaisne) Woodson, Ann. Missouri Bot. Gard. 28: 236–237. 1941. *Dictyanthus* Decaisne in de Candolle, Prodr. 8: 605. 1844. TYPE: *Dictyanthus pavonii* Decaisne.

Tympananthe Hasskarl, Flora 47: 258–259. 1847. TYPE: *Tympananthe suberosa* Hasskarl.

Rytidoloma Turczaninow, Bull. Soc. Imp. Naturalistes Moscou 25(2): 319–320. 1852. TYPE: *Rytidoloma reticulatum* Turczaninow.

Plants erect, trailing, or twining, herbaceous or woody, with or without a woody or fleshy caudex. Woody parts typically with thick, fissured, corky bark. Indumentum variable and often mixed; trichomes multicellular, uniseriate, simple, straight or uncinate, of 3 general types: short nonglandular, short glandular, and long nonglandular. Leaves ovate in general outline, apex mostly acuminate to attenuate, base lobate, with acropetiolar colleters; exstipulate but with an interpetiolar fringe of long trichomes and colleters. Inflorescence extra-axillary, a condensed, simple, helicoid cyme or reduced to a single flower with or without an apparent peduncle. Calyx 5-lobed nearly to base, with 1 or 2 colleters below each sinus within. Corolla deeply to shallowly campanulate; tube mostly convoluted, with raised parts opposite corona lobes and sacs formed between them. Corona digitately 5-lobed, lobes connate below or free, adnate to gynostegium and adnate for their entire length to corolla. Gynostegium stipitate, apex ± pentagonal and concave to apiculate, terminal anther appendages covering margin of apex. Corpusculum sagittate; caudicles winged, hardly distinct from pollinia; pollinia flattened, excavated and hyaline along upper margin, obliquely obovate. Follicles fusiform, with few to numerous, thick to thin, straight to arcuate projections. Seeds obovate, flattened, with a raised, smooth or radially grooved, entire or toothed margin, the surface otherwise verrucate to rugose, pale to dark brown; with a white apical coma.

KEY TO SPECIES OF *MATELEA* SUBG. *DICTYANTHUS*

1a. Corolla tube with parallel vertical lines, these only occasionally with a few cross connections.
  2a. Pedicels less than 6 mm long; corolla lobes less than 7 mm long; corona lobes sagittate in outline, less than half the length of the corolla tube .... 2. *M. tuberosa*
  2b. Pedicels more than 6 mm long; corolla lobes more than 7 mm long; corona lobes linear to linear-spathulate in outline, more than half the length of the corolla tube.
    3a. Calyx and outer surface of corolla glabrous; corolla tube with ca. 5 lines between each corona lobe .... 6. *M. lauta*
    3b. Calyx and outer surface of corolla distinctly hairy; corolla tube with 15 or more lines between each corona lobe.
      4a. Corolla base–sinus length more than 12.5 mm, with a narrow band of short trichomes around corona lobes within; long trichomes of peduncles and pedicels mostly uncinate; twining woody vines without thickened caudices .... 4. *M. pavonii*
      4b. Corolla base–sinus length less than 12.5 mm, glabrous around corona lobes within; long trichomes of peduncles and pedicels straight; erect or weakly twining herbaceous vines with thickened caudices .... 5. *M. macvaughiana*
1b. Corolla tube with circular lines or with distinct reticulations, or without a distinct pattern.
  5a. Corolla entirely glabrous within; corona lobes basally connate and forming a prominent disk; inflorescence bracts more than 1.5 mm wide, elliptic in general shape .... 3. *M. hamata*
  5b. Corolla with dense short trichomes within, at least on limb; corona lobes basally connate or not, but not forming a disk; inflorescence bracts less than 1.5 mm wide, linear or ovate in general shape.
    6a. Corona lobes spathulate, with prominent, purple-black, deeply rugose tips; long trichomes of internodes uncinate.
      7a. Peduncle less than 1 mm long; calyx lobes less than 5 mm long; corolla sharply reflexed from tip of corona lobe to sinus; plants of the Isthmus of Tehuantepec .... 11. *M. suffruticosa*
      7b. Peduncle more than 1 mm long; calyx lobes more than 5 mm long; corolla not reflexed beyond corona lobe tip; plants of the Yucatan Peninsula.
        8a. Corolla lobes 7–12 mm long, length to width (sinus–sinus) ratio greater than 0.80, margins revolute, limb and lobes patent or slightly reflexed; corolla densely gray-purple-reticulate .... 13. *M. yucatanensis*
        8b. Corolla lobes 5–9 mm long, length to width (sinus–sinus) ratio less than 0.80, margins not revolute, limb and lobes ascending; corolla yellow-green when fresh, sometimes drying darker and somewhat reticulate .... 12. *M. aenea*
    6b. Corona lobes of various shapes but never modified as above; long trichomes of internodes rarely uncinate.
      9a. Corolla deeply campanulate, base–sinus length 7 mm or more, margins strongly revolute; corona lobes more than 4.5 mm long, linear or linear-spathulate.
        10a. Corolla tube with circular lines .... 7. *M. standleyana*
        10b. Corolla tube with a reticulate pattern or without a distinct pattern.
          11a. Gynostegium apex apiculate; twining vines without thickened caudices; plants from southeast of the Isthmus of Tehuantepec.
            12a. Corolla limb with irregular roundish reticulations, indumentum within restricted to the reticulations; septa connecting corona lobes to gynostegium each with a prominent tooth; calyx lobes 6 mm or less wide .... 8. *M. ceratopetala*
            12b. Corolla limb with circular lines only occasionally merging, the veins themselves forming a regular angular reticulum, indumentum within uniformly distributed, not restricted to veins; septa of corona entire; calyx lobes 6 mm or more wide .... 9. *M. eximia*
          11b. Gynostegium apex shallowly concave; erect or weakly twining vines, mostly from thickened caudices; plants from northwest of the Isthmus of Tehuantepec .... 10. *M. dictyantha*
      9b. Corolla shallowly campanulate to nearly rotate, base–sinus length 11 mm or less, margins slightly or not at all revolute; corona lobes less than 4.5 mm long, short-spathulate with acute apices .... 1. *M. hemsleyana*

1. **Matelea hemsleyana** Woodson, Ann. Missouri Bot. Gard. 28: 237. 1941, based on *Dictyanthus parviflorus* Hemsley. *Dictyanthus parviflorus* Hemsley, Biol. Cent. Amer., Bot. 2: 329. 1882, not *Matelea parviflora* (Torrey) Woodson. TYPE: México. Chiapas: "les montagnes pres in village indien de Cancunc" [?Cancuc, Mpio. Chilón, Chiapas], June, year not given (fl), *Ghiesbreght 663* (holotype, K, not seen; isotypes, GH, MO, NY). Figure 1.

Dictyanthus prostratus Brandegee, Univ. Calif. Publ. Bot. 7: 329. 1920, not *Matelea prostrata* (Willdenow) Woodson. *Matelea diffusa* Woodson, Ann. Missouri Bot. Gard. 28: 236. 1941, based on *Dictyanthus prostratus* Brandegee. TYPE: México. Veracruz: "Acanoxica" or "Acasonica" [Acaxónica], Aug. 1919 (fl), *Purpus 8411* pro parte (holotype, UC; isotypes, GH, MO, NY, US(2), VT).

Plants erect to trailing or rarely weakly twining. Stems 20–60(–90) cm long, with a woody caudex to 4 cm long and 2 cm wide, this with thin to thick corky bark, also often with short woody stems above caudex, these with or without corky bark, the herbaceous stems with dense short and glandular trichomes and sparse to dense, mostly straight long trichomes to 3 mm long. Leaf blade ovate to very wide-ovate, 13–34 mm long, 13–36 mm wide, with mostly uncinate long trichomes and often with scattered glandular trichomes below, surface smooth, smaller veins sharply raised below, apex acuminate to attenuate or rarely obtuse, base lobate, lobes overlapping to divergent, with 2–6(–8) acropetiolar colleters, margin often somewhat thickened and revolute; petiole 7–18(–26) mm long, with dense short and glandular trichomes and sparse to dense, mostly uncinate long trichomes. Peduncle 1–4 mm long, with dense short and gladular trichomes and sparse to dense, straight or uncinate long trichomes; bracts linear or lorate to lanceolate, 2–4 mm long, with indumentum of leaf or nearly glabrous; pedicel 3–5 mm long, with indumentum of peduncle. Calyx lobes narrow-ovate or occasionally lanceolate, 4–6 mm long, 1.5–2.5 mm wide, apex acute to attenuate, with one colleter below each sinus, abaxial surface with scattered glandular trichomes and scattered to dense, straight or uncinate long trichomes, adaxial surface glabrous. Corolla shallowly campanulate, base to sinus length 3–6 mm, limb not distinct, margin slightly revolute; lobes (3–)4–6(–7) mm long, apex acute or occasionally rounded, patent or slightly reflexed at tip, margin slightly revolute; glabrous within except with dense short trichomes on limb and lobes and these sometimes extending down raised ridges within tube, indumentum on outside of straight long trichomes or sometimes the limb and lobes nearly glabrous; tube convoluted, with the raised parts opposite the corona lobes, forming shallow pockets between them, with corona lobes in distinct pockets in bases of raised parts; moderately to densely brown-purple-reticulate, becoming clear pale purple on and around corona lobes. Corona lobes 1–1.5 mm long, basically short-spathulate with an acute apex, the upper surface with a narrow ridge extending as a short spur to edge of gynostegium. Gynostegium 1–1.5 mm high and 1.5–2 mm wide at apex, short-stipitate, apex convex and slightly bilobed. Corpusculum 0.18–0.22 mm long, 0.08–0.10 mm wide, pollinia 0.58–0.91 mm long, 0.26–0.34 mm wide. Follicles 48–70 mm long, 10–18 mm wide, green with white markings, glabrous or with sparse short and glandular trichomes, with 28–54 projections to 2 mm long, arcuate and somewhat reflexed proximally, straight and leaning forward distally. Seeds ca. 4 mm long, ca. 3 mm wide, with a raised margin, this irregularly toothed distally, inside this margin slightly convex on one side and slightly concave on the opposite side, both sides verrucate, concave side with a narrow ridge from apex to near center, apparently pale brown; coma ca. 25 mm long.

Found in Mexico (Michoacán, Estado de México, Morelos, Veracruz, Chiapas), Guatemala, and El Salvador (Fig. 2). Collected at elevations of somewhat below 800 m to nearly 2,600 m, but mostly 1,000–1,500 m, on slopes and hills, mostly in grasslands, but sometimes in open pine–oak forests, on volcanic cinder and rocky clay soils. Flowering mostly from June through September, but flowering specimens also collected once each in April and November; specimens with mature-sized fruits collected August–December.

Only those specimens of *Purpus 8411* with the locality given as "Acanoxica" or "Acasonica" [Acaxónica] and a date of August 1919 are to be considered types of *Dictyanthus prostratus*.

Collections from the part of the range centered around the state of Morelos differ somewhat from plants in the rest of the range. Woodson, according to his annotations, considered the Morelos plants to be *Matelea hemsleyana* and the others *M. diffusa*. Standley & Williams (1969) also considered the plants from southern Mexico to El Salvador to be *M. diffusa*, but perhaps without seriously considering the plants from Morelos. Standley (1924) considered the two species to be synonymous. Plants from around Morelos tend to be shorter and more erect and to have thicker caudices, larger, more distinctly veined leaves, larger flowers (to nearly

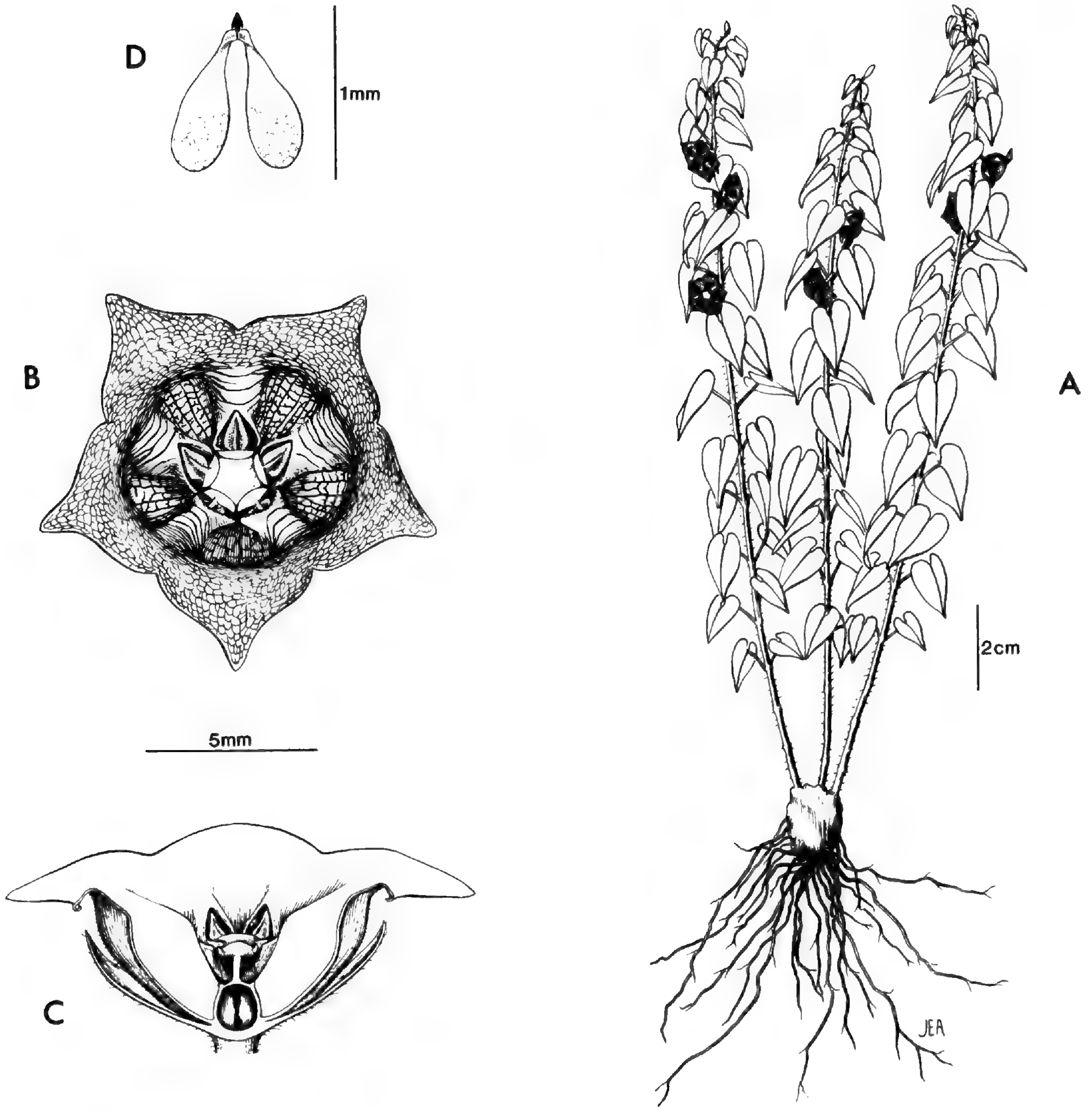


FIGURE 1. Matelea hemsleyana (Stevens C-162, *a cultivated specimen of* Stevens 1399).—*A. Habit.—B, C. Flowers.—D. Bipollinium.*

twice as large), and proportionately longer corona lobes. In describing *Dictyanthus prostratus* (= *Matelea diffusa*), Brandegee considered it to be different from *D. parviflorus* (= *M. hemsleyana*) in having "five minute scales attached to the middle of the gynostegium representing an inner corona." There seems to be no such character, and the "scales" were most likely the remains of the attachments of the corona lobes to the gynostegium, which are typically torn free when the flower is pressed. Despite the differences described above, no known characters faithfully differentiate the two elements. It may well be that further collection will demonstrate that some level of taxonomic recognition is preferable. In this regard, it is curious that this is the only species in the subgenus inhabiting both sides of the continent, a distinctly uncommon phenomenon among the viney milkweeds.

2. **Matelea tuberosa** (Robinson) Woodson, Ann. Missouri Bot. Gard. 28: 237. 1941. *Dictyanthus tuberosus* Robinson, Daedalus 27: 180–181. 1891/1892 [1893]. LECTOTYPE (here chosen): México. Jalisco: slopes of barranca near Guadalajara, 10 Sep. 1891 (fl), *Pringle 3568* (lectotype, GH; isolectotypes, F, VT). Lectoparatype: México. Jalisco: Guadalajara, in ravines, (15 July–3 Aug. fide McVaugh, 1956, p. 215) 1886 (fl), *Palmer*

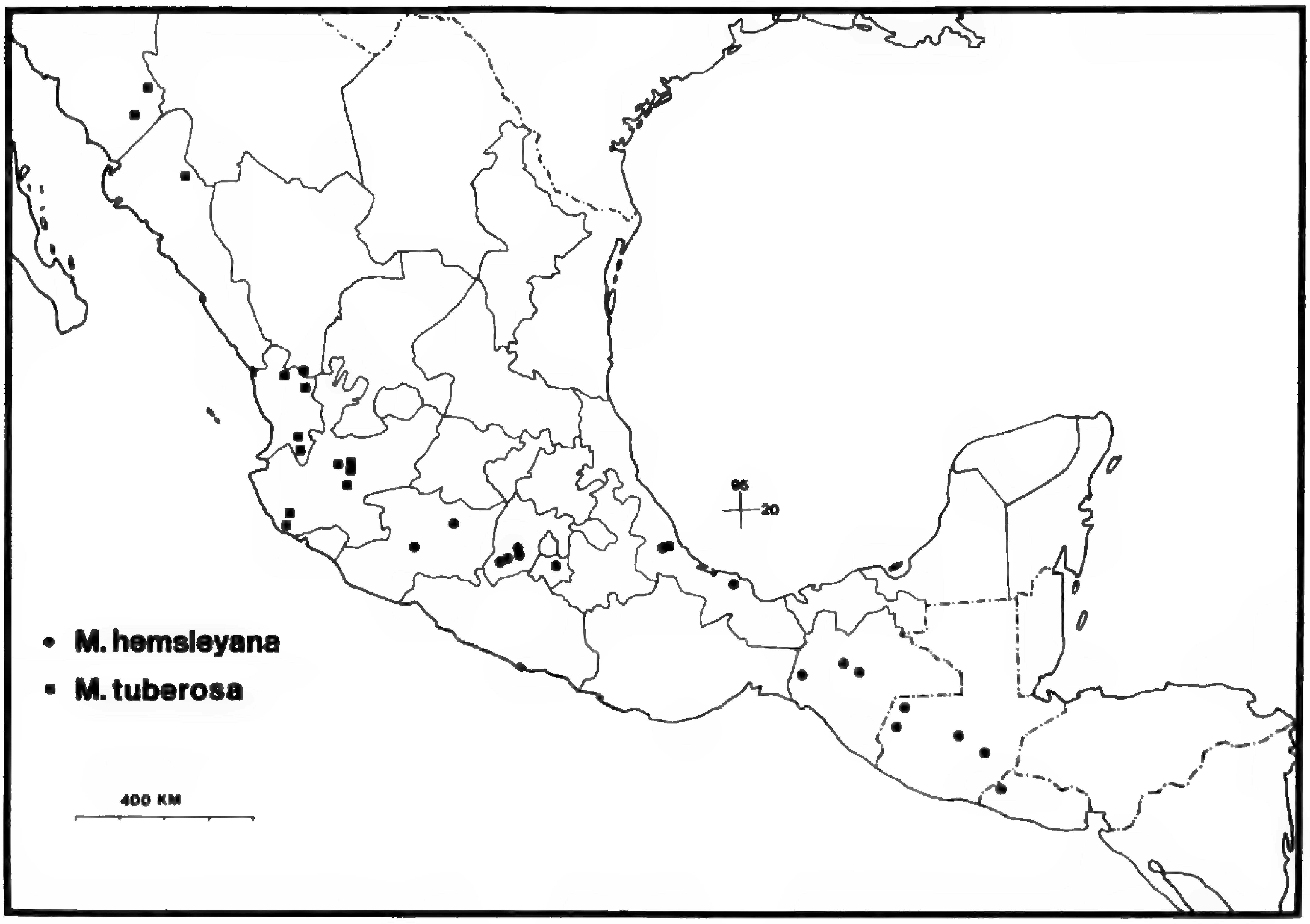


FIGURE 2. *Distributions of* Matelea hemsleyana *and* M. tuberosa.

251 (lectoparatype, GH; isolectoparatypes, ENCB, G, K, MO, ND, NY(2), P, PH, US, WU). Figure 3.

Plants erect to trailing or sometimes weakly twining. Stems 10–70(–100) cm long, with a woody caudex to 5 cm long and 3 cm wide, this with thick corky bark, otherwise typically herbaceous and lacking bark (rarely subshrubs with erect, branched woody stems), with dense short trichomes, very sparse glandular trichomes, and sparse to dense, mostly straight long trichomes to 2 mm long. Leaf blade ovate to very wide-ovate, 17–45 mm long, 17–40 mm wide, with mostly uncinate long trichomes, surface smooth, smaller veins sharply raised below, apex acuminate to attenuate, base lobate, lobes mostly convergent to descending, with 3–6 (–9) acropetiolar colleters, margin often somewhat thickened and revolute; petiole 7–31 mm long, with dense short trichomes, very sparse glandular trichomes, and sparse to dense, mostly uncinate long trichomes. Peduncle 0.5–9 mm long, with dense short trichomes, very sparse glandular trichomes, and sparse to dense, straight or uncinate long trichomes; bracts linear or lorate to lanceolate, 2–8 mm long, with mostly uncinate long trichomes; pedicel 4–5 mm long, with indumentum of peduncle. Calyx lobes lanceolate to narrow-ovate or elliptic, 5–9 mm long, 1.5–3.5 mm wide, apex acute to attenuate, with one colleter below each sinus, abaxial surface with sparse to dense, straight or uncinate long trichomes, adaxial surface glabrous. Corolla deeply campanulate, base to sinus length 6–10 mm, limb revolute; lobes 2.5–6 mm long, apex acute, slightly to strongly reflexed, margins strongly revolute; glabrous within except with dense short trichomes on limb and lobes, indumentum outside of short trichomes on tube and of straight or uncinate long trichomes on limb and lobes, occasionally with a few long trichomes scattered along tube and occasionally distal third of lobes glabrous; with a pair of ridges within tube opposite each corona lobe, ridges of adjacent pairs almost coming together at base and forming pockets at base of corolla, with the corona lobes in distinct pockets in the bases of the furrows between the paired ridges; within the tube with fine gray-brown vertical lines, limb densely gray-brown-reticulate. Corona lobes ca. 2 mm long (but borne distinctly above base of corolla), shape elaborate but basically sagittate in outline, adnate to gynostegium by a thin septum. Gynostegium ca. 2 mm high and ca. 2 mm wide at apex, stipitate, apex broadly and shal-

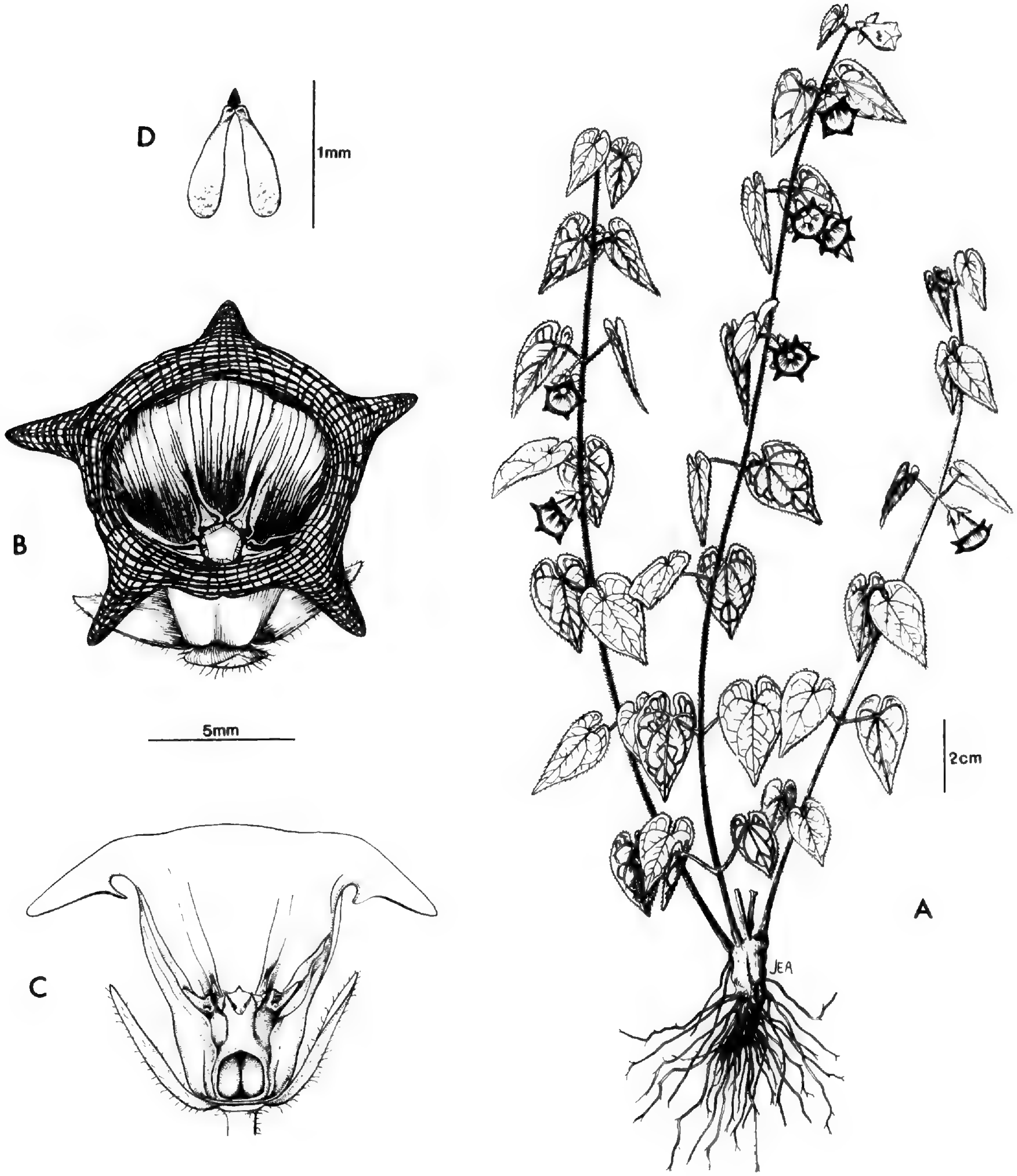


FIGURE 3. Matelea tuberosa (Stevens C-163 *and* C-164, *cultivated specimens of* Stevens 1458 *and* 1473, *respectively, and* Stevens 1473). *—A. Habit.—B, C. Flowers.—D. Bipollinium.*

lowly concave with the corpuscula as high points and slightly convex and bilobed in center. Corpusculum 0.14–0.22 mm long, 0.08–0.13 mm wide, pollinia 0.63–0.86 mm long, 0.29–0.37 mm wide. Follicles 55–65 mm long, 11–19 mm wide, mottled pale and dark green, with scattered short and long trichomes, with 50–110 arcuate projections to 2 mm long. Seeds nearly circular, 5.5–6 mm long, 4.5–5 mm wide, with a raised, radially grooved margin, this entire to shallowly toothed distally, inside this margin slightly convex and verrucate on both sides, one side with a narrow ridge from apex to near center, pale brown; coma ca. 25 mm long.

Collected from southern Sonora to southern Jalisco (Fig. 2) at elevations of 500–1,600 m, in open oak and pine–oak forests and adjacent grasslands, usually in shallow, red, clay soil. Flowering specimens have been collected from late July to early October, and the one specimen with mature seeds was collected in March.

The nearly tubular corolla of this species readily distinguishes it from the other species of this subgenus and is probably unique in the genus *Matelea*.

3. **Matelea hamata** W. D. Stevens, sp. nov. TYPE: México. Guerrero: La Unión, 50 m, 29 July 1898 (fl), *Langlassé 257* (holotype, US; isotypes, GH, P). Figure 4.

Matelea hamata W. D. Stevens; a speciebus ceteris subgeneris *Dictyanthi* pagina interiore corollae glabra et corona disciformi carnosa lutea lobis brevibus (circa 1 mm) corollae adnatis clare distinguenda.

Plants twining vines. Stems woody below, with corky bark, herbaceous stems with moderately dense short and glandular trichomes and sparse to very sparse straight or uncinate long trichomes to 1.5 mm long. Leaf blade narrow-ovate to wide-ovate, 52–113 mm long, 26–52 mm wide, with sparse to dense uncinate long trichomes, surface smooth to minutely pusticulate, apex acute to attenuate, base lobate, lobes slightly convergent to divergent, with 4–9 acropetiolar colleters, margin somewhat thickened and revolute; petiole 23–61 mm long, with moderately dense short and glandular trichomes and sparse, mostly uncinate long trichomes. Inflorescence relatively elongate; peduncle 14–40(–53) mm long, with indumentum of stem; bracts narrow-elliptic to elliptic or lanceolate to narrow-ovate, 4–10 mm long, with indumentum of leaf; pedicel 7–19 mm long, with indumentum of stem. Calyx lobes lanceolate to narrow-ovate or elliptic, 10–17 mm long, 4–6.5 mm wide, apex acute or acuminate, with one colleter below each sinus, abaxial surface with moderately dense, straight or uncinate long trichomes, adaxial surface glabrous. Corolla urceolate-campanulate, base to sinus length 11–16 mm, limb broad, patent; lobes 8–13 mm long, apex obtuse or rounded, slightly recurved, margin patent; glabrous within, indumentum on outside of dense short trichomes and of moderately dense long trichomes on limb and lobes; tube shallowly convoluted, with a pair of ridges opposite and a shallow pit alternate with each corona lobe; with fine, faint, reticulate lines within the tube, limb with fine, distinct circular lines, these becoming reticulate on lobes, these lines gray-brown on a pale yellow-green background. Corona lobes connate and forming a fleshy yellow disk ca. 6.5 mm wide, lobe tips subulate and extending ca. 1 mm above rim of disk, disk adnate to corolla base and lobe tips adnate to corolla between paired ridges, with a fleshy septum from each lobe to the gynostegium, each septum with a fleshy ornate hump. Gynostegium ca. 3 mm high and ca. 3 mm wide at apex, stipitate, apex broadly and shallowly concave with the corpuscula as high points and a slight hump in center. Corpusculum 0.22–0.24 mm long, 0.18–0.19 mm wide, pollinia 1.24–1.49 mm long, 0.41–0.48 mm wide. Fruit and seeds unknown.

Paratypes. MÉXICO. GUERRERO: near el Tuzal, ca. 3.9 mi. SE of Petatlán, ca. 80 m, 25 July 1976 (fl), *Stevens et al. 2538* (ARIZ, DS, DUKE, ENCB, F, G, GH, L, MICH, MO, MSC, NY, P, SD, SMU, TEX, UMO, US, WIS). OAXACA: Distrito de Pochutla, camino a la Bahía de Santa Cruz, 2 km al S de la desviación, 50 m, 25 July 1982 (fl), *Cedillo et al. 1697* (MEXU, MO).

Known only from near the coast (less than 100 m elevation) in Oaxaca and Guerrero (Figure 6), growing in clayey soil. Known flowering in July.

In many ways this is intermediate between *Matelea hemsleyana* and *M. tuberosa* on one hand and the other species of the subgenus on the other. The overall aspect of the plant, the general size and shape of the corolla, the connate corona lobes, and the size and shape of the bipollinia are essentially comparable to the larger group of species. The corona lobes, in this case the tips of the lobes, are more comparable in size, shape, and method of adnation to the corolla of *M. hemsleyana* and *M. tuberosa*. The fleshy corona disk is, however, unique. Also unique are the large, nearly foliaceous bracts, the large elliptic calyx lobes, the broad patent corolla limb, and the relatively short and blunt corolla lobes.

The holotype of this species previously had been tentatively determined as *Dictyanthus stapeliiflorus*; see the discussion of this name under *Matelea pavonii*.

4. **Matelea pavonii** (Decaisne) Woodson, Ann. Missouri Bot. Gard. 28: 237. 1941. *Dictyanthus pavonii* Decaisne in de Candolle, Prodr. 8: 605. 1844. TYPE: "Pavón" (Sessé, Mociño et al. *s.n.*) (holotype, FI, not seen; fragment of holotype, P). Figure 5.

Stapelia campanulata Pavón ex Decaisne in de Candolle, Prodr. 8: 605. 1844, pro syn.

Tympananthe suberosa Hasskarl, Flora 47: 258–259. 1847. TYPE: unknown.

Dictyanthus campanulatus Reichenbach, Selectis e Seminario Horti Academici Dresdensis 4. 1850 (Linnaea 24: 207. 1851), nom. superfl. TYPE: unknown.

Dictyanthus stapeliiflorus Reichenbach, ll.cc. *Matelea stapeliiflora* (Reichenbach) Woodson, Ann. Missouri Bot. Gard. 28: 237. 1941. TYPE: unknown.

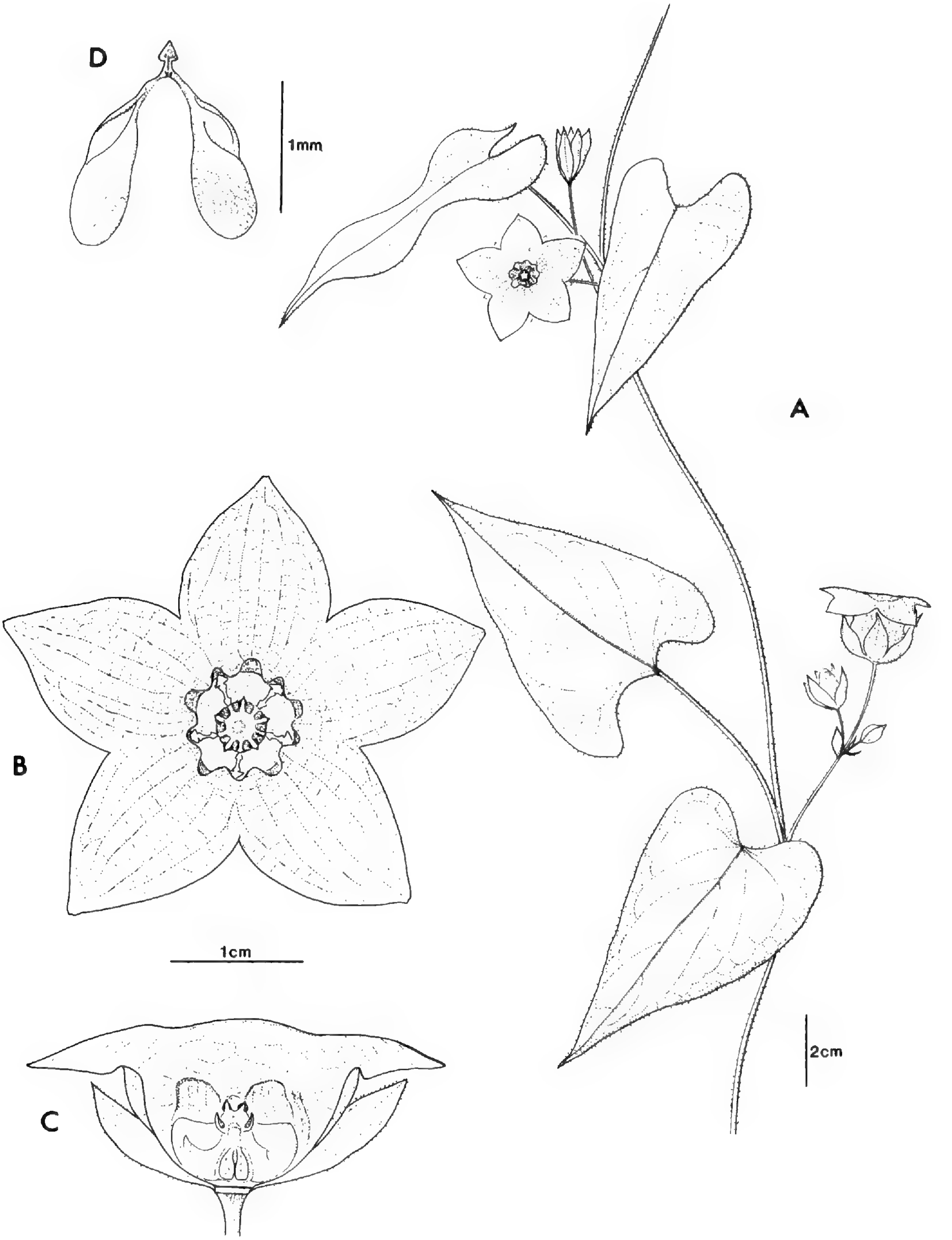


FIGURE 4. Matelea hamata (Stevens et al. 2538).—*A. Section of flowering stem.—B, C. Flowers.—D. Bipollinium.*

Stapelia campanulata Sessé & Mociño, Pl. Nov. Hisp. 41. 1888. TYPE: unknown (Sessé, Mociño et al. *s.n.*, from mountains of Mazatlán, Guerrero).

Plants twining vines. Stems woody below, with thick or occasionally thin corky bark; herbaceous stems with sparse to dense short and glandular trichomes and sparse to dense, straight or uncinate long trichomes to 1.5 mm long, these brittle and often missing from specimens. Leaf blade ovate to wide-ovate or rarely very wide-ovate, (49–)60–128 mm long, 29–100 mm wide, indumentum of sparse to dense uncinate long trichomes, surface pusticulate to minutely pusticulate or occasionally nearly smooth, smaller veins occasionally slightly raised below, apex acuminate to attenuate, base lobate or very rarely cordate, lobes mostly descending to widely divergent, with (0–)1–6(–11) acropetiolar colleters, margin often slightly thickened and revolute; petiole (16–)22–65(–81) mm long, with indumentum of stem. Peduncle 9–60 (–90) mm long, with indumentum of stem or occasionally long trichomes absent; bracts lanceolate or occasionally lorate, narrow-oblong, very narrow-elliptic, narrow-ovate, or ovate, 4–13 mm long, with sparse to dense short and uncinate long trichomes or sometimes nearly glabrous; pedicel (7–) 10–25(–32) mm long, with indumentum of stem or occasionally long trichomes absent. Calyx lobes lanceolate to narrow-ovate or rarely ovate, 9–18 mm long, 3–6(–9) mm wide, apex attenuate, with one colleter below each sinus, abaxial surface with sparse to moderately dense uncinate long trichomes, adaxial surface glabrous. Corolla campanulate, base to sinus length 13–25 mm, limb revolute; lobes 11–25 mm long, apex rounded or occasionally acute or obtuse, patent to slightly reflexed, margin revolute; glabrous within except with moderately dense short trichomes around corona lobes and on limb and lobes, indumentum on outside of very sparse to dense uncinate long trichomes except lobes distally to entirely glabrous; tube convoluted with the raised parts opposite the corona lobes and deep sacs formed between them; with brown, purple, or red vertical lines within tube, these lines becoming finer and circular on base of limb and finely to densely reticulate on distal part of limb and on lobes. Corona lobes 7–13 mm long, linear to linear-spathulate in outline, connate at base, adnate by a thin septum to gynostegium, this septum continuing as a narrow ridge nearly the length of the lobe and often with 1 or rarely 2 distinct teeth on upper margin. Gynostegium 3–6(–7) mm high and 3–4.5 mm wide at apex, stipitate, apex apiculate, the apiculum 0.5–1.5 mm long, slightly shorter than to slightly exceeding corpuscula, appearing to be papillate when dried. Corpusculum 0.31–0.38 mm long, 0.12–0.18 mm wide; pollinia 1.45–1.62 mm long, 0.42–0.48 mm wide. Follicles 70–106 mm long, 22–23 mm wide, green with pale green streaks, with dense short trichomes, bearing 18–54 projections, these thick, straight or slightly arcuate, to 4 mm long. Seeds ca. 6.5 mm long, ca. 3.5 mm wide, with a raised margin, this irregularly crenate distally, inside this margin slightly convex on one side and slightly concave on the opposite side, convex side tuberculate, concave side longitudinally verrucate, dark black-brown; coma ca. 25 mm long.

Collected from southernmost Sinaloa to Oaxaca (Fig. 6). Found mostly at elevations of 900–2,000 m, but also once at 2,500 m and three times at about 600–750 m. Mostly occurring in mountainous areas where pine–oak forests occupy the more exposed sites and tropical deciduous forests occupy the more protected slopes and barrancas. Found in either vegetation type but especially common in disturbed places. Apparently tolerant of a variety of substrates, including limestone, lava, weathered metamorphics, and alluvium. Flowering primarily July–September but also collected in June, October, and November. Mature fruits known only in cultivation (March).

Although there can be no question as to the proper name of this, the type species of *Dictyanthus*, the treatment of the Sessé & Mociño names and specimens has considerably complicated the synonymy. A summary of the Sessé & Mociño specimens relating to *Matelea pavonii* is provided in Table 1. A curious aspect of this summary is that two of the herbarium numbers, *3580* and *3581*, are mixtures of *Matelea pavonii* and *M. standleyana*. Since these species are not known to be sympatric, the mixing probably occurred at some stage of herbarium handling. After both Sessé and Mociño had died, Pavón apparently distributed specimens from their herbarium. It was upon one of these specimens that Decaisne based his genus *Dictyanthus*. The specimen was in the Webb herbarium, which at the time was in Paris (now at FI), but Decaisne kept a fragment which is now at P. I have not seen the specimen at FI, but Dr. Rogers McVaugh has examined it. Decaisne attributed the specimen and the label name, *Stapelia campanulata*, to Pavón. The name was probably actually the same Sessé & Mociño name that was published posthumously in their *Plantae Novae Hispaniae* (1888). In that publication a locality, mountains of Mazatlán, Guerrero, and a plate, "Fl. Mex. Ic. 255," are both cited, but these cannot be associated with any particular one of the Sessé & Mociño herbarium numbers nor with the specimen distributed by Pavón. The plate is apparently the same as the de Candolle plate 804, labeled "255," which is at G (F neg. 30763). A small line drawing taken from the flowers of the de Candolle plate 804 is also at G (F neg. 30406) and is labeled "*Eurybia stapeliaeflora*." This may or may not have been a Sessé & Mociño name, but was never published.

Reichenbach added to the proliferation of names

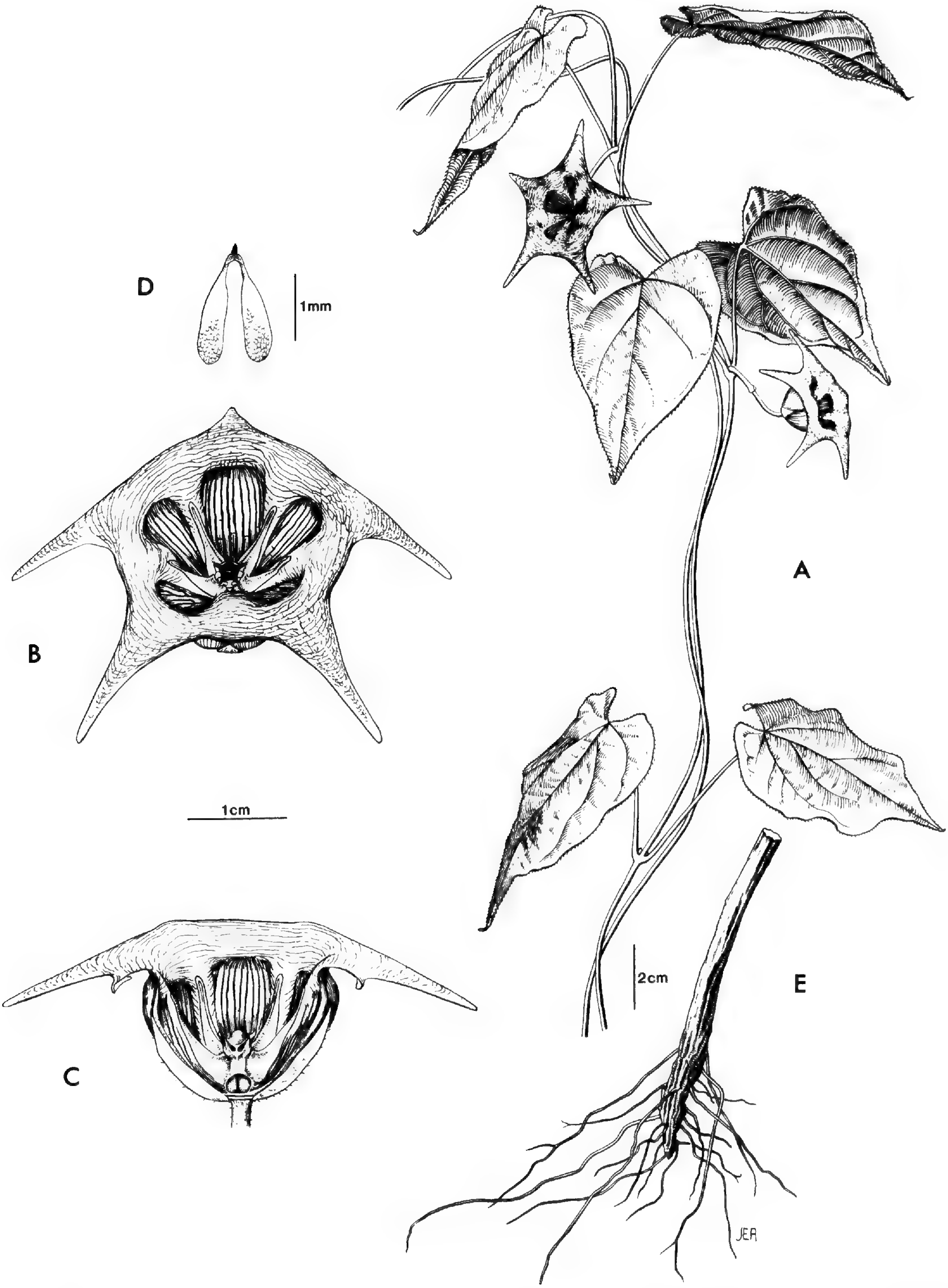


FIGURE 5. Matelea pavonii *(A–D from* Stevens C-160, *a cultivated specimen of* Stevens 1375; *E from* Stevens 1427*).—A. Section of flowering stem.—B, C. Flowers.—D. Bipollinium.—E. Base of stem.*

TABLE 1. *Sessé & Mociño collections pertinent to* Matelea pavonii.

Sessé & Mociño Herbarium Number	Herbarium	F Negative Number	Sessé & Mociño Label Names	Woodson's Determinations	Determinations According to This Treatment
829	MA	41470	*Stapelia campanulata*	*Matelea pavonii*	not determinable from photo, probably not subgenus *Dictyanthus*, perhaps not *Matelea*
835	MA	41471	*Cynanchum violaceum*	*M. pavonii*	probably at least partly *M. pavonii*
838	F	—	—	*M. pavonii*	*M. pavonii*
838	MA	41472	*C. campanulatum*	*M. pavonii*	*M. pavonii*
1253	MA	41473	*C. campanulatum* & *C. punctatum*	*M. pavonii*	*M. standleyana*
3580	F	—	—	*M. pavonii*	*M. standleyana*
3580	MA	41474	*S. campanulata*	*M. pavonii*	*M. pavonii*
3581	F	—	—	*M. pavonii*	*M. pavonii* plus *M. standleyana*
3581	MA	41475	*C. campanulatum*	*M. pavonii*	*M. pavonii* plus *M. standleyana*
s.n.	FI	—	*S. campanulata*	—	*M. pavonii* (not seen)
s.n.	P	—	—	—	*M. pavonii*

by describing *Dictyanthus campanulatus* and *D. stapeliiflorus.* The former, apparently as an early attempt to apply the idea of priority, is a superfluous name, since Reichenbach cited "*Stapelia campanulata* Pavón. *D. pavonii* DC. prodr. *Tympananthe suberosa* Haskarl." *Dictyanthus stapeliiflorus* is a most problematic name. Reichenbach described both of his species from plants growing at a botanical garden in Dresden from seeds collected in Mexico at the foot of the Sierra Madre, near Durango. Apparently no specimens were prepared and neither description is alone adequate for identifying the species, but both could apply to *Matelea pavonii* and the source area would be more appropriate for that species than for any of the other larger-flowered species of subgenus *Dictyanthus.* Partly on the basis of this weak evidence and partly because of a later reference (Anonymous, 1857), I have tentatively considered *D. stapeliiflorus* to be synonymous with *Matelea pavonii.* This Anonymous (1857) reference purports to provide the first illustration of *D. stapeliiflorus.* It is implied but not stated that the illustration, taken from a living plant, is from the original material. Considering that the plant was apparently also growing in a German botanical garden and that only seven years had passed since Reichenbach's description, it could well have been from original material. The illustration does not precisely fit any species of *Matelea,* but most resembles *M. pavonii.* It is conceivable that this represents a distinct species that has never been re-collected, but, in the absence of specimens, I consider it an atypical representative of the variable *M. pavonii.* Although Woodson (1941) made a new combination, *Matelea stapeliiflora,* one cannot be certain as to what he intended the name to apply. In some cases he annotated specimens of *M. tuberosa* with this name, probably following Gray's misapplication of the name (in Watson, 1887). In one other case, Woodson applied the name to a specimen of *M. yucatanensis,* a duplicate of which he properly determined. He also almost certainly had examined the specimen of *Langlassé 257* at US, which had been tentatively determined as *D. stapeliiflorus,* but which is here described as a new species, *Matelea hamata.* Standley (1924) apparently (but tentatively) described the equivalent of my *M. hamata* under *D. stapeliiflorus,* and this could also have accounted for Woodson's concept of the species.

In the late 1840s this species was introduced into European botanical gardens and was apparently a popular plant for about ten years. During this period, at least seven illustrations, mostly colored plates, were published in horticultural journals (Anonymous, 1852; Anonymous & Beaton, 1852; Morren, 1852; Planchon & Van Houtte, 1852–

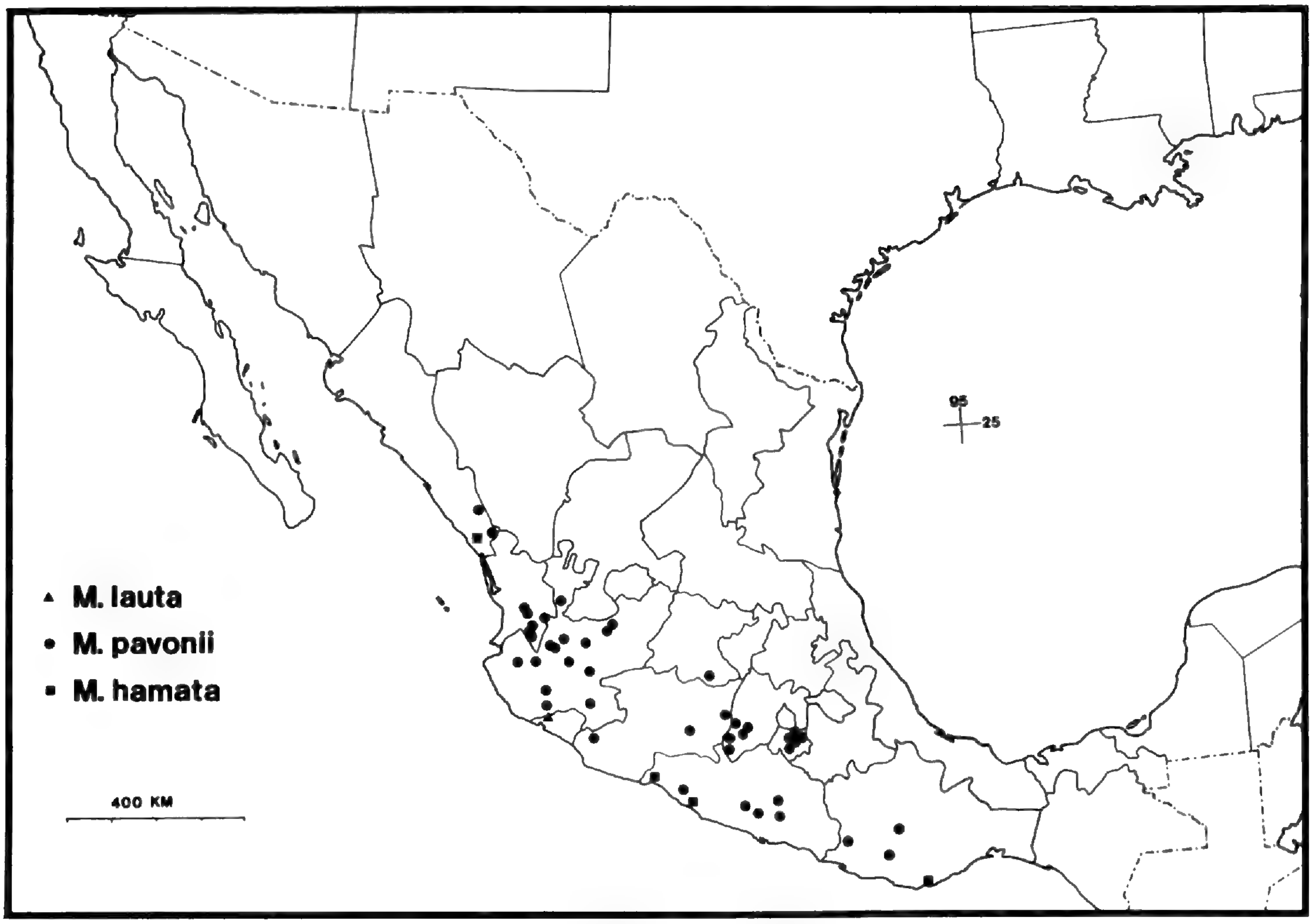


FIGURE 6. *Distributions of* Matelea lauta, M. pavonii, *and* M. hamata.

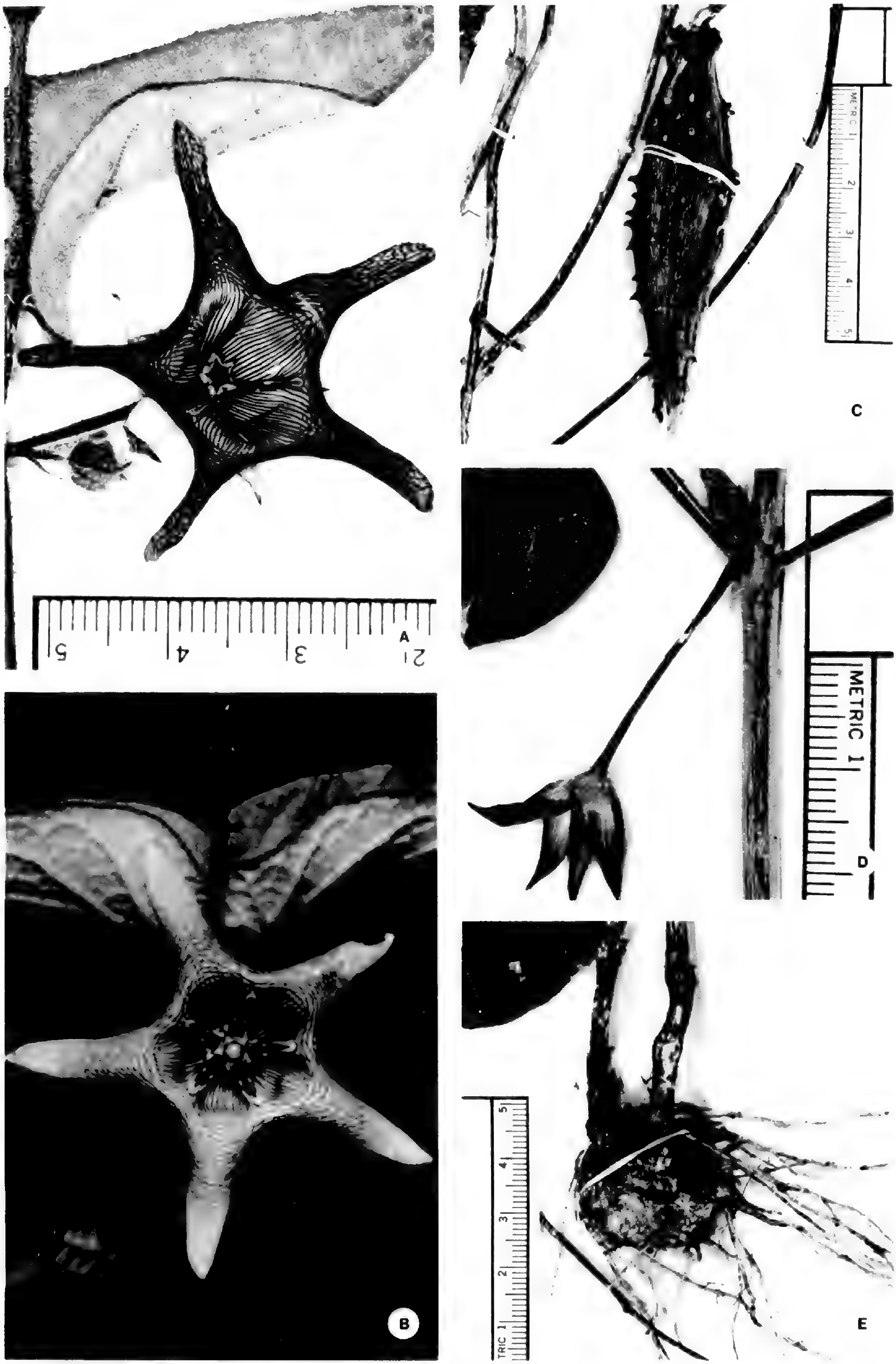
1853; Anonymous, 1853; Anonymous, 1857; Anonymous, 1862). The plants probably originated from one or two introductions, but little reliable information was provided.

This is the most common species of subgenus *Dictyanthus* and exhibits considerable floral variation throughout its range. The most conspicuous variation is in the background color of the corolla and in the color and density of corolla reticulations, but the basic color pattern is essentially constant. The presence or absence of teeth on the septum connecting the corona lobe to the gynostegium appears to have some geographical basis, all of the toothed specimens occurring from Jalisco and northward, but untoothed specimens occur throughout the range. In some populations, examples can be found with prominent teeth, with very small teeth, and with no teeth.

5. **Matelea macvaughiana** W. D. Stevens, sp. nov. TYPE: México. Jalisco: moist slopes near Guadalajara (between El Castillo and Juanacatlán, fide Davis, 1936, p. 199), 5 Aug. 1902 (fl), *Pringle 8629* (holotype, MSC; isotypes, ENCB, F, G(4), GH, L(2), MEXU, MO, NY, P, PH(2), POM, UC, US(2), VT, W). Figure 7.

Matelea macvaughiana W. D. Stevens; *M. pavonii* affinis, a qua imprimis differt caulibus annuis erectis vel leniter volubilibus et caudice perenni ligneo, pagina folii laevi, pedunculis plerumque brevioribus (0–16 mm), trichomatibus longis pedunculorum et pedicellorum rectis, tubo corollae breviore (9–12 mm e basi ad sinum), dentibus lateralibus loborum coronae duobus parvis et prominentiis folliculorum numerosioribus.

Plants erect to occasionally twining. Stems 20–85 cm long, with an herbaceous or woody caudex to 4 cm long and 2 cm wide, this with thin to moderately thick corky bark, occasionally with short woody stems above caudex, these with or without thin corky bark, herbaceous stems with dense short trichomes, sparse to dense glandular trichomes, and sparse to dense straight long trichomes to 3 mm long, these thin and often broken off on lower and older stems. Leaf blade ovate to wide-ovate or rarely narrow-ovate or very wide-ovate, 30–95 mm long, 21–72 mm wide, with sparse to dense uncinate long trichomes, surface smooth, smaller veins sharply raised below, apex acuminate to attenuate, base lobate, lobes mostly descending to widely divergent, with 2–6(–8) acropetiolar colleters, margin often somewhat thickened and revolute; petiole 9–37(–48) mm long, with dense short trichomes, sparse to dense glandular trichomes,


A
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E

and sparse to dense uncinate long trichomes. Inflorescence often reduced to a single flower (then with or rarely apparently without a rudimentary peduncle); peduncle absent–16 mm long, with indumentum of stem or occasionally with long trichomes nearly absent; bracts linear to lorate or lanceolate, (2–)4–7 mm long, abaxial surface with dense short trichomes, sparse to dense glandular trichomes, and sparse to dense, straight or uncinate long trichomes, adaxial surface glabrous or with scattered short trichomes distally; pedicel (5.5–)8–20 mm long, with indumentum of peduncle. Calyx lobes lanceolate to narrow-ovate, 8–12 mm long, 3–4.5 mm wide, apex attenuate, with 1(2) colleter(s) below each sinus, abaxial surface with dense short trichomes, sparse to dense glandular trichomes, and sparse to dense, straight or uncinate long trichomes, adaxial surface glabrous. Corolla campanulate, base to sinus length 9–12 mm, limb revolute; lobes 9–17 mm long, apex rounded or occasionally obtuse, patent, margin revolute; glabrous within except limb and lobes with moderately dense to dense short trichomes, indumentum outside of dense short trichomes on tube and limb and sparse to moderately dense uncinate long trichomes on limb and lobes; tube convoluted with the raised parts opposite the corona lobes and sacs formed between them; with gray or black vertical lines within the tube, these becoming circular on base of limb and reticulate on distal part of limb and lobes. Corona lobes (6–)7–9(–10) mm long, linear to linear-spathulate in outline, connate at base, adnate by a thin septum to gynostegium, this septum continuing as a narrow ridge about half the length of the lobe and with a pair of small thick teeth lateral to the upper margin near center. Gynostegium (2.5–)3–4 mm high and (3–)4–5 mm wide at apex, stipitate, apex broadly convex or nearly apiculate, the center apparently slightly shorter than to equaling the corpuscula. Corpusculum 0.23–0.26 mm long, 0.12–0.15 mm wide, pollinia 1.46–1.68 mm long, 0.43–0.49 mm wide. Follicles ca. 83 mm long, ca. 20 mm wide, striped pale and dark green, with dense short and glandular trichomes, with 118–144 arcuate projections to 3 mm long. Seeds 5.5–6 mm long, ca. 4.5 mm wide, with a raised, faintly radially grooved margin, this entire or weakly toothed distally, inside this margin both sides flat or slightly convex, both sides verrucate to rugose, one side with a slight ridge from apex to near center, pale brown; coma 25–30 mm long.

Paratypes. MÉXICO. JALISCO: Huejotitán, July 1912 (fl), *Diquet s.n.* (MICH (2, one mixed with *Matelea pavonii*), P, US); ranch near Coyula (near Tonalá) ca. 12 mi. E of Guadalajara, July 1963 (fl), *Faberge s.n.* (TEX); wet seepage area 23 mi. S of Guadalajara on Hwy. 15, 5,300 ft., 13 July 1963 (fl), *Molseed & Rice 220* (ARIZ, MEXU, MICH, MO, NY, UC); wet meadows near Guadalajara (El Castillo, according to Davis, 1936, p. 118), 22 Aug. 1893 (fl), *Pringle 5431* (GH, VT). *Michoacán*: cultivated fields 6–7 km N of Jaripó, roadside thickets, 1,600 m, 1 Dec. 1970 (fr), *McVaugh 24934* (MICH, MSC).

The known collection localities are essentially centered in the region of Lago de Chapala at an elevation of about 1,600 m (Fig. 10). Apparently growing in seasonally wet meadows and grasslands; the erect or weakly twining habit and ground-level perennating parts are consistent with this open type of vegetation. Flowering July–August. Specimens with mature-sized fruit collected in December.

This species is named in honor of Dr. Rogers McVaugh for his extraordinary contributions to the flora of the part of Mexico in which this species is found, not the least of which are the many fine specimens of *Matelea*.

It is something of a quirk that this species requires description. Woodson recognized the species, but according to his annotation of the MO specimen of *Pringle 8629*, he considered it to be *Matelea dictyantha* Woodson, a new name based on *Rytidoloma reticulatum* Turcz. This apparently resulted from the fact that the two Pringle collections of this species were misdetermined as *Dictyanthus reticulatus* (Turcz.) Bentham & Hooker f. ex Hemsley (actually "*Dictyanthus reticulatus* Turcz. (ex char.)" in the case of *Pringle 5431* and "*Dictyanthus reticulatus* B. & H." in the case of *Pringle 8629*). Woodson, in providing the new name, cited both Turczaninow's name and type (*Jürgensen 692*), leaving no question as to the application of the name. *Jürgensen 692*, which Woodson apparently never examined, represents another species of *Matelea*, which according to his

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FIGURE 7. *Representative features of* Matelea macvaughiana.—*A. Flower (*Pringle 8629, *US)*.—*B. Living flower, ca. same scale as A, negative taken from color positive, courtesy of Dr. Robert W. Cruden.*—*C. Fruit* (McVaugh 24934, *MICH)*.—*D. Inflorescence reduced to a single flower (past anthesis), without a bract to indicate the presence of a peduncle—contrast with more typical inflorescence of A (*Pringle 8629, *VT)*.—*E. Caudex (*McVaugh 24934, *MICH)*.

annotations he did not recognize, but which must nevertheless bear the name *M. dictyantha*. This left the species he did recognize without a description, type, or name, which are herewith provided.

Matelea macvaughiana is likely to be confused with *Matelea pavonii* because of the similarity of the shape and color pattern of the corolla but is amply distinct, most prominently by having a caudex, an erect or weakly twining habit, straight rather than uncinate long trichomes on several structures, smaller flowers on more reduced inflorescences, paired lateral teeth on the corona lobes, indumentum absent around the corona lobes, and more numerous and arcuate projections on the follicles.

6. Matelea lauta W. D. Stevens, sp. nov. TYPE: México. Colima: steep ravines in gorge of Río Cihuatlán, near bridge 13 mi. N of Santiago, 200–300 m, 27 July 1957 (fl), *McVaugh 15826* (holotype, MICH). Figure 8.

Matelea lauta W. D. Stevens; differt a *M. pavonii* ordinatione venationes corolla, habitatione, pedunculis pedicellisque brevioribus, bracteis floribusque parvioribus; a speciebus omnibus subgeneris *Dictyanthi* calyce et pagina exteriore corollae glabra facile dignoscenda.

Plants twining vines. Stems woody below, with thick corky bark, herbaceous stems with dense, short, sparse glandular trichomes and sparse straight or uncinate long trichomes to 1 mm long. Leaf blade ovate to wide-ovate, 107–130 mm long, 71–88 mm wide, indumentum of sparse uncinate long trichomes above and dense uncinate long trichomes below, surface pusticulate along the veins, apex acuminate, base lobate, lobes descending to widely divergent, with 4–6 acropetiolar colleters; petiole 47–81 mm long, with indumentum of stem. Peduncle 1–4 mm long, with moderately dense short and glandular trichomes; bracts lanceolate, 2.5–5 mm long, with sparse short trichomes abaxially, adaxially glabrous; pedicel 3–4.5 mm long, with moderately dense short and glandular trichomes. Calyx lobes lanceolate, 8–9.4 mm long, 2–3 mm wide, apex acute, with one colleter below each sinus, glabrous. Corolla campanulate, base to sinus length 15–18 mm, limb patent; lobes 14–18 mm long, apex acute, patent, margin revolute; glabrous within except with sparse short trichomes on lobes and in a line around corona lobes, glabrous without; tube convoluted with the raised parts opposite the corona lobes and deep sacs formed between them; with gray-brown vertical lines within tube, these becoming ± angularly and uniformly reticulate on limb and lobes. Corona lobes 7–8 mm long, linear-spathulate in outline, connate at base, adnate by a thin septum to gynostegium. Gynostegium ca. 4.5 mm high and 3 mm wide at apex, stipitate, apex apiculate, the apiculum ca. 0.5 mm long, equaling corpuscula, shriveled and apparently papillate when dried. Corpusculum ca. 0.33 mm long, 0.20 mm wide, pollinia ca. 1.27 mm long, 0.40 mm wide. Fruit and seeds unknown.

Known only from the type collection in lowland Colima (Fig. 6), flowering in July.

This new species appears to be closest to *M. pavonii* but can be immediately distinguished by the pattern of reticulations of the corolla. Most inflorescence and floral measurements of this species are notably smaller than the corresponding measurements of *M. pavonii*, and the glabrous calyx and outer surface of the corolla are unique in the subgenus. Additionally, the single collection was made at a significantly lower elevation than any known collection of *M. pavonii*.

7. Matelea standleyana Woodson, Ann. Missouri Bot. Gard. 28: 237. 1941, based on *Dictyanthus tigrinus* Conzatti & Standley. *Dictyanthus tigrinus* Conzatti & Standley in Standley, Contr. U.S. Natl. Herb. 23: 1183–1184. 1924, not *Matelea tigrina* (Grisebach) Woodson. TYPE: México. Oaxaca: Dist. Tuxtepec, Laguna de Ojitlán, 350 m, 31 Oct. 1919 (fl), *Conzatti 3760* (holotype, US; isotype, GH). Figure 9.

Plants twining vines. Stems herbaceous and lacking bark, or sometimes rhizomes slightly woody and with thin corky bark; rhizomes thin, horizontal; stem indumentum of sparse to dense short and glandular trichomes and sparse to very sparse straight long trichomes to 1.5 mm long, these very brittle and mostly missing from specimens. Leaf blade wide-ovate to very wide-ovate or occasionally ovate, 48–104 mm long, 36–102 mm wide, indumentum of sparse uncinate long trichomes above and dense uncinate long trichomes below, surface smooth, apex acuminate to attenuate, base lobate, lobes mostly convergent to descending, with 1–7 acropetiolar colleters; petiole 35–112 mm long, with sparse to dense short and glandular trichomes and sparse to very sparse, straight or uncinate long trichomes. Peduncle 5–18(–25) mm long, with indumentum of stem or often with long trichomes absent; bracts linear to lanceolate, 2–6 mm long, with dense short and sparse straight long trichomes; pedicel 7–16 mm long, with indumentum of stem. Calyx lobes narrow-ovate or occasionally lanceolate

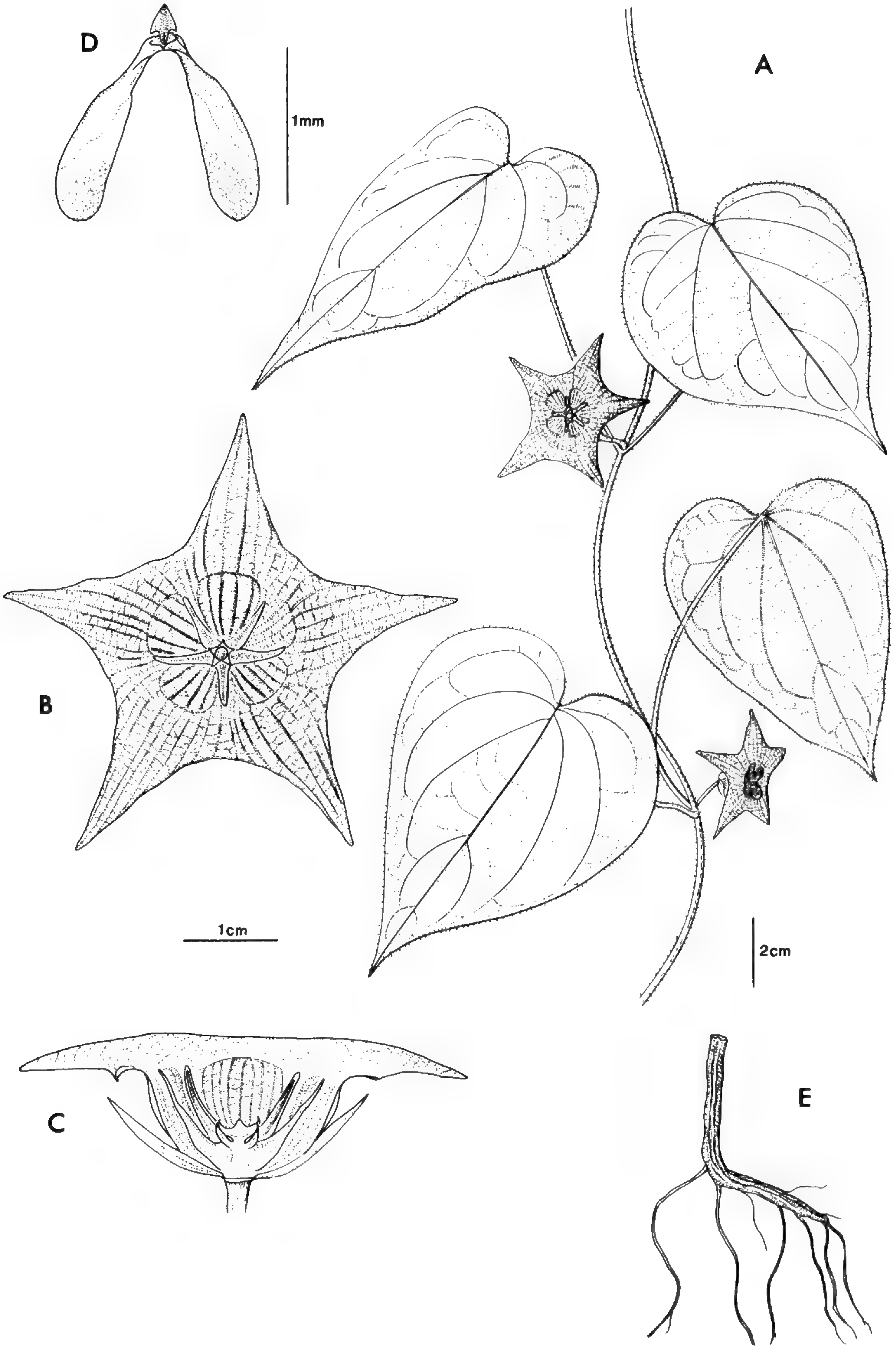

FIGURE 8. Matelea lauta (McVaugh 15826).—*A. Section of flowering stem.—B, C. Flowers.—D. Bipollinium.—E. Base of stem.*

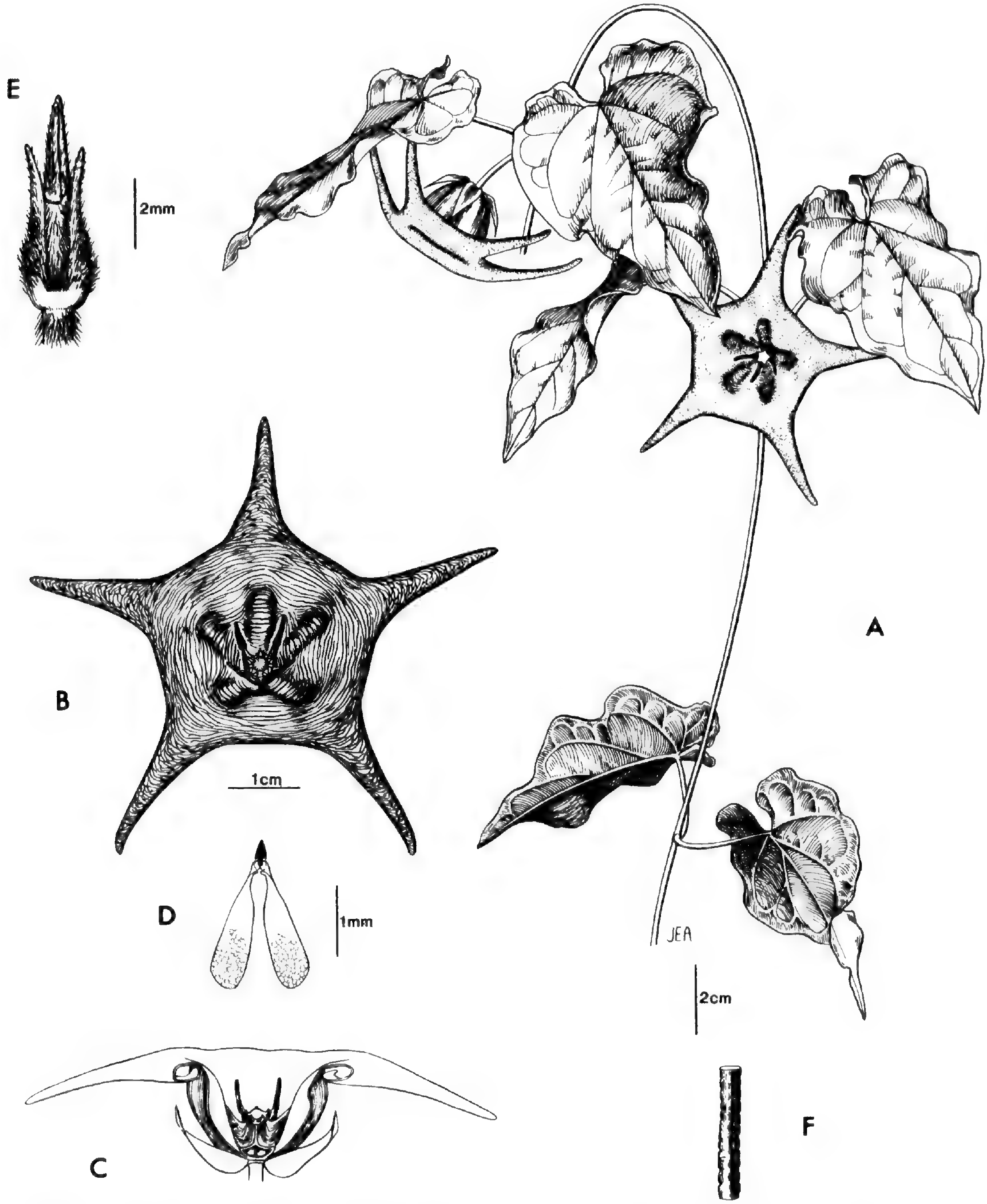

FIGURE 9. Matelea standleyana (Stevens C-161, *a cultivated specimen of* Stevens 1392*).—A. Section of flowering stem.—B, C. Flowers.—D. Bipollinium.—E. Base of stem.—F. Base of adaxial surface of leaf blade,*

or ovate, (8.5–)12–18 mm long, 4–6.5 mm wide, apex attenuate, with one colleter below each sinus, abaxial surface with dense short trichomes, margin with sparse straight or uncinate long trichomes, adaxial surface glabrous. Corolla deeply campanulate, base to sinus length (14–)17–31 mm, limb revolute; lobes 17–28 mm long, apex acute, patent to reflexed, margin revolute; glabrous within except with moderately dense to dense short trichomes on lobes, limb, and around corona lobes, indumentum on outside of sparse to dense short trichomes; tube convoluted with the raised parts opposite the co-

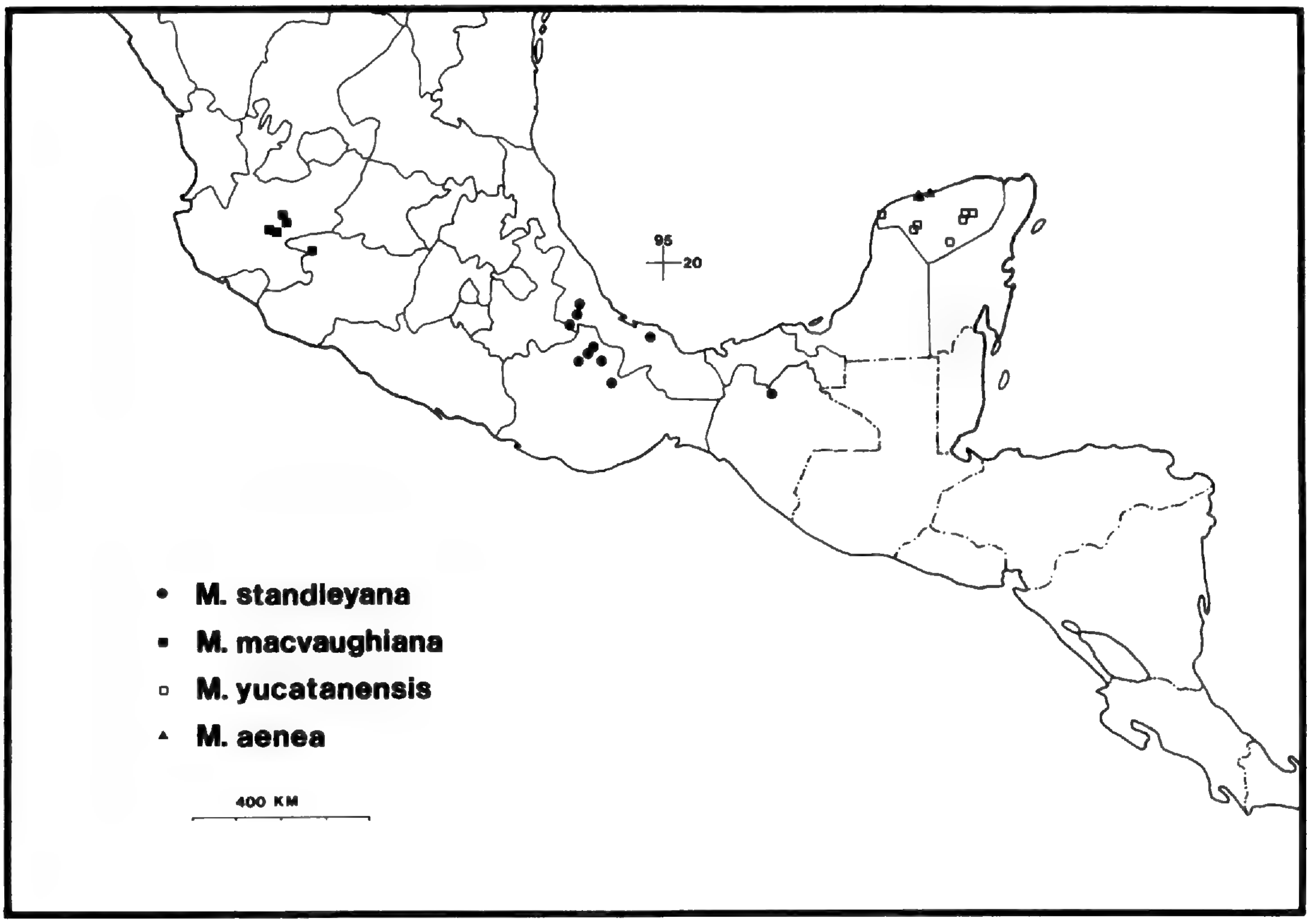

FIGURE 10. *Distributions of* Matelea standleyana, M. macvaughiana, M. yucatanensis, *and* M. aenea.

rona lobes and sacs formed between them; with thick, brown-red, circular lines within tube, these becoming thinner and reticulate on distal part of limb and lobes. Corona lobes 9–13 mm long, linear in outline, connate at base, adnate by a thin septum to gynostegium. Gynostegium (3–)4–5 mm high and 3–4.5 mm wide at apex, stipitate, apex with a blunt projection (formed from apices of anther wings) below each corpusculum and exceeding them laterally, apex convex with tip flattened and slightly bilobed and slightly exceeding corpuscula, terminal anther appendages covering ca. 1/3 of apex. Corpusculum 0.48–0.55 mm long, 0.23–0.28 mm wide, pollinia 1.54–1.88 mm long, 0.45–0.63 mm wide. Mature follicles unknown, immature follicles fusiform, to 85 mm long, to 28 mm wide, apparently green, with dense short trichomes, with ca. 50 very thick, straight projections to 7 mm long. Seeds unknown.

Apparently a plant of moist thickets restricted to northern Oaxaca and adjacent Veracruz, with one collection in northern Chiapas (Fig. 10), at elevations up to 1,220 m. Flowering specimens collected mainly in July and August, but also once each in June and late October. The one immature fruit was collected in August. Flowers of a greenhouse-grown specimen were noticed to produce a faint foetid odor in late afternoon.

This species is readily identifiable because of the large, deeply campanulate corolla with circular markings within the tube. It is likely the largest-flowered New World asclepiad. Well-formed leaves of this species are, along with those of *Matelea pavonii*, the largest of the subgenus and have a uniquely angular sinus.

For a discussion of the Sessé & Mociño collections of this species, see *Matelea pavonii.*

8. **Matelea ceratopetala** (J. D. Smith) Woodson, Ann. Missouri Bot. Gard. 28: 236. 1941. *Dictyanthus ceratopetalus* J. D. Smith, Bot. Gaz. (Crawfordsville) 18: 208. 1893. TYPE: Guatemala. Santa Rosa: Santa Rosa, 3,000 ft., Aug. 1892 (fl), *Heyde & Lux ex J. D. Smith 3999* (holotype, US; isotypes, G, GH, K, NY, US). Figure 11.

Plants twining or occasionally trailing or erect, frequently rooting at lower nodes. Stems 25–55 cm long when erect, woody and with thin to thick corky bark below or occasionally entirely herbaceous, herbaceous stems with dense short trichomes, lacking to dense glandular trichomes, and very sparse to moderately dense, mostly straight long trichomes to 2 mm long. Leaf blade ovate to very wide-ovate, 25–63 mm long, 15–55 mm wide, indumentum above of sparse to occasionally dense straight or uncinate long trichomes and occasionally also sparse short trichomes, or rarely glabrous, indumentum below of sparse to dense mostly uncinate long trichomes, glandular trichomes lacking to sparse, surface smooth, smaller veins often moderately to sharply raised below, apex acute to attenuate, base lobate, lobes mostly convergent, with 1–4(–7) acropetiolar colleters, margin often somewhat thickened and revolute; petiole 13–60(–70) mm long, with dense short trichomes, sparse to dense glandular trichomes, and very sparse to moderately dense, mostly uncinate long trichomes. Inflorescence sometimes reduced to a single flower but with a distinct peduncle; peduncle 1–15(–27) mm long, with dense short trichomes, sparse to dense glandular trichomes, and very sparse to moderately dense, straight or uncinate long trichomes; bracts linear to lanceolate, 3–5(–7) mm long, abaxial surface with short, glandular, and long trichomes, adaxial surface with short and occasionally also scattered long trichomes; pedicel 3–12(–15) mm long, sometimes accrescent in fruit, with indumentum of peduncle. Calyx lobes narrow-ovate or occasionally lanceolate, 9–13 mm long, 3.5–6 mm wide, apex acute or attenuate, with one colleter below each sinus, abaxial surface with scattered straight or uncinate long trichomes, adaxial surface glabrous. Corolla campanulate, base to sinus length 12–20 mm, limb revolute; lobes 11–18 mm long, apex acute, patent to reflexed, margin revolute; glabrous within except with scattered short trichomes on lobes, on limb (on veins only), and around corona lobes, indumentum on outside of sparse to dense short and scattered long trichomes; tube convoluted with the raised parts opposite the corona lobes and deep sacs formed between them; brown- or red-purple-reticulate, reticulations wider within tube. Corona lobes 8–11 mm long, linear-spathulate in outline, connate at base, adnate by a thin septum to gynostegium, this septum with a distinct tooth near center of upper margin. Gynostegium 3.5–5.5 mm high and 3–4.5 mm wide at apex, stipitate, apex apiculate, the apiculum 1–2 mm long and exceeding corpuscula. Corpusculum 0.41–0.46 mm long, 0.18–0.22 mm wide, pollinia 1.52–1.63 mm long, 0.40–0.49 mm wide. Follicles 75–90(–103) mm long, 20–27 mm wide, striped dark green and pale green or white, with short and glandular trichomes, with (36–)48–60 straight or occasionally arcuate projections to 7 mm long. Seeds ca. 4.5 mm long and 2.5–3.5 mm wide, with a raised, radially grooved margin, this weakly toothed distally, inside this margin convex and verrucate on one side, concave and verrucate to rugose on the opposite side, concave side with a slight ridge extending ca. 1 mm from apex; coma 20–30 mm long.

Collected from southern Guatemala to southern Nicaragua (Fig. 13), mostly at elevations of 800–1,000 m but occasionally up to 1,400 m and down to near sea level, both extremes occurring in Nicaragua. Apparently not found on forests but rather in moist or dry fields, thickets, fencerows, streamsides, and roadsides. Mostly associated with rocky volcanic soils but once noted as occurring on a salt flat. Flowering mostly mid July to early October but as early as June and as late as November. Collected with mature-sized fruit from mid September to December.

Until now, the plants here considered to be *Matelea dictyantha* have been included in this taxon. The two species are actually quite distinct, and *M. ceratopetala* has its closest affinities with *M. pavonii*. This problem is further discussed under *M. dictyantha*.

9. **Matelea eximia** W. D. Stevens, sp. nov.

TYPE: México. Chiapas: Fca. Fuarez, Esc. (Finca Unión Juárez, fide M. Sousa S., pers. comm.), 12 Aug. 1937 (fl), *Matuda 1778* (holotype, MICH; isotype, MEXU). Figure 12.

Matelea eximia W. D. Stevens; differt a *M. ceratopetala* ordinatione venationis super limbo corollae ordinate circulari (in illa irregulater reticulata), trichomatibus super limbo corollae aequaliter distributis (in illa limitatis ad reticulum), septis coronae integris, apiculo styli breviore, floribus ubique grandioribus.

Plants twining or trailing, rooting at lower nodes. Stems slightly woody below and with thin corky bark, herbaceous stems with dense short trichomes and very sparse straight long trichomes to 0.5 mm long. Leaf blade ovate, 45–58 mm long, 36–41 mm wide, indumentum above of sparse straight or uncinate long trichomes, indumentum below of dense uncinate long trichomes, surface smooth, apex acuminate to attenuate, base lobate, lobes convergent, with 1–4 acropetiolar colleters, margin somewhat thickened and revolute; petiole 44–65 mm long, with dense short trichomes, sparse glandular trichomes, and sparse to dense (only distally) uncinate long trichomes. Peduncle 3–8 mm long, with dense short trichomes; bracts lanceolate to narrow-ovate, 2–3 mm long (probably larger, primary bracts unknown), with dense short and sparse long trichomes; pedicels 7–9 mm long, with dense

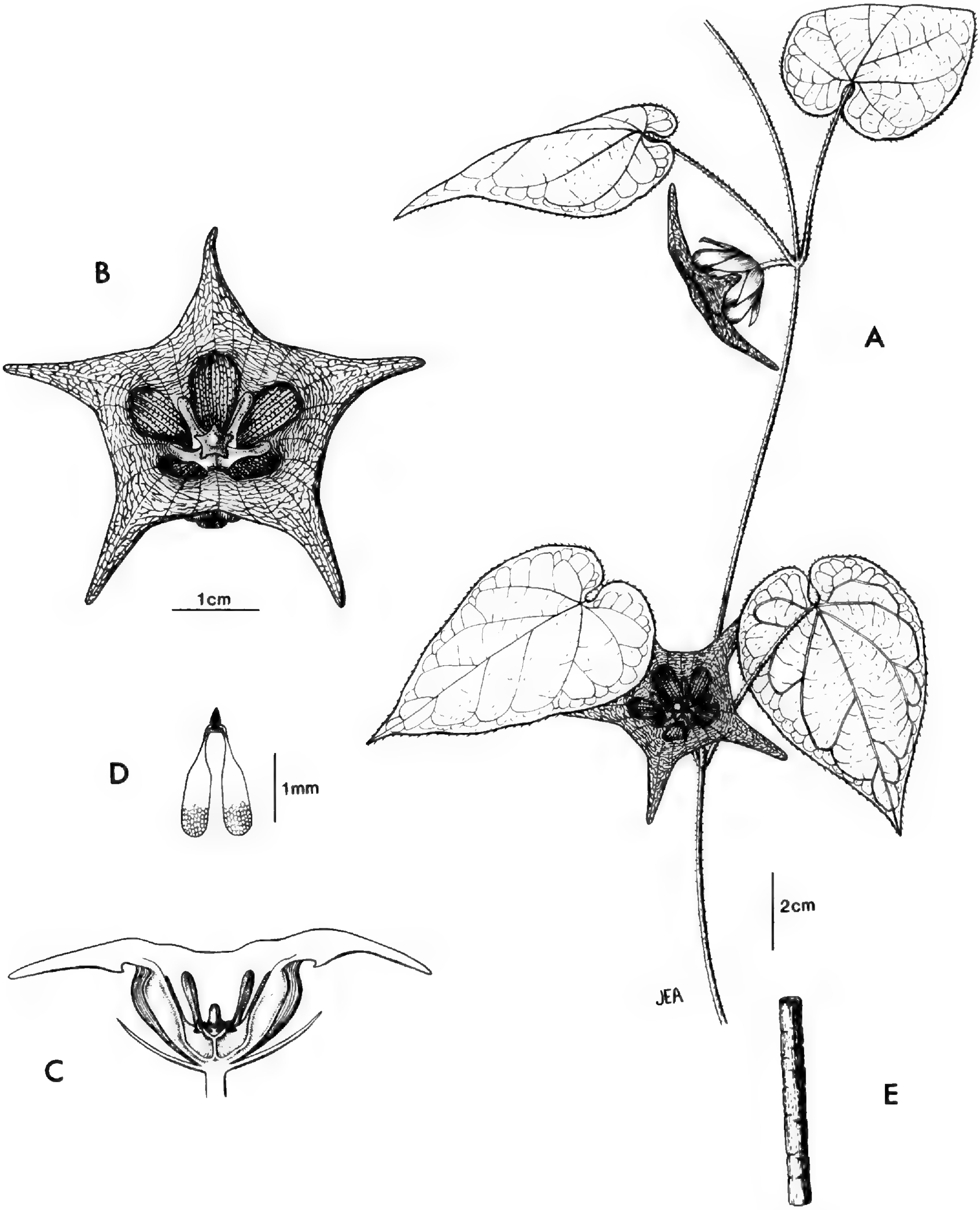

FIGURE 11. Matelea ceratopetala (Stevens 1245).—*A. Section of flowering stem.—B, C. Flowers.—D. Bipollinium.—E. Section of old stem.*

short trichomes and sparse straight long trichomes (only distally). Calyx lobes narrow-ovate to ovate, 9–15 mm long, 6–7.2 mm wide, apex acute or attenuate, with 1 colleter below each sinus, abaxial surface with scattered short trichomes and sparse straight or uncinate long trichomes, adaxial surface glabrous. Corolla campanulate, base to sinus length 16–20 mm, margin apparently revolute; lobes 14–23 mm long, apex acute, apparently reflexed with margin revolute; with uniformly distributed, moderately dense short trichomes within except glabrous in tube between corona lobes, indumentum outside of dense short trichomes; tube convoluted with the raised parts opposite the corona lobes and

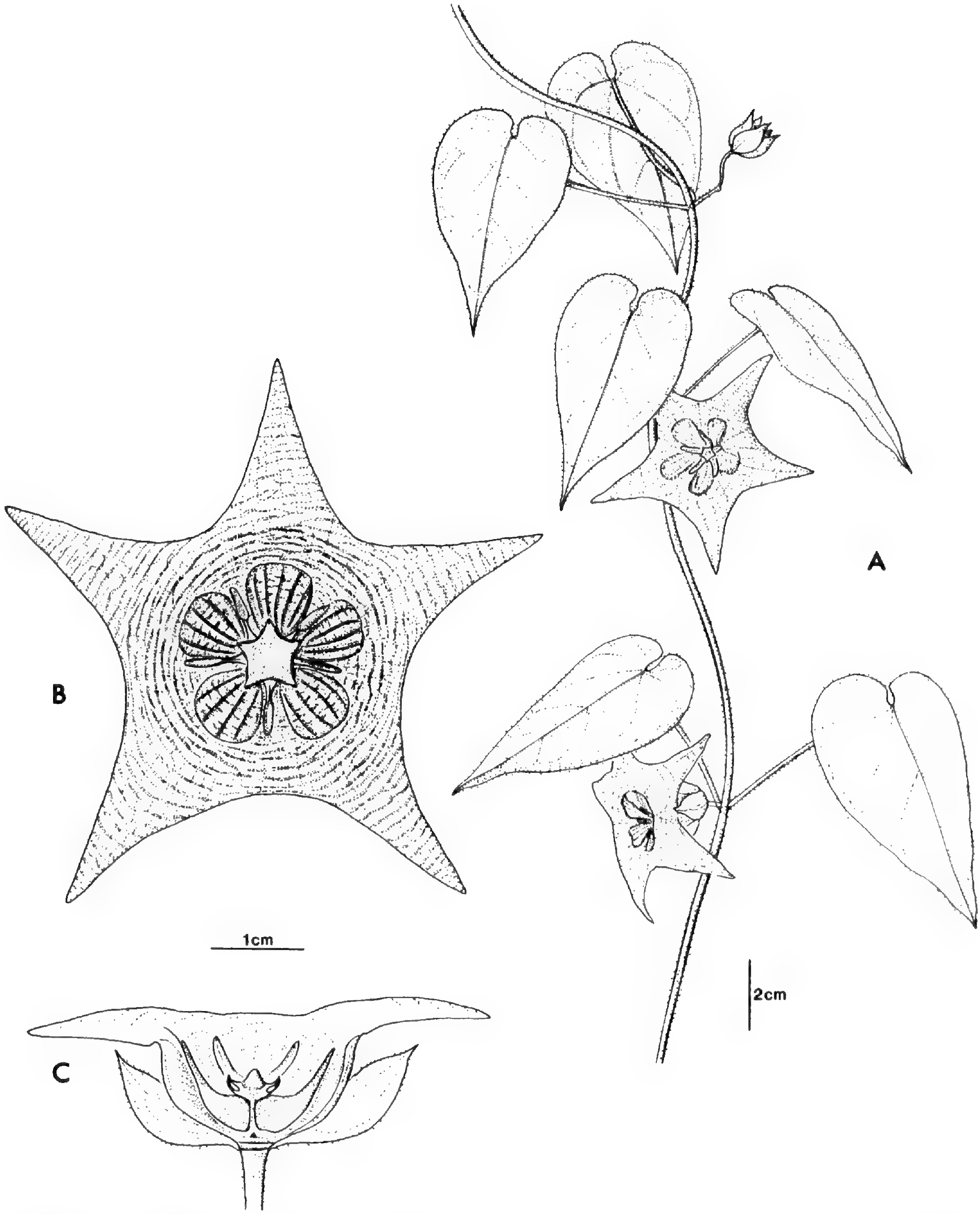

FIGURE 12. Matelea eximia *(*Breedlove 28682 *and* Matuda 1778*).—A. Section of flowering stem.—B, C. Flowers.*

deep sacs formed between them; apparently purple-reticulate. Corona lobes 6–7 mm long, linear-spathulate in outline, connate at base, adnate by a thin, entire septum to gynostegium. Gynostegium 4.5–5 mm high and 2.7–3 mm wide at apex, stipitate, apex apiculate, the apiculum ca. 0.8 mm long and exceeded by corpuscula. Corpusculum ca. 0.37 mm long, 0.23 mm wide, pollinia ca. 1.17 mm long, 0.30 mm wide. Fruits and seeds unknown.

Paratype. MÉXICO. CHIAPAS: Mpio. de Motozintla de Mendoza, 25–27 km NE of Huixtla along road to Mo-

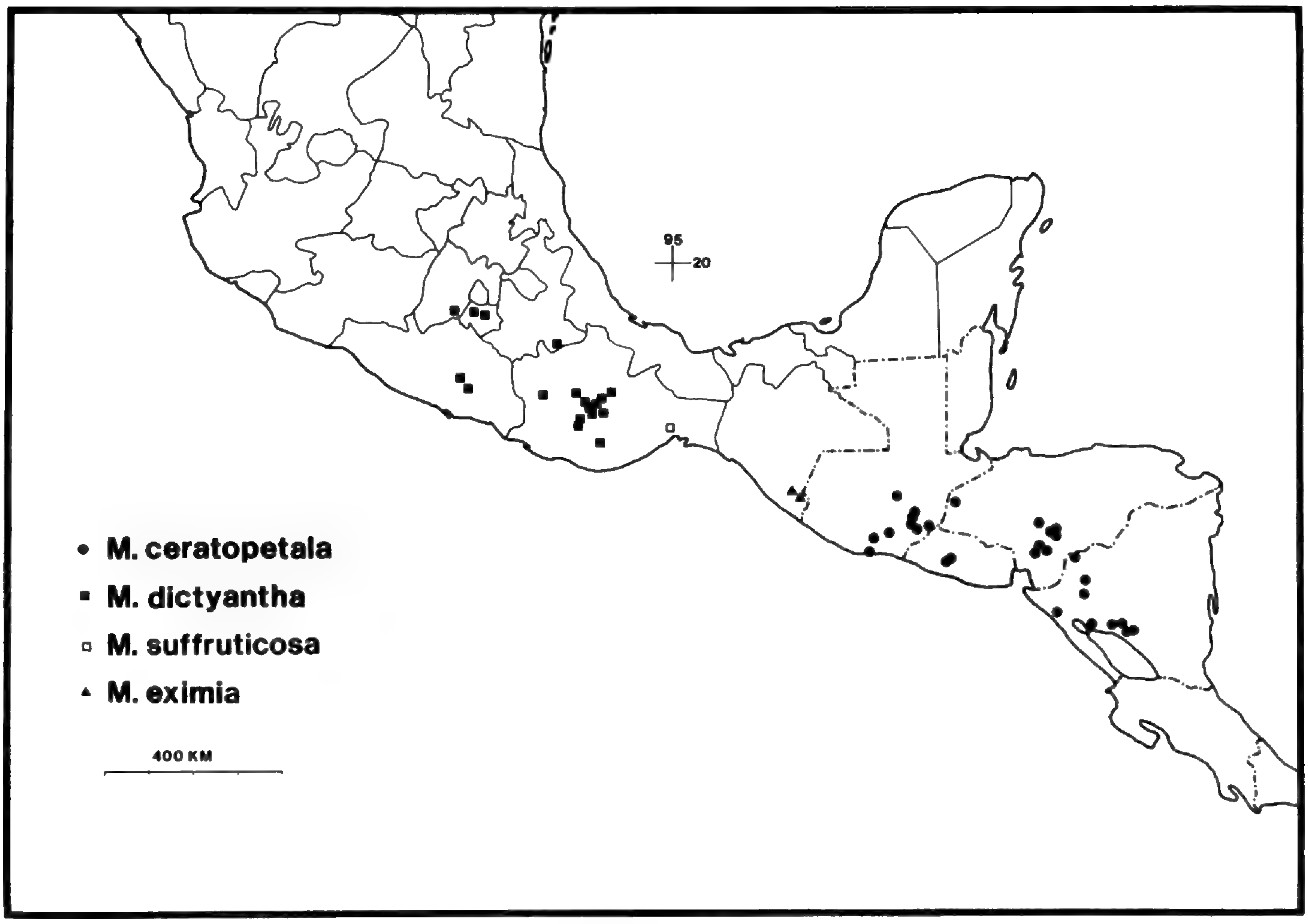

FIGURE 13. *Distributions of* Matelea ceratopetala, M. dictyantha, M. suffruticosa, *and* M. eximia.

tozintla SW of Toliman, 700 m, 7 Oct. 1972 (fl), *Breedlove 28682* (DS).

Known only from the type collection and one other, both from the southern corner of Chiapas (Fig. 13).

This new species is clearly related to *Matelea ceratopetala,* with which it has a contiguous but apparently allopatric range. These two species are quite similar in general aspect and are the only ones in the subgenus where the trailing stems typically root at the nodes. The flowers of the two known collections of *M. eximia* are rather different in appearance, perhaps because the Matuda collection was bleached of corolla coloration during preservation. The Matuda collection thus has a corolla limb with the regular circular veins intersecting the vertical veins and producing a regular angular reticulation; the Breedlove collection has the same pattern of veins but the circular veins are pigmented while the vertical are not, resulting in a circular pattern. Both are different, however, from the irregular roundish pigmented reticulations of *M. ceratopetala.* The additional differences in limb indumentum, corona septa, and style apex apiculum leave little doubt that neither collection pertains to *M. ceratopetala,* nor to any other species of subgenus *Dictyanthus*; but until *M. eximia* is better known, there must remain some doubt that the two collections are properly associated.

10. Matelea dictyantha Woodson, Ann. Missouri Bot. Gard. 28: 236. 1941, based on *Rytidoloma reticulatum* Turczaninow. *Rytidoloma reticultum* Turczaninow, Bull. Soc. Imp. Naturalistes Moscou 25(2): 319–320. 1852, not *Matelea reticulata* (Engelmann ex A. Gray) Woodson. *Dictyanthus reticulatus* (Turczaninow) Bentham & Hooker f. ex Hemsley, Biol. Cent.-Amer., Bot. 2: 329. 1882. TYPE: México. Oaxaca: "Sierra San Pedro Nolasco, Talea, etc.," 1843–1844 (fl), *Jürgensen 692* (holotype, KW, not seen; isotype, K). Figure 14.

Plants erect to trailing or twining. Stems 15–70(–150+) cm long, with a woody caudex to 5 cm long and 3 cm wide, this with thin to thick corky bark, or occasionally with an elongate woody rhizome, also often with woody stems above caudex or rhizome, these usually with thin corky bark and up to ca. 5 cm long but occasionally up to 20 cm long, herbaceous stems with dense short and glandular trichomes and sparse to dense, mostly straight long trichomes to 3 mm long. Leaf blade wide-ovate to very wide-ovate, 26–62(–103) mm long, 24–52(–76) mm wide, with long uncinate trichomes and also often glandular trichomes on veins below, surface smooth, smaller veins sharply raised below, apex acute to attenuate or rarely obtuse, base lobate, lobes mostly convergent to descending, with 1–6(–8) acropetiolar colleters, margin often somewhat thickened and revolute; petiole (11–)14–34(–57) mm long, with dense short and glandular trichomes and sparse to dense uncinate long trichomes. Inflorescence sometimes reduced to a single flower with or apparently without a rudimentary peduncle; peduncle absent–10 mm long, with indumentum of petiole; bracts linear to lanceolate, 2.5–7 mm long, abaxial surface with indumentum of stem, adaxial surface glabrous; pedicel 5–12 (–16) mm long, sometimes markedly accrescent in fruit, with indumentum of stem. Calyx lobes narrow-ovate or occasionally lanceolate or ovate, 6–11 mm long, 2.5–6 mm wide, apex acute to attenuate, with one colleter below each sinus or occasionally these somewhat above sinus near margin of lobe, abaxial surface with indumentum of stem, adaxial surface glabrous. Corolla campanulate, base to sinus length (7–)9–16 mm, limb revolute; lobes 8–14 mm long, apex acute or sometimes rounded, patent to strongly reflexed, margin revolute; glabrous within except with sparse to dense short trichomes around corona lobes and on limb and bases of lobes or sometimes over whole surface of lobes, indumentum on outside of short trichomes and occasionally also with long trichomes on limb and bases of lobes, or occasionally tube and tips of lobes nearly glabrous; tube convoluted with the raised parts opposite the corona lobes and deep sacs formed between them; faintly to densely gray-purple-reticulate, reticulations wider within tube. Corona lobes (5–)6–8 mm long, linear in outline with a raised margin, connate at base, adnate by a thin septum to gynostegium, this septum continuing as a narrow ridge nearly the length of lobe. Gynostegium 3–4 mm high and 3–3.5 mm wide at apex, stipitate, apex broadly and shallowly concave with corpuscula as high points. Corpusculum 0.22–0.35 mm long, 0.09–0.17 mm wide, pollinia 1.17–1.45 mm long, 0.29–0.38 mm wide. Follicles (45–)55–70 mm long, 10–22 mm wide, pale green with a few dark green stripes, with short and glandular trichomes, with (30–)50–110 straight to arcuate projections to 3 mm long. Seeds ca. 5.5 mm long and 4–4.5 mm wide, with a raised, radially grooved margin, this weakly toothed distally, inside this margin flat or slightly concave and verrucate on one side, convex and verrucate on the opposite side, the flat side with a slight ridge from apex to near center, pale brown to brown; coma 25–30 mm long.

Collected in the mountains of four more or less discrete areas: around Cuernavaca (Morelos and adjacent state of Mexico), around Chilpancingo (Guerrero), around Oaxaca (Oaxaca), and in southwestern Puebla (Fig. 13). Found at elevations of ca. 1,500–2,500 m. About a third of the collections are noted as being on or associated with limestone, and many of the other localities are in limestone areas, but whether or not *Matelea dictyantha* is restricted to limestone is uncertain. Mostly in low, open oak, pine, or pine–oak forests, especially where disturbed. Flowering mid June to mid September. Mature-sized fruits collected August–December, mature seeds only in December.

As mentioned under *Matelea macvaughiana*, Woodson provided the epithet for *M. dictyantha* quite by accident. He did not distinguish it from *M. ceratopetala*, to which it bears some resemblance in the shape and color pattern of the corolla and the size and shape of the leaves. The major characteristics distinguishing *M. dictyantha* from *M. ceratopetala* include the woody caudex and predominantly shorter habit, the smaller flowers, the lack of a tooth on the septum connecting the corona lobe to the gynostegium, the concave rather than apiculate gynostegium apex, and the smaller follicles with smaller and more numerous projections. The geographic ranges of the two species are also distinct. The distinctiveness of *M. dictyantha* from *M. ceratopetala* has been noted on two specimens, *Conzatti 2168* at F (unsigned and undated) and *Pringle 4768* at GH (J. M. Greenman, 18 Sep. 1890). Standley (1924) considered *Rytidoloma reticulatum* to be synonymous with *Matelea pavonii*.

The form of Turczaninow's protologue (1852) has led to some confusion. The apparent generic description is actually a description of the genus and its single species and cites *Jürgensen 692*. Immediately following the genus–species description is the entry "18. *R. reticulatum*. Altera species hujus generis, quantum e flore unico, Ptino corrupto, dijudicare possum, adest in collectione Galeottiana ex Oaxaca sub n. 1563." This led Langman (1964: 748) to state that *Rytidoloma reticulatum* was based on a Galeotti collection. Turczaninow was actually indicating that he recognized another

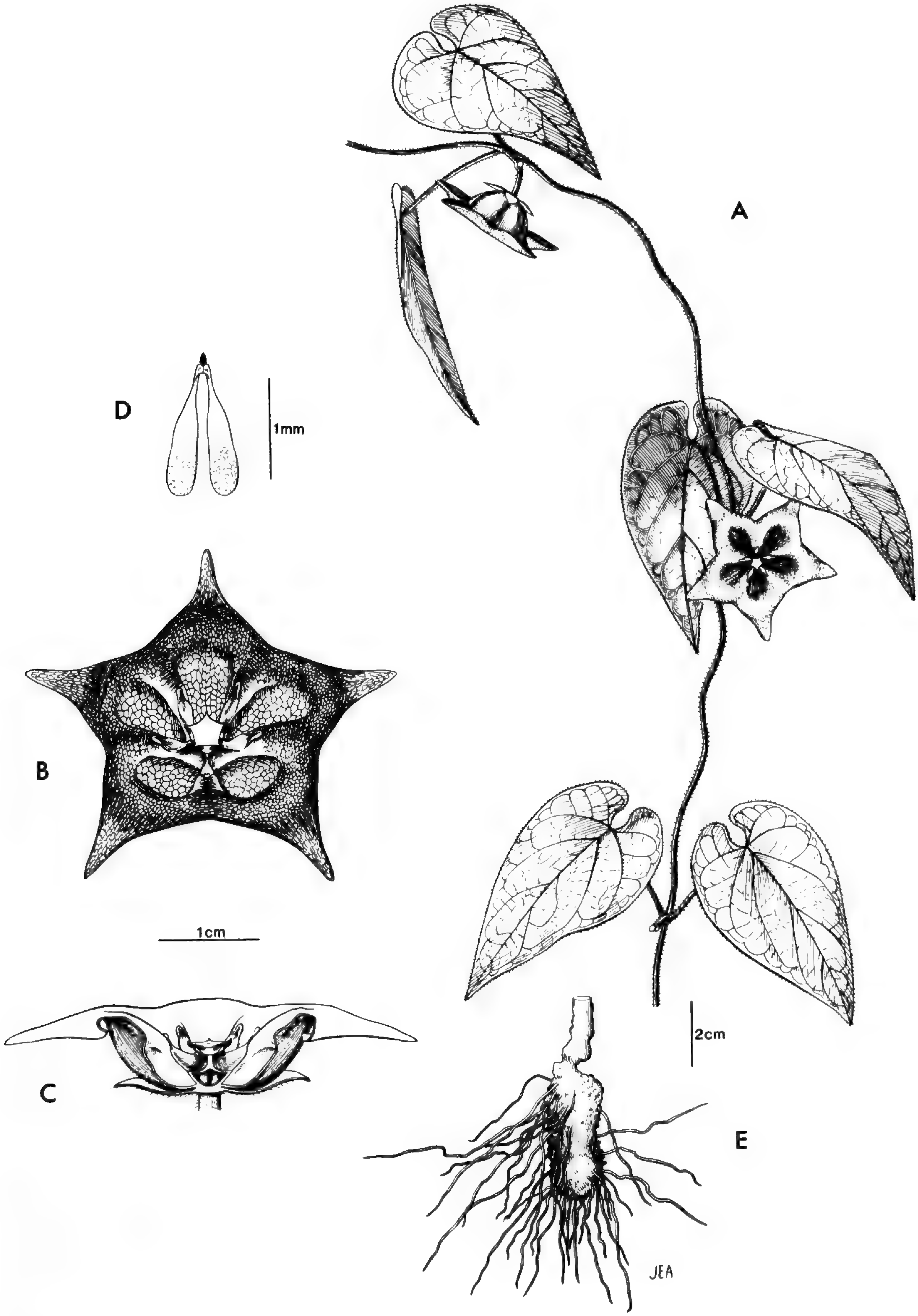

FIGURE 14. Matelea dictyantha *(A–D from* Stevens C-105, *a cultivated specimen of* Graham 1231; *E from* Stevens 1311*)*.—*A. Section of flowering stem.*—*B, C. Flowers.*—*D. Bipollinium.*—*E. Caudex.*

species in his new genus, but he neither named nor described it. *Galeotti 1563* is indeed a different species, *Matelea standleyana.*

As with *M. hemsleyana,* two somewhat distinctive elements of *M. dictyantha* can be recognized, but it does not seem that they warrant taxonomic recognition on the basis of currently available material. The flowers of the Morelos and Guerrero element tend to be larger, more shallowly campanulate, and much lighter in color than the Puebla-Oaxaca element. In this case the ranges are apparently distinct, but I have found no objective way of describing the difference in dried specimens. Perhaps with additional field study their separation will become more feasible. In this connection, it is most likely that the specimens of *Ghiesbreght s.n.* from "province d'Oaxaca" were actually collected at Cuernavaca, Morelos; such mixing of labels apparently often occurred with Ghiesbreght specimens.

11. Matelea suffruticosa W. D. Stevens, sp. nov. TYPE: México. Oaxaca: 4 mi. W of junction of Mex. 185 with Mex. 190, near La Ventosa, 17 Aug. 1971 (fl), *Wunderlin, Dwyer, Spellman & Vaughn 800* (holotype, MO; isotype, MEXU). Figure 15.

Matelea suffruticosa W. D. Stevens; *M. yucatanensis* atque *M. aeneae* affinis coronae apicibus propriis sed inter species subgeneris *Dictyanthi* forma corollae (tubo anguste campanulato, limbo in sinibus abrupte reflexo, lobis erectiusculis) notabilis.

Plants apparently suffrutescent with twining tips. Woody stems with thin corky bark, herbaceous stems with dense short and glandular trichomes and moderately dense uncinate long trichomes to 1.5 mm long. Leaf blade ovate to wide-ovate, 40–51 mm long, 27–39 mm wide, indumentum of short and glandular trichomes on and near major veins and moderately dense (above) to dense (below) uncinate long trichomes, surface smooth, apex acuminate, base lobate, lobes descending, with 5–7 acropetiolar colleters, margin somewhat thickened, revolute, and crispate; petiole 36–53 mm long, with indumentum of stem. Inflorescence sometimes with a smaller adjacent cyme apparently produced lateral to the axillary bud, that is, originating between the axillary bud and the normal extra-axillary inflorescence; peduncle to 1 mm long, with dense short and glandular trichomes; bracts linear to lorate, margins mostly revolute, 1–2 mm long, with short, glandular, and uncinate long trichomes abaxially, glabrous adaxially; pedicel 1.5–2.5 mm long, with indumentum of stem. Calyx lobes decurrent on pedicel, elliptic to wide-elliptic, 3.3–4.5 mm long, 1.6–1.7 mm wide, apex acute, with one colleter below each sinus, abaxial surface with dense short, glandular, and uncinate long trichomes, adaxial surface glabrous. Corolla narrowly campanulate, base to sinus length 5.5–6.5 mm, limb sharply reflexed at each sinus; lobes 4–5 mm long, apex rounded, apparently erect, margins revolute; tube glabrous within, limb and lobes with stiff, erect, glassy, apparently unicellular trichomes 0.1–0.2 mm long, outer surface of corolla with dense short, glandular, and uncinate long trichomes; tube apparently suffused with deep purple, becoming purple-reticulate on limb and lobes. Corona lobes 3–3.5 mm long, linear-spathulate with tip deeply convoluted, glistening purple-black, separate to base, base (below style apex) yellow and glistening. Gynostegium ca. 2 mm high and 1.5 mm wide at apex, short-stipitate, apex nearly plane with corpuscula forming high points and center slightly convex, terminal anther appendages covering about half of apex. Corpusculum ca. 0.25 mm long, 0.17 mm wide, pollinia ca. 0.53 mm long, 0.37 mm wide. Fruits and seeds unknown.

Known only from the type collection, from the south side of the Isthmus of Tehuantepec (Fig. 13), probably below 100 m elevation.

This new species has some striking innovations but nonetheless fits easily into the subgenus and, despite its distinctive appearance, is probably closely related to the two species from the Yucatan. The exaggerated development of the corolla limb at the sinuses, which even at the bud stage is obvious as the sinuses have the appearance of recurved horns, causes the modified tips of the corona lobes to be presented in a unique fashion, at the distal margin of the limb, with which they contrast in color, between the erect and revolute corolla lobes. The hairs on the inside of the corolla, the occasional subsidiary inflorescences, and the roundish (rather than pentagonal) style apices appear to be unique in the subgenus but not in the genus as a whole. The highly modified tips of the corona lobes suggest a link between this species and the two Yucatan species, as does similarity in indumentum.

12. Matelea aenea (Woodson) W. D. Stevens, comb. nov. *Dictyanthus aeneus* Woodson, Amer. J. Bot. 22: 691, pl. 1, fig. 4. 1935. TYPE: México. Yucatán: Progreso, 11–15 Aug. 1932 (fl), *Steere 3005* (holotype, MO; isotype, MICH). Figure 16.

Plants twining vines. Stems woody below, with thin to thick corky bark, herbaceous stems with

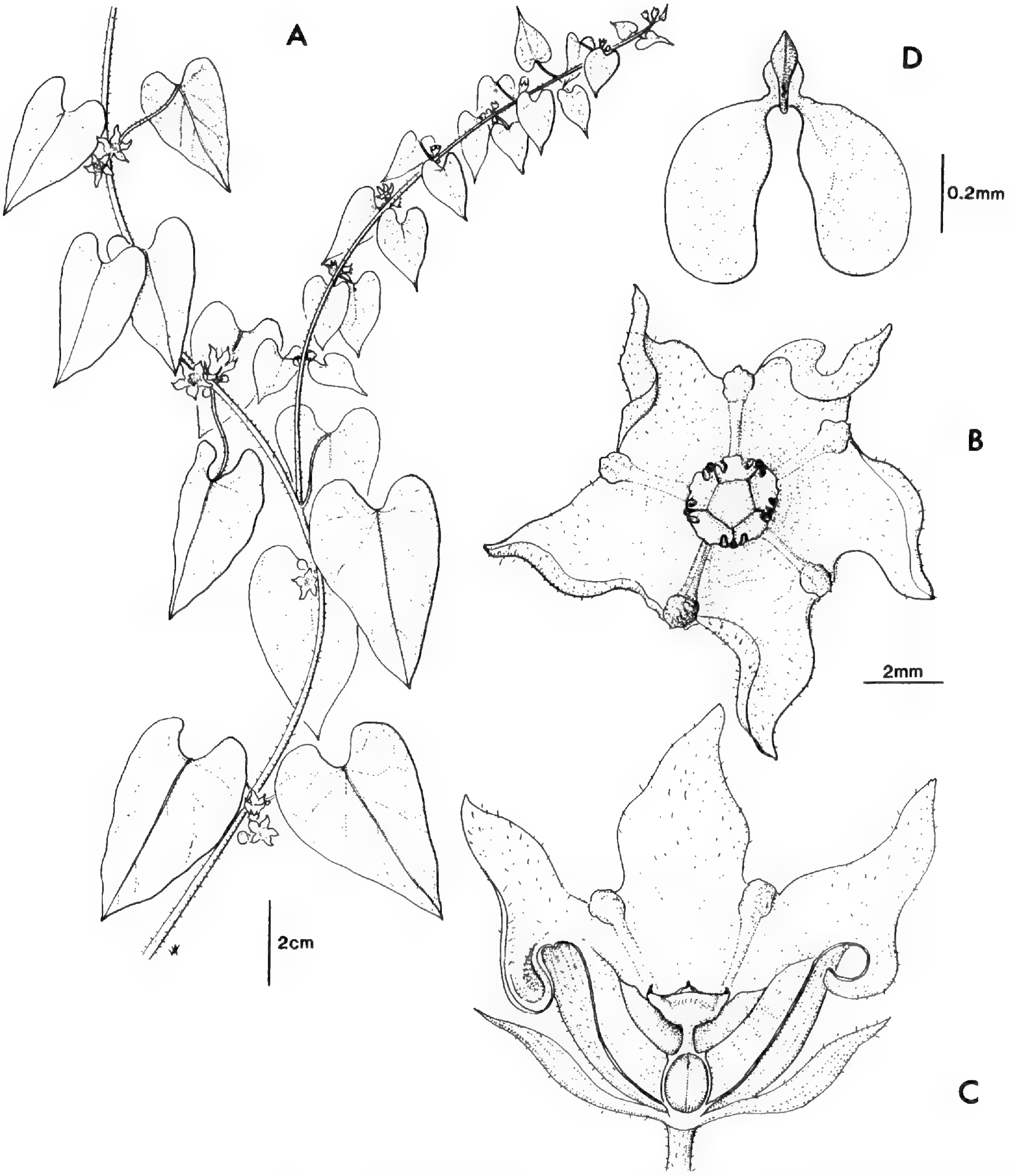

FIGURE 15. Matelea suffruticosa (Wunderlin et al. 800).—*A. Section of flowering stem.—B, C. Flowers.— D. Bipollinium.*

dense short and glandular trichomes and dense uncinate long trichomes to 2.5 mm. Leaf blade wide-ovate to very wide-ovate or occasionally ovate, 35–98 mm long, 26–70 mm wide, indumentum of uncinate long trichomes and of glandular trichomes on veins below, surface smooth, apex acute to acuminate, base lobate, lobes convergent to widely divergent, with 4–11 acropetiolar colleters, often crispate; petiole 21–62 mm long, with indumentum of stem. Peduncle 4–11 mm long, with indumentum of stem; bracts linear to lanceolate, 3–4 mm long, with indumentum of stem or occasionally glabrous on adaxial surface; pedicel ca. 4 mm long, with indumentum of stem. Calyx lobes lanceolate to narrow-ovate, 6–9 mm long, 2–4.5 mm wide, apex acute to attenuate, with 1(2) colleter(s) below each sinus, abaxial surface with dense short, glandular, and uncinate long trichomes, adaxial surface

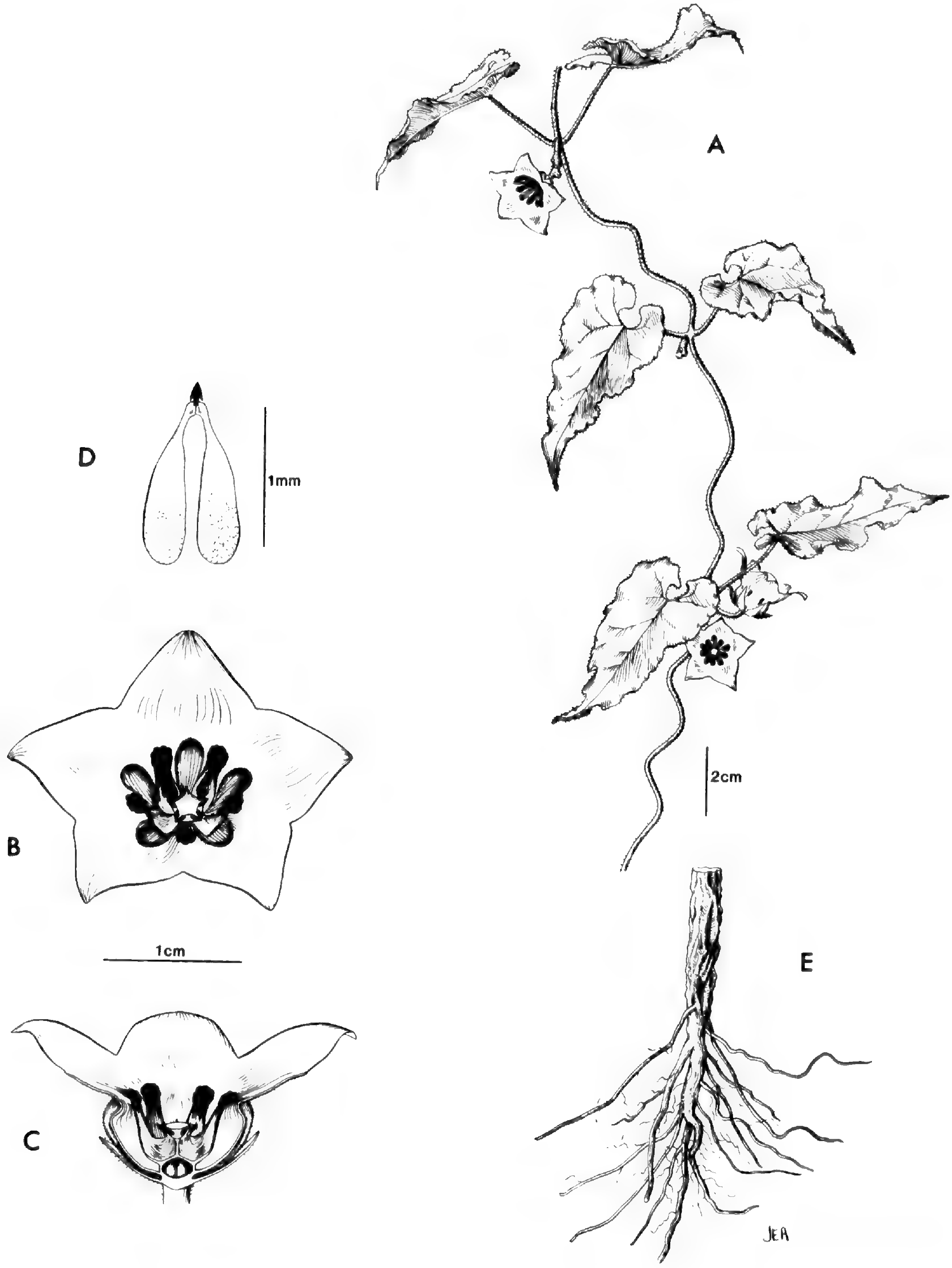

FIGURE 16. Matelea aenea *(A–D from* Stevens C-157, *a cultivated specimen of* Stevens 1145; *E from* Stevens 1145*).—A. Section of flowering stem.—B, C. Flowers.—D. Bipollinium.—E. Base of stem.*

glabrous. Corolla campanulate, base to sinus length (6–)8–12 mm, limb ascending to nearly patent, not revolute; lobes 5–9 mm long, length to width (sinus–sinus) ratio 0.67–0.78, apex acute or rounded, ascending to slightly reflexed at tip, margin not revolute; glabrous within except with dense short trichomes on limb and lobes, indumentum on outside of short, glandular, and uncinate long trichomes; tube convoluted with raised parts opposite corona lobes and forming deep sacs between them; pale yellow-green, sometimes with faint reticulations, these often drying darker. Corona lobes 6–8 mm long, linear-spathulate in outline with tip deeply rugose and glistening purple-black, otherwise yellow-green or tinted purple, connate at base, adnate by a thin septum to gynostegium, this septum continuing as a narrow ridge nearly the length of the lobe. Gynostegium ca. 3 mm high and ca. 2.5 mm wide at apex, stipitate, apex broadly and shallowly concave with corpuscula as high points and occasionally also slightly convex in center, terminal anther appendages hardly covering margin of apex. Corpusculum 0.21–0.28 mm long, 0.12–0.15 mm wide, pollinia 1.08–1.18 mm long, 0.35–0.37 mm wide. Follicles ca. 95 mm long, ca. 20 mm wide, finely mottled, probably green and white, with scattered short and glandular trichomes, with ca. 40 thick projections to 2 mm long. Seeds ca. 4.5 mm long and 3 mm wide, with a raised, radially grooved margin, this essentially entire, inside this margin essentially flat on one side and convex on the other, both sides deeply verrucate to deeply rugose, dark brown; coma ca. 40 mm long.

Collected only in the vicinity of Progreso, on the tip of the Yucatan Peninsula (Fig. 10), at near sea level. Growing in low scrub vegetation in thin, limestone-derived soils, apparently where not particularly saline. Collected flowering June–August and in December.

In describing *Dictyanthus aeneus*, Woodson (1935) summarized the differences as follows: "*T. aeneus* differs from *T. yucatanensis* Standl. [sic] superficially in the smaller and more shortly petiolate leaves with paler color and hispidulous or strigillose surfaces, and smaller, paler corollas with a more pronounced campanulate tube. Structural differences of the corolla and corona are conspicuous as well." Later, Woodson (1941) considered *Dictyanthus aeneus* to be a synonym of *Matelea yucatanensis* (Standley) Woodson and so annotated the type specimen. I concur with his original recognition of *Dictyanthus aeneus*, but unfortunately his characters are not very diagnostic and, in fact, his drawing of the flower (Woodson, 1935; pl. 1, fig. 4a) has the shape of *Matelea yucatanensis* and the size of *M. aenea*. The best characters for separating the two species are most easily observable in fresh flowers. The corolla limb and lobes of *Matelea yucatanensis* form essentially a right angle with the tube and have revolute margins, while those of *M. aenea* are ascending and do not have revolute margins. This difference can often still be seen in dried specimens when not carefully pressed. The corolla color is also strikingly different in fresh flowers, being yellow-green with faint reticulations in *M. aenea* and densely gray-purple-reticulate in *M. yucatanensis*. Unfortunately, *M. aenea* sometimes darkens in drying and this difference is partially obscured. The most dependable floral characters in pressed specimens are the size and shape of the corolla lobes, but even with these the flowers often require boiling to be measured accurately. As noted in the descriptions, *M. aenea* has shorter and proportionately wider corolla lobes. There seem to be certain vegetative differences as well, but the variation within each species is large and there are too few specimens to make possible any meaningful conclusions. *Matelea aenea* tends to have denser long trichomes on the vegetative parts and smaller, wider, more crispate, and less purple-pigmented leaves. Although obviously very closely related and the only two species of the subgenus *Dictyanthus* occurring on the Yucatan Peninsula, *M. aenea* appears to be restricted to the coastal area immediately around Progreso, while *M. yucatanensis* is found at scattered, mostly inland, localities. Both species are too poorly collected, however, to support much conjecture on their relative distributions.

13. Matelea yucatanensis (Standley) Woodson, Ann. Missouri Bot. Gard. 28: 237. 1941. *Dictyanthus yucatanensis* Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 37. 1930. TYPE: México. Yucatán: without precise locality or date (fl), *Gaumer 933* (holotype, F; fragment of holotype, G). Figure 17.

Plants twining vines. Stems woody below, with thin to thick corky bark, herbaceous stems with dense short and glandular trichomes and dense uncinate long trichomes to 2.5 mm long. Leaf blade ovate to wide-ovate or occasionally very wide-ovate, (39–)45–95 mm long, 24–81 mm wide, indumentum of uncinate long trichomes and also glandular trichomes on veins below, surface smooth, apex acuminate to attenuate, base lobate, lobes mostly

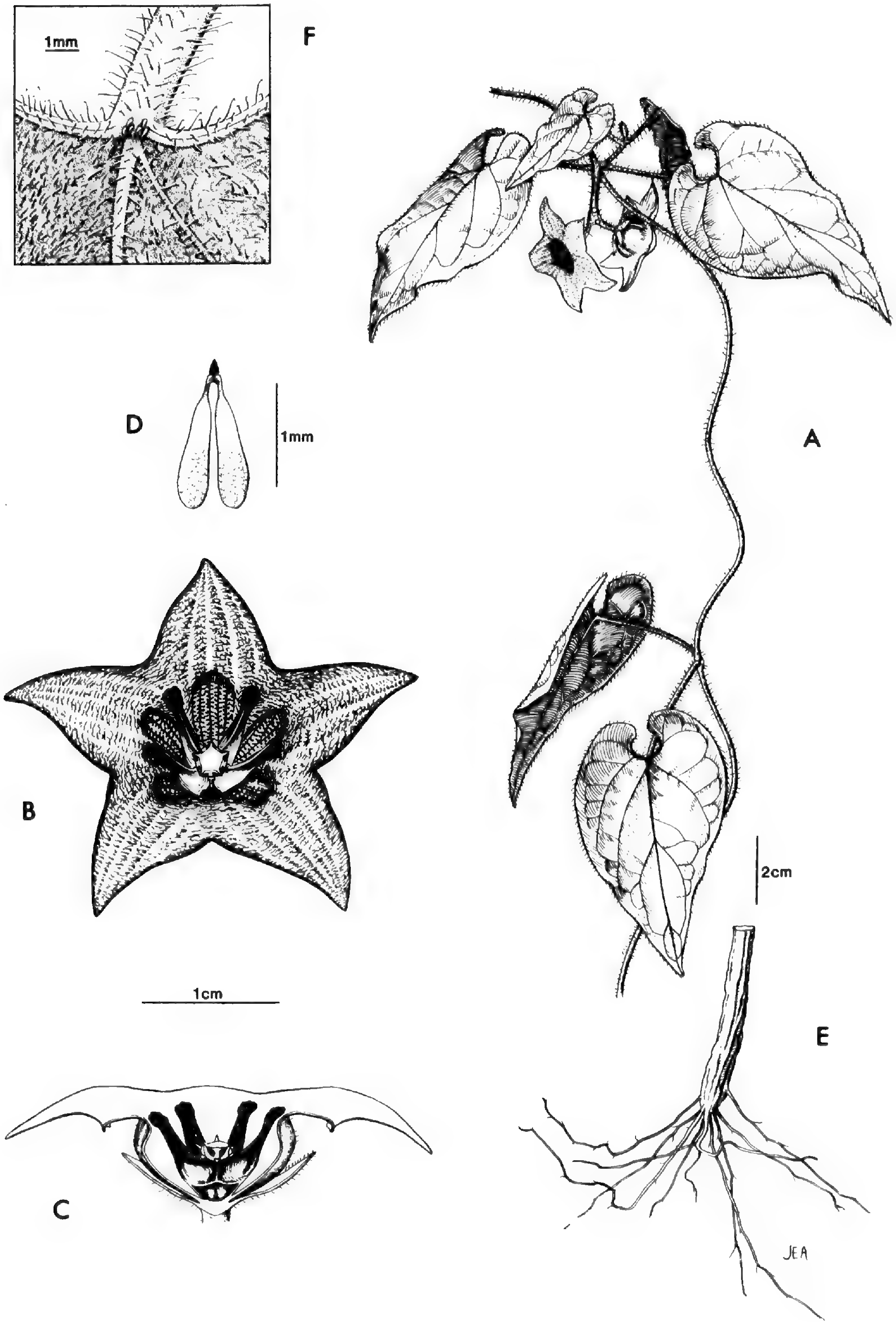

FIGURE 17. Matelea yucatanensis (Stevens C-158, *a cultivated specimen of* Stevens 1168).—*A. Section of flowering stem.—B, C. Flowers.—D. Bipollinium.—E. Base of stem.—F. Base of adaxial surface of leaf blade, showing acropetiolar colleters.*

convergent to descending, with 4–10 acropetiolar colleters, margin often crispate; petiole (22–)42–57(–82) mm long, with indumentum of stem. Peduncle 2–9 mm long, with indumentum of stem; bracts linear to lanceolate, 3–5 mm long, with indumentum of stem or sometimes with long trichomes on margin only and glabrous on adaxial surface; pedicel 3–5(–7) mm long, with indumentum of stem. Calyx lobes lanceolate to narrow-ovate, 7–10 mm long, 2–3.5 mm wide, apex acute to attenuate, with 1(2) colleter(s) below each sinus, abaxial surface with scattered short trichomes, dense glandular trichomes, and scattered uncinate long trichomes or occasionally nearly glabrous, adaxial surface glabrous. Corolla campanulate, base to sinus length (7–)10–11 mm, limb patent, revolute; lobes 7–12 mm long, length to width (sinus–sinus) ratio 0.83–1.20, apex acute, patent or slightly reflexed at tip, margin revolute; glabrous within except with sparse to dense short trichomes on limb and lobes, indumentum on outside of short, glandular, and uncinate long trichomes; tube convoluted with raised parts opposite corona lobes and forming deep sacs between them; densely gray-purple-reticulate, reticulations wider in tube. Corona lobes (4–)5–7 mm long, linear-spathulate in outline with tip deeply rugose and glistening purple-black, otherwise deep purple, connate at base, adnate by a thin septum to gynostegium, this septum continuing as a narrow ridge nearly the length of lobe. Gynostegium 3–3.5 mm high and 2.5–3 mm wide at apex, stipitate, apex broadly and shallowly concave with corpuscula as high points and occasionally also slightly convex in center, terminal anther appendages hardly covering margin of apex. Corpusculum 0.24–0.26 mm long, 0.12–0.15 mm wide, pollinia 1.11–1.26 mm long, 0.28–0.35 mm wide. Follicles ca. 95 mm long, ca. 15 mm wide, finely mottled green and white, with scattered short and glandular trichomes, with ca. 55 thick projections to 4 mm long. Seeds ca. 4.5 mm long and 3.5 mm wide, with a raised, faintly radially grooved margin, this entire, inside this margin essentially flat on one side and convex on the other, both sides deeply verrucate to deeply rugose, dark brown; coma ca. 35 mm long.

The identifiable collection localities are scattered in the state of Yucatan (Fig. 10), at elevations probably well below 200 m. Almost certainly to be expected in the adjacent areas of Campeche and Quintana Roo. Growing in low forests and second growth and probably always in limestone-derived soils. Collected flowering in June, July, and October and fruiting in October.

Most closely related to *Matelea aenea*; for comparison see discussion under that species. These two species form a distinct unit morphologically and are geographically isolated from the other species of subgenus *Dictyanthus*. They are obviously related to *M. suffruticosa* and the several species grouped with *M. pavonii* but have clear affinities only with the former. Their most conspicuous innovation, besides occupying a unique region and a unique environment (karst limestone), is the highly modified tip of the corona lobe. These tips glisten as if they are wet but apparently produce no secretion. They may function as "pseudonectaries." It should be noted, however, that the sides of the corona lobes are secretory in apparently the same manner as the species grouped with *M. pavonii*. These two species, along with *M. suffruticosa*, are also unique in having predominantly uncinate long trichomes on the internodes, the other species considered here having either entirely straight or only occasionally a few uncinate long trichomes on the internodes.

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FLORA OF THE VENEZUELAN GUAYANA—VI[1]

Julian A. Steyermark[2]

ABSTRACT

Studies in the genus Sloanea *(Elaeocarpaceae) for the* Flora of the Venezuelan Guayana *have yielded changes in nomenclature and taxonomic concepts in addition to the following new taxa:* Sloanea bolivarensis, S. cataniapensis, S. davidsei, S. longiaristata, S. merevariensis, S. parvifructa, S. sipapoana, S. steyermarkii *subsp.* autanae, S. steyermarkii *subsp.* jauaensis, S. subpsilocarpa, *and* S. wurdackii. *Notes pertaining to the families Rapateaceae, Bombacaceae, and Theaceae are included.*

RAPATEACEAE

In preparing the treatment of Rapateaceae for the *Flora of the Venezuelan Guayana*, a number of discrepancies have been noted in the previous treatments by Maguire (1958, 1982). In the interest of placing these observations on record before the publication of the flora, the following data are presented.

AMPHIPHYLLUM

Amphiphyllum rigidum Gl.

Maguire (1982: 105) gave the length of the involucral bracts as 3–4 cm long. On the three specimens in VEN they measure 2–2.5 cm long.

CEPHALOSTEMON

Cephalostemon vs. *Duckea*

Maguire (1958) separated *Duckea* on the basis of the exappendiculate seeds. I am unable to separate *Duckea* from *Cephalostemon* on gross morphological characters. They merge as noted in such species as *Duckea squarrosa* and *Cephalostemon gracilis* and should be combined under the earlier-published *Cephalostemon*.

Duckea flava becomes *Cephalostemon flavus* (Link) Steyerm., a new combination.

Cephalostemon flavus (Link) Steyerm., comb. nov. *Duckea flava* (Link) Mag., Mem. New York Bot. Gard. 10(1): 43. 1958.

Cephalostemon junciformis (Mag.) Steyerm., comb. nov. *Duckea junciformis* Mag., Mem. New York Bot. Gard. 10(1): 43, fig. 1. 1958.

Cephalostemon flavus vs. *Cephalostemon junciformis*

The bracteole apex is acute in *C. junciformis* and obtuse to rounded in the commoner *C. flavus*. Maguire (1958) distinguished them on the basis of the globose inflorescence 1–1.4 cm long of *C. junciformis* contrasted with the oblong inflorescence 2–4 cm long of *C. flavus*. This difference does not hold true: several collections of *C. flavus* have short globose inflorescences 1 cm long. Measurements show the following intergradation:

C. junciformis: heads 0.8–1.5 cm high, broadly hemispherical or subhemispherical.

C. flavus: heads 1–4 cm high, depressed subglobose to cylindric-oblong.

The depressed or subglobose short inflorescences of *C. flavus* are represented by the collections of *Maguire et al. 30800, 37662, 30487*; *Huber 4860, 3115, 3129*; and *Vareschi & Magdefrau 6718, 6590.*

Cephalostemon cyperaceoides vs. *Cephalostemon squarrosus*

In general, heads in *C. cyperaceoides* are 1–1.5 cm broad and smaller than in *C. squarrosus* with heads 2–2.5 cm broad. Yet heads in *C. cyperaceoides* vary in size and may reach 2 cm wide in such collections as *Huber & Medina 5905*. In others, such as *Maguire 29276* (identified as *C. squarrosus*), the heads are 2.5 cm wide, while the mature bracteoles are nerved and long attenuate or subulate but not squarrose. Although the bracteoles of *Steyermark 75323* are strongly nerved, they show varying degrees of squarroseness, some

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[2] *Deceased, October 15, 1988.*

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scarcely or not at all squarrose, others only slightly so.

Also in *C. squarrosus*, specimens are found with strongly nerved squarrose bracteoles, but with small heads only 1.3 cm broad, as in *Vareschi & Magdefrau 6611* (VEN), so that overlapping appears in the sizes of the heads and in the degree of squarroseness. In *Maguire et al. 30799* (identified as *C. squarrosus*), the bracteoles are strongly nerved but are mainly ascending at maturity.

Moreover, *C. squarrosus* and *C. cyperaceoides* do not differ in the type of apex of the bracteole between as described by Maguire in his keys (1958: 42): "bracteoles . . . , apex strongly aristate" in *Duckea cyperaceoides* vs. "bracteoles . . . , apex merely acuminate" in *Duckea squarrosa*. Both have attenuate apices, and no fine distinction can be drawn: the two taxa may have to be merged eventually.

KUNHARDTIA

Kunhardtia rhodantha Mag., Mem. New York Bot. Gard. 10(1): 32, figs. 5, 6. 1958.

Schoenocephalium sipapoanum Mag., Acta Bot. Venez. 14(3): 17. 1984.

Schoenocephalium sipapoanum was based on a collection (*Steyermark et al. 124534*) from the summit of Cerro Sipapo. Although Maguire (1984—see above) noted that it had a general similar aspect to that of *Kunhardtia*, he placed the specimen in *Schoenocephalium* on the basis primarily of its anthers opening by four apical pores instead of being two-celled as in *Kunhardtia*. Other differences thought by Maguire to distinguish the two genera were the conspicuous exsertion of the porrect corollas and depressed-subglobose heads of *Kunhardtia* contrasted with the included corollas and sphaeroidal heads with the mature flowers radiate of *Schoenocephalium*.

These gross morphological characters were observed by the author at the time the type collection was made, and having already seen thousands of individuals of *Kunhardtia rhodantha* on the summit of the nearby Cerro Autana (Steyermark, 1974), the Sipapo collection was noted to be in all respects the same as the common *Kunhardtia rhodantha*. The depressed-subglobose, deep red heads with red, conspicuously exserted porrect flowers, and strongly imbricated leaf sheaths abruptly narrowed at their summits of the Sipapo collection match perfectly the numerous specimens in the colonies of *Kunhardtia rhodantha* seen on the summit of Cerro Autana.

Reexamination and careful comparison of the type collection of *Schoenocephalium sipapoanum* and *Kunhardtia rhodantha* does not reveal any further difference between them. Reexamination of the anthers in the type material of *Schoenocephalium sipapoanum* and *Kunhardtia rhodantha* shows no difference between the two. Moreover, the other characters pertaining to *Kunhardtia* as emphasized by Maguire, together with an examination of additional herbarium specimens, emphasizes the conspecifity of the two taxa.

MONOTREMA

Monotrema aemulans vs. *M. affine*

The key difference separating *M. aemulans* from *M. affine* in Maguire (1958: 46) is that in the former the primary bracts of the inflorescence do not exceed the head or do so only inconspicuously, whereas in *M. affine* they conspicuously exceed the head. However, specimens cited by Maguire, such as *Maguire et al. 30491* from Yapacana savanna, have the bracts somewhat exceeding the heads and are 13 mm long. Thus, *Maguire et al. 30491* could be placed in *M. affine* instead of *M. aemulans*. *Monotrema affine* may have the primary bracts only 10–15 mm long. The isotype of *M. affine*, from Yapacana at VEN, has the longest bracts only 15–16 mm long and barely exceeding the head. The leaves of *M. affine* vary in width from 5–9 mm up to 16 mm in *Huber 5939*, those of *M. aemulans* from 6 to 10(–15) mm. In *M. bracteatum* var. *bracteatum* the leaves are only 2–4(–5) mm wide except in var. *major*, where they are 6–12 mm wide.

Some specimens of *M. aemulans* have bracts usually 8–12 mm long, but in early stages preceding anthesis, as in *Steyermark et al. 130334* from Cerro Vinilla (VEN), they are only 1–5.5 mm long and equal the head, or they are slightly shorter to only slightly longer than the head. The two taxa are otherwise similar vegetatively and occur in the same Yapacana savanna.

The collections *Huber & Tillett 2965* (identified by Huber as *M. xyridoides*) and *Huber & Medina 5939* (identified by Maguire as "*M. affine* with broad leaf blades *vel valde aff.*") are forms with leaves 1.4–1.5 cm wide and leaf sheaths 14–15 cm long, whereas other collections of *M. affine* vary in leaf width from only 0.5 to 0.9 cm. The broadly ovoid heads are also longer than broad as in *M. xyridoides* and are 17–21 mm long × 12 mm broad at the middle. The outer involucral bract is 21 mm long and barely longer than the head. Perhaps these represent introgressive collections of *M. xyridoides* and *M. affine*. *Huber 1640*, identified as *M. bracteatum*, has the shorter broader outer bracts of *M. affine* and the shorter secondary bracts of *M. affine*.

A third species, *M. bracteatum*, with all the bracts elongated, occurs in the Yapacana savanna and occasionally is confused with *M. affine* which has shorter, broader outer bracts.

A fourth species, *M. xyridoides*, with heads usually longer than broad having bracteoles rounded or obtuse, likewise occurs in the Yapacana savanna.

Monotrema bracteatum may be confused with *Cephalostemon cyperacoides* on account of the outer bracts, which in *C. cyperacoides* are reflexed, whereas those of *M. bracteatum* and *M. affine* are spreading to ascending.

Monotrema bracteatum subsp. *bracteatum*

Huber 3268 from W of Serranía El Tigre (identified as *M. affine* by Maguire) represents *M. bracteatum* subsp. *bracteatum* with the bracts and bracteoles long pointed.

Monotrema arthrophyllum (Seub.) Maguire, Mem. New York Bot. Gard. 10(3): 47. 1958. *Schoenocephalium arthrophyllum* Seub. in Mart., Fl. Bras. 3(1): 131. 1847.

This species was originally described from Arara-Coara, Río Caquetá, Colombia. *Maguire et al. 44109* from scrub savanna, Araracuara, identified by Maguire as *M. aemulans* Körnicke, is a topotype of *Schoenocephalium arthrophyllum*. In his English key (1958, p. 46) Maguire gave "5–10-flowered" for *M. arthrophyllum*, as contrasted with "numerous" and "50–75-flowered" for *M. aemulans* in both his English (1958) and Spanish (1982) treatments. This collection matches the photo of the type of *M. arthrophyllum* in shape and width of leaf, abrupt contracted leaf sheath summit at the base of the leaf blade, and much shorter leaves compared with the peduncle length. The leaf blades are strongly 11-nerved on the lower side, 13–14 mm wide, 14–22 cm long, and show the leaf sheath strongly 7–8 nerved. This compares well with the type photo of *M. arthrophyllum*. Although *Maguire et al. 44109* has strongly nerved leaf sheaths, they do appear, although not very sharply, on the type photo of *Schoenocephalium arthrophyllum*.

A specimen from Yavita, Territorio Federal Amazonas (*Williams 14086*, VEN), originally identified by Maguire in 1950 as *M. arthrophyllum*, was later identified by him as *M. aemulans*. Although never cited by Maguire (1958, 1982), this specimen partly agrees with the description and key characters assigned by him (1958) to *M. arthrophyllum* in having fewer spikelets with heads which are not subdidymous. However, the linear leaves are only 3.5–7 mm wide, whereas in the photo of the type of *Schoenocephalium arthrophyllum* they are broader. The *Williams 14086* specimen from Yavita does not match either the photo or the *Maguire et al.* collection from Colombia. Its much narrower leaves 3.5–7 mm wide merge, but not abruptly, at the base into the leaf sheath, which is 6 cm long and 4 mm wide. Also, the leaf blade and sheath are not strongly nerved as in the Colombian collections and are 21–25 cm long. The head is 8 mm wide and hemispheric as in *M. aemulans*, but the head is too small and few-flowered to be placed in *M. aemulans*. Probably, as Huber concluded, the specimen represents a depauperate inflorescence form of *M. xyridoides* rather than a form of *M. aemulans*, as *M. arthrophyllum* was interpreted by Maguire.

PHELPSIELLA

Phelpsiella ptericaulis Maguire

The genus is described in Maguire's (1958) generic key as having yellow petals, but the *Hoyos & Morillo 518* collection from Laguna Asisa, Cerro Asisa, Serranía Parú indicates that the flowers are white. The winged strongly compressed stem and narrow leaf blades are strongly reminiscent of *Stegolepis breweri* Mag.

SCHOENOCEPHALIUM

Schoenocephalium cucullatum vs. *coriaceum*

The distinctions made between *S. cucullatum* and *S. coriaceum* (in Maguire's key, 1958: 37) were based on the relative distance separating the upper bracteoles and the tip of the sepals (in *S. coriaceum* the sepals exceed "the upper bracteoles by (3)4–5 mm in length," whereas in *S. cucullatum* the sepals exceed the upper bracteoles "2(3) mm or less in length." Also, the width of 14–16 mm is given for the leaf blades of *S. coriaceum* contrasted with that of "2.0–3.5 cm" for *S. cucullatum*. These differences have been found inconstant. It should be noted that although Maguire described the leaves of *S. cucullatum* in his key as "2.0–3.5 cm broad," none of the specimens from VEN, including the paratype (*Maguire et al. 37631*) and the isotype (*Maguire et al. 30486*) of *S. cucullatum* have leaf blades exceeding 1 cm.

Moreover, of all the specimens examined at VEN of *S. cucullatum* determined by Maguire, the leaf blades vary from 0.8 to 1.7 cm broad, those in *S. coriaceum* varying from 0.5 to 1.3 cm. With the material at hand, the specimens cannot be separated on either of these characters and, in combining them as conspecific, I am employing the binomial *Schoenocephalium cucullatum.*

It should also be noted that in *S. teretifolium* the sepals exceed the upper bracteoles by distances of 6–10 mm instead of, as stated, by "(3–)4–5 mm" (1958). The same error occurs in *S. cucullatum,* where the sepals exceed the upper bracteoles by 2–4 mm and in *S. coriaceum* by 2–6 mm.

Schoenocephalium martianum Seub.

It is probable that *S. martianum* Seub. may eventually be considered synonymous with *S. cucullatum,* in which case *S. cucullatum* has priority. However, differences in sepal length in relation to the bracteoles, leaf sheaths, and leaf blades appear to justify their separation for the present. The leaf sheaths in *S. cucullatum* are shorter and terminate more abruptly at the base of the leaf blade, whereas in *S. martianum* the leaf sheaths are more elongated and merge at their summit more directly with the leaf blade. In *S. martianum* the sepals exceed the upper bracteoles by 7–10 mm. Also, the leaves are longer in *S. martianum* than in *S. cucullatum* and *S. coriaceum.* I have seen a topotype of *S. martianum* from Colombia (*Maguire et al. 44179* VEN, scrub savanna Araracuara, Vaupés).

SAXOFRIDERICIA

Saxofridericia duidae vs. *S. grandis*

The separation of *S. grandis* from *S. duidae* on the basis of the presence of a petiole between the base of the leaf blade and the summit of the leaf sheath is not evident on some specimens. In his (1958) key, Maguire differentiated them as follows:

Petioles absent, the leaf passing directly from the summit of the leaf sheath to the leaf blade . . *S. duidae*
Petioles 10–15 cm long, uniting the summit of the leaf sheath with the leaf blade proper . . . . . *S. grandis*

However, in *Huber 4426,* a topotype of *S. grandis* from Serranía Parú, the length of the petiolar portion varies from only 1 to 2 cm long to as much as 8.5 cm long in *Huber 4347,* also from Parú. Although the description of *S. grandis* gives 10–15 cm as the length of the petiolar portion, the isotype (*Cowan & Wurdack 31115*) at VEN has the petiolar portion only 4 cm long. Maguire (1958) stated that *S. grandis* is the only species of subgenus *Saxofridericia* to have developed a distinct petiole. In Huber's specimens the summit of the peduncle beneath the head is sharply angled, flattened, glaucous, and broadened to 2–2.7 cm. The leaf blades in *S. grandis* vary from 3.5 to 4.5 cm wide (4–5.5 cm wide according to Maguire). The sheath in *S. grandis* is strongly indurated and 4–7 cm wide.

Saxofridericia duidae, confused with *S. grandis,* does not possess a petiolar portion between the summit of the sheath and the base of the leaf blade, the sheath is narrower (2–3 cm wide), less indurated, conspicuously carinate dorsally, the peduncle below the head narrower (1.2–1.7 cm wide), less conspicuously ampliated, with stronger ribbing, and the leaf blades mainly narrower (2.5–3.5–4) cm, but overlapping the measurements of *S. grandis.* However, although the other specimens of *S. duidae* lack petiolar interruptions between the leaf sheath and the leaf blade, the VEN paratype of *S. duidae* (*Maguire & Maguire, Jr. 29122*) has an elongated petiolar portion 10–18 cm long, although it has the narrower leaf blades, narrower leaf sheath with dorsal keel, and narrower apical part of the peduncle characteristic of *S. duidae.* The base of the leaf blade in this specimen is so narrowly attenuate as to appear petiolate and could be interpreted as sufficiently petiolate as the material seen of *S. grandis.*

An additional character, however, for differentiating the two taxa is that in *S. duidae* the bracteoles surrounding each flower are more conspicuously pungent and more conspicuously imbricate with looser, longer, narrower apices, whereas in *S. grandis* the bracteoles are more appressed, with shorter, less pungent tips from a more broadly shaped contour. This paratype thus breaks down the distinctions between the two taxa, which are otherwise separated by the differences enumerated above.

Saxofridericia compressa vs. *S. spongiosa*

Maguire's dimensions given for the diameter of the heads, peduncles below the summit of the head, and the leaf width do not apply to collections from VEN not seen or not annotated by him. Thus, the width of leaf blades separating *S. compressa* and *S. spongiosa* (4–5 cm against 7–10 cm broad respectively) must be changed to 3–8 cm and 4.5–9 cm, respectively.

Saxofridericia petiolata vs. *S. inermis*

The fibrous marcescent character of the leaf sheaths of *S. petiolata* versus the nonmarcescent, nonfibrous character of *S. inermis* is not apparent on specimens identified by Maguire. Although used as one of the separating key characters (1958), it does not serve to identify most extant herbarium material.

STEGOLEPIS

Stegolepis microcephala Maguire

This is keyed out by Maguire as having the "mature sheaths hardened and nerveless." However, the type specimen has the sheath clearly nerved.

Stegolepis membranacea Maguire

The bracteoles are described as somewhat obtuse, but in *Steyermark et al. 129658* from Marahuaca, the bracteoles are subacute, and the sheath and the summit of the auricle have thin brown margins. The specimen is referred to *S. membranacea* because of the nerved sheath (in the upper part) and lack of broad white scarious auricle.

Stegolepis neblinensis Maguire

This species was placed in the section having spikelets 5–50, but in *S. neblinensis* the spikelets are only 1–3 (peduncles 2–4). In the Spanish key (*Fl. Ven.*) there is confusion in the couplet "10" which gives "sepals" not reflexed.

If the indurated sepals are absent, and only the bracteoles remain, then the length measurement is only 2 cm instead of the "2.5–3.5 cm" given for this species.

Stegolepis parvipetala Steyerm.

On the basis of the number of spikelets, supposed to be "70–100," the isotype (VEN) cannot be properly disposed, since the spikelets are less than 70 (actually there are 50 or fewer), thus relegating it to another part of the key. The key on p. 109 (1982, *Fl. Ven.*) gives the length of the spikelets as "10–16" mm. However the text (p. 120) gives "14–16" mm. In the key to the subspecies, the spikelets are "14–15" in subsp. *parvipetala* and "10–12" in subsp. *chimantensis*.

Stegolepis parvipetala is characterized by the rounded or broadly obtuse apices of the lower and middle bracteoles, blunt apex of the spikelet, thick diameter of the peduncle, conspicuously swollen summit of the trigonous summit of the peduncle, and small petals.

Stegolepis pauciflora Gleason

Although this species is placed by Maguire in that part of the key (1982, *Fl. Ven.*, p. 111) having "auricles of the sheath not ligulate," actually they may attain a length of 25 mm, whereas in *S. hitchcockii* they are ca. 10 mm long.

Stegolepis ptaritepuiensis Steyerm.

The key (1958) gives leaf blades "2–2.5 cm" wide, but the text states "2–4.5 cm" wide.

Stegolepis pungens Gleason

The key in *Fl. Ven.* (1982: 110) gives spikelet measurement "3–8.8" cm. It should be "3–3.8" cm as given in the text. Actually some spikelets are less than 3 cm (2.5–2.8 cm).

Stegolepis steyermarkii Maguire

This species is poorly segregated in the key on the basis of the nervation of the leaf sheaths and their relative thickness or induration. Although nerves may be present along the margin, they are not always present on the rest of the sheath as in some other species. The sheaths may be indurated, as in *Steyermark et al. 92498*, making it difficult to determine into which part of the key to place the specimen.

Stegolepis steyermarkii vs. *S. ferruginea*

Although these two species are very similar, they may be distinguished by the key characters given by Maguire (1965: 71), with *S. steyermarkii* having narrower and longer leaf sheaths, glabrous vs. minutely puberulent petals, narrower leaf blades (not given by Maguire), a more conspicuous, broader, and more elevated midrib below, and a more attenuate narrower leaf apex.

Although the two species are apparently distinct, it should be noted that the length of some leaf sheaths of *S. steyermarkii* is not as long as that originally stated, i.e., 15–20 × 4.5 cm in text (18–20 × 3.5–4.5 cm in key). The type specimen shows the basal part of the plant with the sheath length complete. However, one of the paratypes (*Steyermark & Nilsson 296* NY) has a lone sheath only 12.5 cm long, taken from an inner relatively shorter sheath. Other collections, such as *Croat*

53998, have sheaths 16 cm long. The latter specimen has the sheathing portion cut off above the base so that the length shown is not complete.

Stegolepis vivipara

Examination of the isotype (*Steyermark & Wurdack 332*) at VEN shows only 15–20 spikelets and not 25–35 as stated in the original description. The heads are 3.5 cm in diameter. The bracteoles are ± 20–25 and not "ca.16" as given by Maguire (1965). They are orbicular or orbicular-ovate, as stated, and pale brown with scarious margins. The midnerve is prominent below with many fine nerves, but much less manifest than in *S. parvipetala* and subsp. *chimantensis*. The upper leaf surface has many fine nerves with a sulcate midrib as in *S. parvipetala*. The leaf sheath is soft, papyraceous, or submembranaceous and has many fine, closely crowded nerves. The leaf apex is subacute or narrowed to an obtuse or subobtuse apex. The broadly obovate petals, described as 22–24 mm long by Maguire (1965), are only 15 mm long and 12 mm wide in the dried state. The sepals are many-costate and 3.5–5 mm wide (3–4 mm as given by Maguire).

All the bracts of a spikelet are more or less uniformly broadly suborbicular-ovate, obtuse, or subobtuse, whereas in *S. angustata* the upper ones are more narrowed to a subobtuse or subacutely obtuse apex and are relatively longer than broad. In *S. vivipara* the bracts are more uniform and only slightly longer than broad. Also, the bracts of *S. vivipara* are paler and have more scarious margins and a brown apex when contrasted with *S. angustata*, in which the bracts are darker brown and lack scarious margins and a brown apex.

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NOTES ON *SLOANEA* (ELAEOCARPACEAE) IN THE VENEZUELAN GUAYANA

The following notes are based on a treatment of the genus *Sloanea* in preparation for a *Flora of the Venezuelan Guayana*. This has necessitated a study of newly collected material obtained from recently completed expeditions to previously unexplored areas, as well as a restudy of specimens identified by previous workers. I am grateful to the curators of F, GH, NY, US, and VEN for the loan of critical material.

As a result of the present study, nine new species are recognized, and critical comments on other species are given. The revision by C. E. Smith (1954) on the New World species of *Sloanea* elaborated 62 species, of which nine included taxa from the Venezuelan Guayana and eight species from other parts of Venezuela. An additional species, *S. floribunda* Spruce ex Benth., collected at San Carlos de Rio Negro, was erroneously ascribed to Brazil instead of Venezuela. Two additional species from the Venezelan Guayana, *S. crassifolia* and *S. steyermarkii*, were published by Smith in 1962 and 1967, respectively. Steyermark and Marcano-Berti described *S. megacarpa* from the Guayana in 1966, and additional taxa originating from the Venezuelan Guayana were described by Steyermark in 1976 and 1978. Species not originally cited by Smith are now known to occur in the Venezuelan Guayana as a result of recent expeditions into that territory. They include, in addition to those published since Smith's revision and the nine described below, *S. caribaea*, *S. guianensis*, *S. pubescens*, *S. multiflora*, *S. robusta*, *S. synandra*, and *S. terniflora*. *Sloanea pitttieriana* and *S. ptariana*, previously included by Smith as synonyms of other taxa, have been newly studied and found to merit specific recognition.

Sloanea floribunda Spruce ex Benth., J. Linn. Soc., Bot. 5: suppl. 66. 1861.

Sloanea maroana Steyerm., Pittieria 7: 14. 1978.

A reexamination of *S. maroana* Steyerm. shows that it cannot be maintained apart from *S. floribunda*.

Sloanea laurifolia (Benth.) Benth., J. Linn. Soc., Bot. 5: suppl. 70. 1861.

This species was treated by Smith (1954) as highly variable and included *S. oppositifolia* Spruce ex Benth. as well as the collection *Cardona 1951* from the Venezuelan Guayana along the Río Merevari, which was assigned an herbarium name by Pittier but never published. *Schomburgk 936*, upon which *Dasynema laurifolium* Benth. (basionym of *Sloanea laurifolia*) was based, has opposite, acuminate leaf blades identical with that of *Spruce 3689*, the type of *Sloanea oppositifolia* Spruce ex Benth. The leaf blades in both collections are glabrous throughout and ovate- or oblong-lanceolate. *Cardona 1951*, on the other hand, is distinct in having alternate, obovate, rounded leaf blades that are densely tomentose on the upper and lower midnerves. It further differs from the collections of both *S. oppositifolia* and *Dasynema laurifolium* in having acute instead of obtuse awns on the anthers, and styles free to the base instead of shortly parted only at the apex.

Sloanea macrophylla Benth. ex Turcz., Bull. Soc. Imp. Naturalistes Moscow 31(1): 224. 1858.

The dimensions given by C. E. Smith (1954) for the stamens of this species were taken from flowers in a very early stage of anthesis. He described the stamens as "4–6 mm long; filaments 0.5–1 mm long, usually flattened laterally, minutely puberulent; anthers 2–4 mm long, lanceolate, minutely puberulent, connective prolonged into a glabrous awn 0.3–0.5 mm long." However, in other collections referred to this species (*Liesner et al. 20919*) it was noted that as the flowers mature the filaments and appendages of the anthers became more elongated. *Sloanea caudata* Steyerm., placed by Smith (1954) in the synonymy of *S. macrophylla* also has much longer staminal dimensions than those described for that species.

Sloanea pittieriana Steyerm., Fieldiana, Bot. 28: 359. 1952.

This species was reduced to synonymy by Smith (1954) under *Sloanea fendleriana* Benth. *Sloanea fendleriana* was based originally on a specimen collected by Fendler (*2489*) from the Coastal Cordillera of northern Venezuela. *Sloanea pittieriana* was described from a collection originating in the Venezuelan Guayana Highland, some 700 kilometers distant. Reexamination of the type material of these two taxa and study of additional collections shows them to be quite distinct. Although vegetative differences occur, the chief distinctions are found in the termination of the anther and in the spines of the capsule. In *S. pittieriana* the apex of the anther is obtuse and has an obsolete, minute, scarcely discernable knob. By contrast, the anther of *S. fendleriana* terminates in a shortly acuminate summit, originally described by Bentham (1861) as "breviter acuminatae," or as "prolonged into a small puberulent knob or short awn," as described by Smith (1954). Fruiting material of *S. fendleriana* collected near the type locality in Estado Aragua (Pittier National Park, *Pittier & Nakichenovich 15425* VEN), identified by Smith, has merely granulose capsules lacking spines, whereas capsules obtained within the distributional area of *S. pittieriana* and referred to that species have slender, rigid, glabrous spines.

Vegetative differences are likewise evident. In *Sloanea fendleriana* the lateral secondary nerves terminate dichotomously 3–8 mm from the leaf margins, and the veinlets of the lower surface are prominently reticulate. As opposed to this, the lateral nerves of *S. pittieriana*, best observed on the lower leaf surface, usually extend to the margins without branching, although some branching may be present 3–5 mm from the margin. Furthermore, the tertiary venation of the lower surface is less conspicuous, less elevated, and more impressed. Finally, the lateral nerves of *S. pittieriana* are more equidistant than in *S. fendleriana*, the latter with the nerves irregularly spaced.

The following specimens, all from the Venezuelan Guayana, pertain to *Sloanea pittieriana*: BOLÍVAR: Ptari-tepui, *Steyermark 59984* (holotype, F; isotype, VEN); Ptari-tepui, *Steyermark 60261* (F); between Eldorado and Luepa, plateau of Cerro Venamo, *Steyermark & Nilsson 799* (VEN); Amaruay-tepui, *Holst & Liesner 2840* (MO, VEN).

Sloanea ptariana Steyerm., Fieldiana, Bot. 28: 360. 1952.

This taxon, described from Ptari-tepui in the Venezuelan Guayana, was reduced to synonymy by C. E. Smith (1954) under *Sloanea picapica* Standley, a species based on fruiting material from Honduras. The holotype of *S. picapica* (*C. & W. von Hagen 1390* NY), together with additional paratype specimens from Central America, identified as *S. picapica* by Smith, have been restudied by the author. No flowering material of *S. picapica* has been collected up to the present, but Damon Andrew Smith stated in his unpublished thesis (1985) on the Costa Rican species of *Sloanea*, that, although no flowers of *S. picapica* had been seen, stamens were found adhering to very young fruits. He described them as being short-tomentose. His detailed description of the stamens is as follows: "filaments at least 1.7 mm long, 0.04 mm in diameter; anthers 0.6–0.9 mm long, about 0.2 mm wide, basally slightly cordate; anther sacs opening along entire length, but most widely at apex; awn about 0.04–0.08 mm long, obtuse."

Although no flowers of Central American specimens of *Sloanea picapica* were available to C. E. Smith for study, he based his detailed description of the flowers upon the flowering collection of the holotype of *S. ptariana*. However, the stamens of

S. ptariana are quite unlike those found by Damon Smith in *S. picapica.* Although the stamens of *S. ptariana* were originally described as pubescent, reexamination, as verified by C. E. Smith (1954), showed that they were glabrous throughout. In addition to the glabrity of the stamens in *S. ptariana,* the filaments of that taxon are longer (3–3.5 mm) than those of *S. picapica.*

Additional differences between these two taxa may be observed in their leaves. In *Sloanea ptariana* the lateral nerves extend nearly unbranched to the margin and anastomose 1–3 mm from it. In the Central American specimens of *S. picapica* the lateral nerves branch farther from the margin (in *Little 25400,* 4–6 mm from the margin before anastomosing). The apex of the leaf in *S. ptariana,* moreover, is also longer and narrower throughout its length, and 3–6 mm wide at the base; in the Central American specimens of *S. picapica* the apex averages shorter and broader at the base, where it is 7–9 mm wide.

Based upon the staminal and vegetative differences noted between *Sloanea ptariana* and *S. picapica,* I am reinstating the former as a distinct species. This eliminates the previously held erroneous concept of a disjunct geographical range for *S. picapica,* a disjunct range not normally found between Central American and Guayana Highland taxa.

Sloanea bolivarensis Steyerm., sp. nov. TYPE: Venezuela. Bolívar: 7 km NE of Ciudad Píar, 7°28'N, 63°14'W, 350–500 m, 10 Apr. 1981, *Ronald Liesner & Angel Gonzalez 11479* (holotype, VEN; isotypes, MO, NY). Figure 1.

Arbor 25 m, foliorum laminis obovatis apice obtuse acutis basi acutis majoribus 17–20 cm longis 8–11 cm latis, marginibus utroque latere 11–18 repando-dentatis subtus costa media nervis lateralibusque hirsutulis; petiolis 1.7–2.5 cm longis dense hirtellis; inflorescentiis lateralibus umbellatim 2–3-floris, pedunculis 1.5–2 cm longis dense hirtellis; pedicellis 10–15 mm longis dense hirtellis; sepalis quattuor aequalibus 7–9 mm longis; antheris 1.8–2.1 mm longis hispidulis connectivo in acumen hispidulum 1.5 mm longum producto; filamentis 1.2–1.5 mm longis dense hirsutulis; ovario hispidulo, stylo torto glabro.

Tree, 25 m tall, the branches hirtellous. Leaves alternate or subalternate. Petioles 1.7–2.5 cm long, densely hirtellous; leaf blades obovate, obtusely acute at the abruptly prolonged apex, narrowed to an acute base, the larger ones 17–20 cm long, 8–11 cm wide, the margins each side 11–18 repand-dentate or coarsely obtusely dentate; lower midrib and lateral nerves hirsutulous, upper midrib minutely hirtellous, glabrous elsewhere on lower and upper leaf surfaces; lateral nerves 12–16 each side, ascending at 25–30°; tertiary venation finely elevated, minutely reticulate both sides. Inflorescence lateral, near summit of branch, umbellately 2–3-flowered; peduncle 1.5–2 cm long, densely gray-hirtellous; pedicels 10–15 mm long, densely gray-hirtellous. Sepals 4, equal, ovate, acute, 7–9 mm long, 3–5 mm wide, both sides minutely puberulous. Anthers lanceolate, 1.8–2.1 mm long, hispidulous, dehiscing laterally, the connective prolonged into a hispidulous awn 1.5 mm long, somewhat shorter than the body of the anther; filaments 1.2–1.5 mm long, densely hirsutulous. Ovary hispidulous; style 2.5–2.8 mm long, twisted, glabrous. Capsule not seen.

The twisted style and umbellately few-flowered inflorescence relate this new taxon to *Sloanea garckeana* Schum., from which it differs in having anther awns uniformly pubescent; densely pubescent, shorter pedicels and peduncles; and wider repand-dentate to coarsely dentate leaf blades.

Specimens of *Sloanea garckeana* identified by C. E. Smith and D. Alforo Castañeda show a range of variation. The species, originally based on the collection *Riedel 888* from the province of Rio de Janeiro, has entire or subentire, oblong or oblong-lanceolate, acuminate leaf blades 2–5 cm wide, 2–3-flowered inflorescences on elongated peduncles 5–6 cm long, sepals 8–9 × 4–4.5 mm, anthers (including the apical appendage) 5 mm long with the appendage described as glabrous, and tomentose filaments 3–4 mm long. Although Smith (1954) allowed for a range in variation of the anther appendage from sparsely pubescent to glabrous, the material I have examined has glabrous awns principally. Smith (1954) also allowed for a wide range of variation in glabrity and length of peduncles and pedicels.

Sloanea cataniapensis Steyerm., sp. nov. TYPE: Venezuela. T. F. Amazonas: Dept. Atures, N side of Río Cataniapo, 48 km SE of Puerto Ayacucho, 5°35'N, 67°15'W, 200–300 m, 10 May 1980, *Julian A. Steyermark, Gerrit Davidse & Francisco Guanchez 122215* (holotype, VEN; isotype, MO). Figure 2.

Arbor 15 m, foliorum laminis elliptico-ovatis vel oblongo-ellipticis apice abrupte acutis basi acutis vel subobtusis 7–12.5 cm longis 3.5–6.5 cm latis integerrimis praeter costam mediam subtus minute puberulentem glabris; inflorescentiis 3–7-floris, pendunculis primariis semel ramosis 5.5–9 cm longis dense puberulentibus omnibus umbellatim 3-pedicellatis, axibus lateralibus 1-floris; pedicellis 2–4 cm longis dense puberulentibus; sepalis quattuor

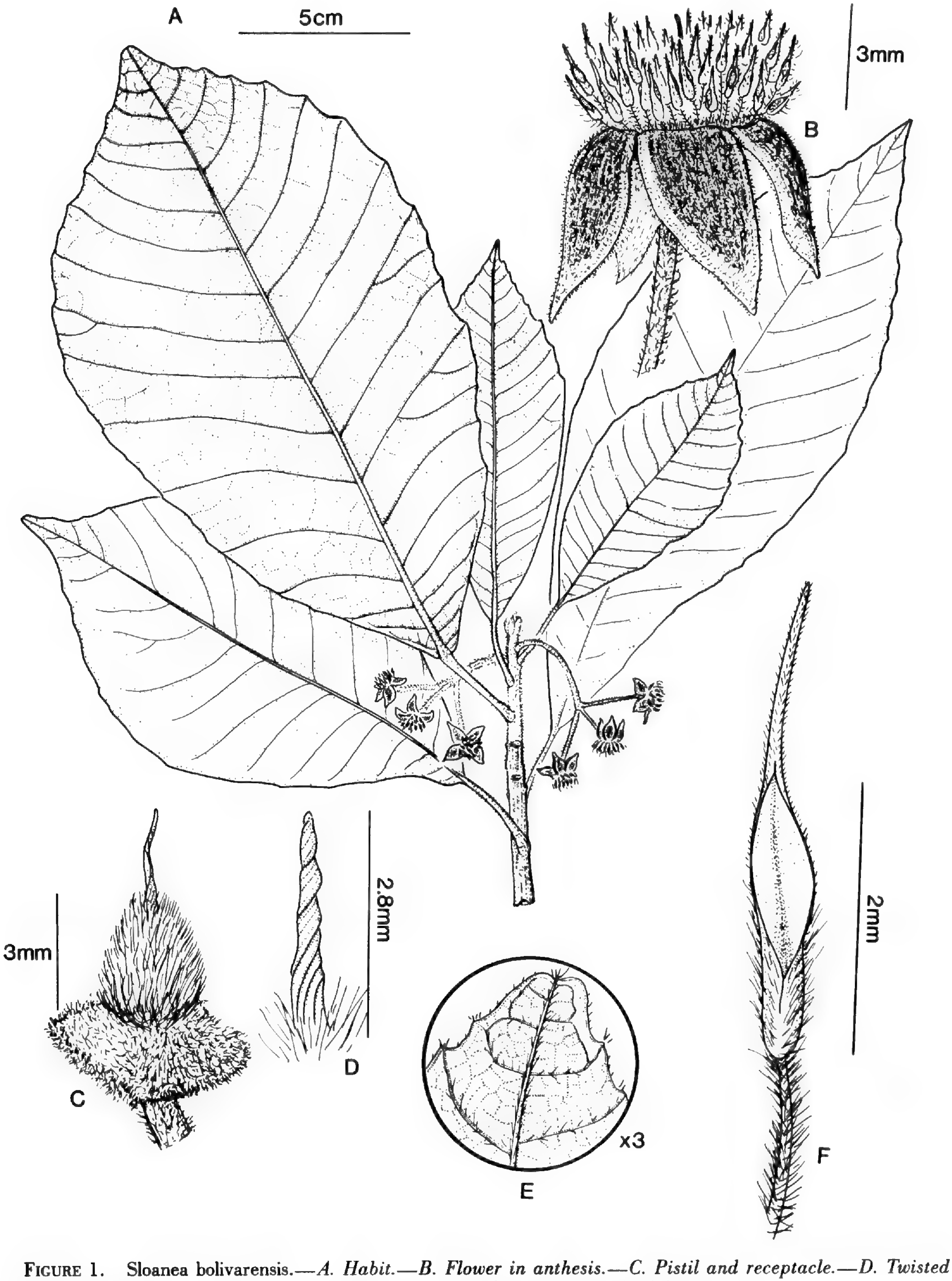

FIGURE 1. Sloanea bolivarensis.—*A. Habit.—B. Flower in anthesis.—C. Pistil and receptacle.—D. Twisted style.—E. Leaf blade, detail of apical abaxial side.—F. Stamen, laterally dehiscent.*

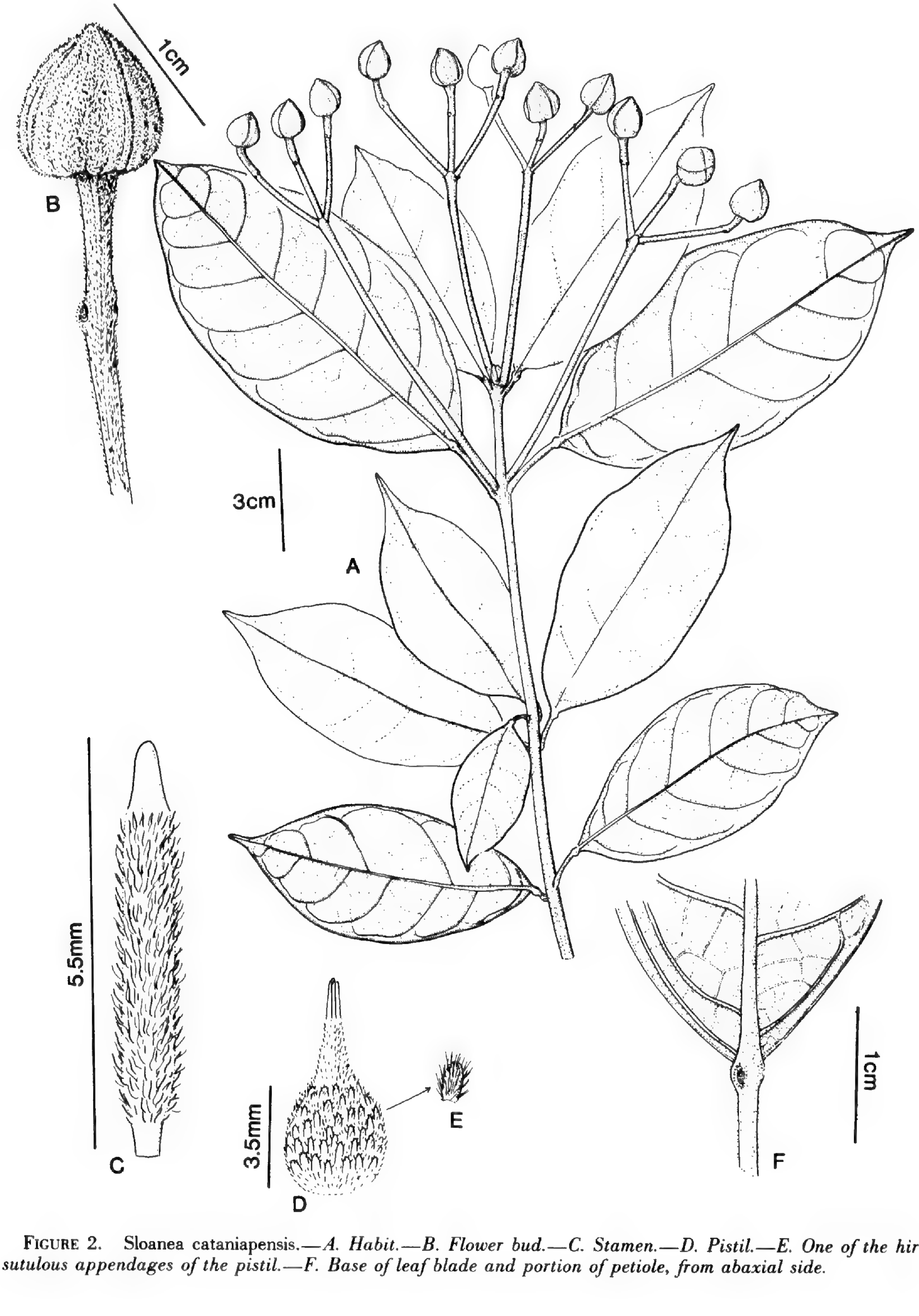

FIGURE 2. Sloanea cataniapensis.—*A. Habit.—B. Flower bud.—C. Stamen.—D. Pistil.—E. One of the hirsutulous appendages of the pistil.—F. Base of leaf blade and portion of petiole, from abaxial side.*

aequalibus 10 mm longis 7.5 mm latis; antheris (alabastro) linearibus 5.5 mm longis dense hirsutulis connectivo in acumen rotundatum glabrum 0.7–1 mm longum productis; filamentis (alabastro) 0.5–0.7 mm longis glabris.

Tree 15 m tall, upper portion of branchlets densely puberulent. Leaves alternate or opposite. Petioles 1–2 cm long, densely fulvous puberulent; leaf blades chartaceous, elliptic-ovate or oblong-elliptic, abruptly acute at apex, acute to subobtuse at base, 7–12.5 cm long, 3.5–6.5 cm wide, entire, glabrous except for the densely minutely puberulent midrib on the lower side; lateral nerves 5–6 each side, elevated below; subsulcate above, ascending at a 45° angle, terminating and anastomosing 1–2 mm from the margin; tertiary venation subelevated reticulate below, subrugulose above. Inflorescence umbellate to paniculate, 3–7-flowered; primary peduncles elongate, 5.5–9 cm long, 2.5–3 mm wide; secondary axes unbranched, 1-flowered, densely fulvous-puberulent; pedicels 2–4 cm long, 1.5–2 mm wide, densely fulvous-puberulent. Flower bud suborbicular, slightly acute at apex, 1 cm long, 1 cm wide basally. Sepals 4, covering the rest of the flowering parts in bud, equal, thickish, with thickened margins, broadly ovate, obtusely acute at apex, 10 mm long, 7.5 mm wide, densely fulvous-puberulent without, sericeous within. Stamens ca. 60; anthers (in bud) linear, 5.5 mm long (including apical appendage), 0.7–0.8 mm wide, densely hirsutulous upward, dehiscent by an apical pore, the connective prolonged into a rounded glabrous awn 0.7–1.1 mm long; filaments (in bud) 0.5–0.7 mm long, glabrous. Ovary broadly ovoid, 3.5 mm long, minutely hispidulous; style conic-linear, 2 mm long, densely hispidulous-appressed in the basal portion, elsewhere glabrous; stamens 4, glabrous.

Related taxa, such as *Sloanea laxiflora* Spruce ex Benth. and *S. synandra* Spruce ex Benth., have branched lateral or secondary axes of the primary peduncles, whereas in *S. cataniapensis* the primary peduncles branch only at their summits into three pedicellate flowers. Other differences are shown by the longer pedicels, shorter filaments, more densely pubescent anthers with longer ascending pubescence, sepals obtusely acute, and more densely puberulous lower midrib of the leaf blade.

Sloanea davidsei Steyermark, sp. nov. TYPE: Venezuela. T. F. Amazonas: Depto. Río Negro, Río Pacimoni, between its mouth and its junction with the Río Baria and Río Yatua, 1°53′–1°27′N, 66°35′–66°32′W, 80 m, 23–25 July 1984, *Gerrit Davidse 27733* (holotype, VEN; isotype, MO). Figure 3.

Arbor 4–15 m, ramulis superne dense patenti-pilosis; foliorum laminis maturis oblongo-obovatis apice rotundatis basi acutis obtusis vel rotundatis 7–14 cm longis (3.5–) 4–9 cm latis integerrimis, costa media nervis lateralibusque pilis patentibus dense munitis, superficie inferiore pilis minutis dense tomentosa; inflorescentiis simplicibus umbellatim 3–4-floris; pedunculis 0.5–3.5 cm longis dense pilosulis; pedicellis (6–)10–20 mm longis dense pilosulis; sepalis quattuor aequalibus late ovatis 5–8 mm longis; antheris 1.5–2 mm longis; connectivo in appendicem hirsutulum 0.7–1 mm longum producto; filamentis 1.2–2.8 mm longis; stylis liberis glabris; capsulis ovoideis 2.2–3 cm longis, spinis setulosis acicularibus inaequalibus majoribus 12–50 mm longis.

Tree 4–15 m tall, upper part of branches minutely and densely pilosulous with spreading hairs. Leaves alternate or opposite. Petioles 1.2–3 cm long, densely tomentose; leaf blades oblong-obovate, rounded at apex, acute, obtuse, or rounded at base, 7–14 cm long, (3.5–)4–9 cm wide, entire; lateral nerves 10–14 each side, elevated below, sulcate above, ascending at a 45° angle, anastomosing at the margins; midrib and lateral nerves below densely pilosulous with spreading hairs; midrib above sulcate, densely tomentellose; lateral nerves above slightly pubescent. Inflorescence lateral or terminal, simply 3–4-umbellately flowered, (2–)4–5.5 cm long; peduncle 0.5–3.5 cm long, densely pilosulous with spreading hairs; bracts at base of pedicels linear-lanceolate, acute, 3.5 mm long, densely tomentose without, sparsely appressed within; pedicels (6–)10–20 mm long, densely pilosulous. Sepals 4, equal, enclosing the flower in preanthesis, ovate, acute, 5–8 mm long, 2.5–5 mm wide, densely cinereous-pubescent without, more sparsely appressed pubescent within, the margins thickened, densely pubescent. Anthers oblong-elliptic or oblong-lanceolate, including the awn 1.5–2 mm long, densely hirsutulous, laterally dehiscent, the connective prolonged into a hirsutulous subobtuse awn 0.7–1 mm long; filaments 1.2–2.8 mm long, equaling or longer than the anther. Ovary ovoid or suborbicular-ovoid, 3.5–4 mm long, 3 mm wide, brown-hispidulous, 4-angled; styles 4, free, divergent, glabrous, 1.5–2 mm long. Capsule ovoid, 2.2–3 cm long, densely covered with usually red, acicular, unequal, straight spines, the longer ones 12–50 mm long with appressed setulose projections along their length, the shorter bristles 3–4 mm long, overlying surface of dense, pale hispidulous hairs; mesocarp reddish. Seed golden, reddish proximally.

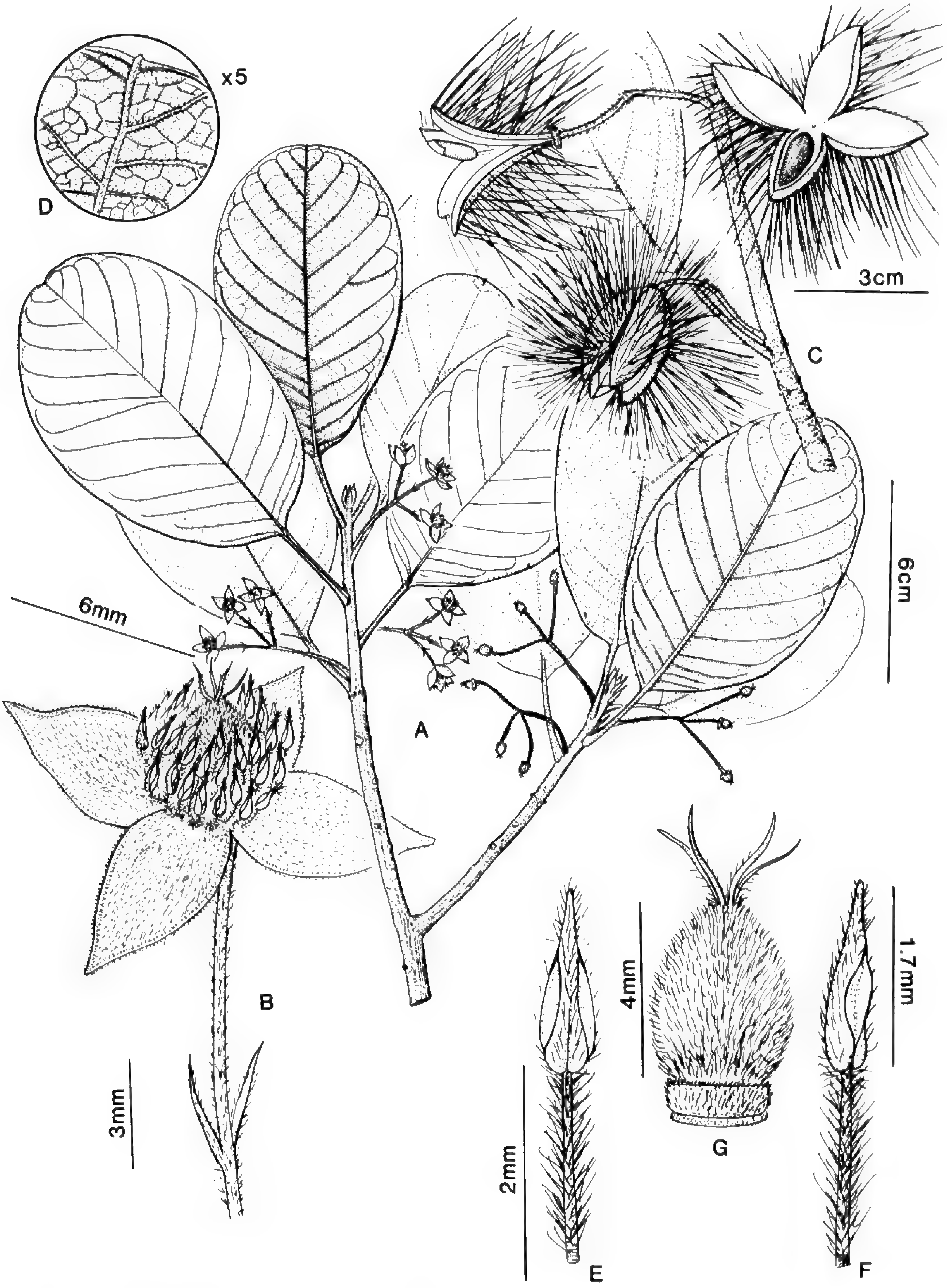

FIGURE 3. Sloanea davidsei.—*A. Habit.—B. Flower and pedicel, in anthesis with bracts.—C. Portion of infructescence.—D. Portion of lower leaf surface.—E. Stamen, with lateral dehiscence, ventral view.—F. Stamen, lateral view.—G. Pistil.*

Paratypes. VENEZUELA. T. F. AMAZONAS: Río Guainía between San Miguel and Maroa, 100–400 m, 30 June 1959, *Wurdack & Adderley 43260* (MO, NY); DEPT. RÍO NEGRO: selva pluvial por las orillas del Medio Pacimoni, 1°40'N, 66°35'W, 3 Dec. 1984, *Stergios & Aymard 7582, 7583* (MO, PORT); 0.5 km N of mouth of Río Casiquiare, 1°57'N, 67°7'W, 5 Feb. 1980, *Liesner & Clark 9140* (MO, VEN); igapó forests along Caño Cuweje, 32 km S of San Carlos, 1°56'N, 67°03'W, 119 m, 4 Apr. 1980, *Clark 7480* (MO); laja on right bank of Caño Cupueni, opposite mouth of Río Atabapo, 120–130 m, 12 Nov. 1953, *Maguire, Wurdack & Bunting 36219* (MO, NY).

Common names. Uruch, onoto rebalsero; onotillo, urucurana.

The common names are derived from the superficial resemblance to the spinose fruits of *Bixa orellana* and *B. urucurana.* The species is related to *Sloanea kuhlmanii* Ducke of Amazonian Brazil but differs in the absence of a corrugated receptacle, in the shorter stamens with densely hirsutulous anthers and their appendages, in the entire leaf margins nonemarginate at the apex, in the densely pubescent peduncles and pedicels, and in the densely pubescent lower leaf surfaces, especially on the nerves. The younger leaves of *Davidse 27733* and *Wurdack & Adderley 43260* have a more abundant tomentum on the lower leaf surface. The pubescence of the older, more mature leaf blades tends to be more sparse and shortly ascending or spreading along the midrib and/or nerves, whereas the lower surface itself, including the tertiary veins, remains glabrous or essentially so.

Sloanea longiaristata Steyerm., sp. nov. TYPE: Venezuela. T. F. Amazonas: Depto. Atabapo, forested slopes, Cerro Marahuaca, 1–2 km N of Sima Camp, 3°43'N, 65°31'W, 1,100 m, 8–9 Mar. 1985, *Ronald Liesner 18455* (holotype, VEN; isotype, MO). Figure 4.

Arbor 5–15 m, ramulis juvenilibus tomentosis; petiolis 0.7–2 cm longis dense tomentosis; foliorum laminis late oblongo-obovatis vel elliptico-oblongis apice rotundatis vel breviter obtusis basi acutis vel subacutis 10–15 cm longis 5–11 cm latis praeter utrinque costam mediam nervos lateralesque tomentosis glabris integris vel subundulatis; inflorescentiis lateralibus racemosis 1.5–4.5 cm longis 3–8-floris dense hirtellis pilis patentibus munitis; pedunculis 5–7 mm longis dense hirsutulis; pedicellis 4–15 mm longis dense hirsutulis pilis patentibus munitis; sepalis quattuor reflexis lanceolatis acutis 2.5–4 mm longis, utrinque hirsutulis; antheris elliptico- vel ovoideo-oblongis 0.7–1 mm longis dense hirsutulis lateraliter dehiscentibus; connectivo in aristam glabram elongatam 1.3–2 mm longam producto; filamentis 1.5–2.1 mm longis dense hirsutulis; stylis quadripartitis vel basi vix connatis 2.8–4 mm longis praeter basim adpresso-hispidulam glabris; capsulis ignotis.

Tree 5–15 m high, the young branches tomentose. Leaves alternate, crowded at the summit of the branches. Petioles 0.7–2 cm long, densely tomentose; leaf blades coriaceous, broadly oblong-obovate or elliptic-oblong, rounded at summit, or with a short broadly obtuse projection, cuneately acute or subacute at base, 10–15 cm long, 5–11 cm wide, the leaf surfaces glabrous, but the upper and lower midribs tomentose and the lower lateral nerves slightly pubescent, the margins entire to subundulate; lateral nerves 6–8 each side, elevated below, slightly impressed above, ascending at 45–60°, terminating mainly at the margins or unbranched before reaching margins; tertiary venation forming obliquely parallel connecting veins with the lateral nerves of the lower side, slightly elevated or impressed below. Inflorescence lateral, racemose, 1.5–4.5 cm long, 2.5 cm wide, 3–8-flowered, rachis moderately hirtellous with spreading hairs. Peduncles 5–7 mm long, densely hirsutulous. Bracts subtending pedicels, alternate, linear, 2 mm long, densely hirtellous. Pedicels 4–15 mm long, densely hirsutulous with spreading hairs. Sepals 4, reflexed, lanceolate, acute, 2.5–4 mm long, densely hirsutulous without, less pubescent within. Anthers elliptic or ovoid-oblong, 0.7–1 mm long, densely hirsutulous, laterally dehiscent, the connective prolonged into a conspicuously elongated glabrous awn 1.3–2 mm long; filaments 1.5–2.1 mm long, densely hirsutulous, much exceeding the anther body. Ovary ovoid-subglobose or ovoid-oblong, 3–3.5 mm long, 2–2.5 mm wide, densely hispidulous; styles 4, deeply divided or connate at the base, 2.8–4 mm long, glabrous except in the appressed-pubescent basal portion. Young capsule 4-celled.

Paratypes. VENEZUELA. T. F. AMAZONAS: 1–2 km SE and E of San Carlos, 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°3'W, 120 m, 22 Apr. 1979, *Liesner 6875* (MO, VEN). DEPT. ATABAPO: Cerro Marahuaca, Sima Camp, S-central portion of forested slopes along E branch of Caño Negro, 3°43'N, 65°31'W, 1,140 m, 21–22 Feb. 1985, *Steyermark & Holst 130507* (MO, VEN).

This species is most closely related to *Sloanea duckei* C. E. Smith and *S. rufa* Planch. ex Benth. From *S. rufa* it differs in the longer anthers and longer awns, more elongated inflorescences and pedicels, broadly rounded leaf apices, glabrous lower leaf surface, and styles more divided. From *S. duckei* it differs in the longer awns; longer filaments; pubescent petioles, midribs, and secondary nerves of the leaf blades; broadly obovate or oblong-obovate leaf blades acute or subacute at base; shorter peduncles; and 4 instead of 5–7 sepals. From

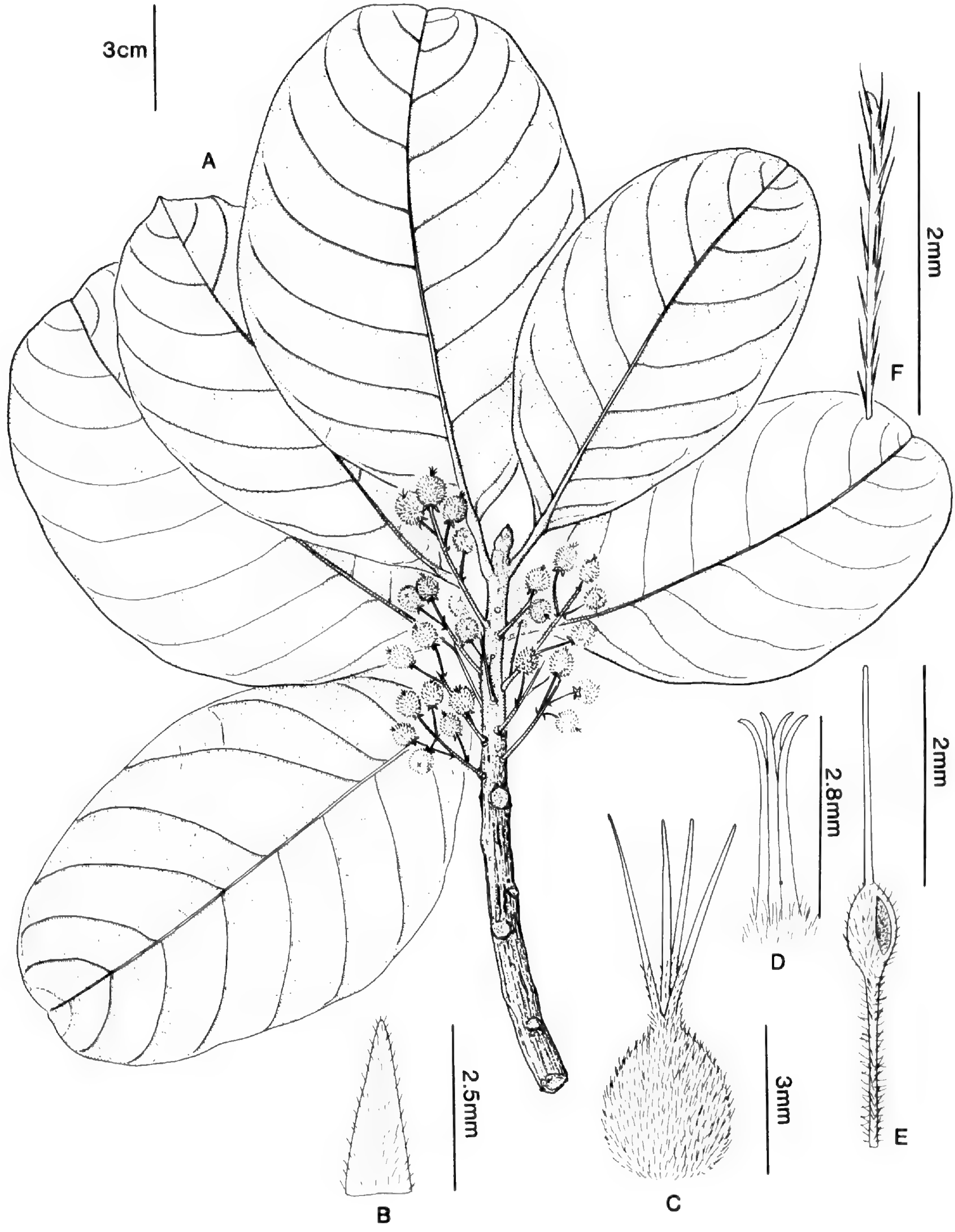

FIGURE 4. Sloanea longiaristata.—*A. Habit.—B. Sepal, exterior view.—C. Pistil, showing free styles.—D. Pistil, showing coherent styles.—E. Stamen.—F. Portion of bristly hairs of young fruit.*

other related species belonging to section *Brevispicae* C. E. Smith, such as *S. stipitata* Spruce ex Benth. and *S. robusta* Uittien, it is distinguished by the elongate awns longer than the anther body, shorter petioles, and differences in the leaf blades.

The collection *Liesner 6875* from the region of San Carlos is doubtfully assigned to this taxon. It differs in having the styles more united and smaller, glabrous leaf blades with the apices more obtusely prolonged rather than rounded and with more-undulate margins.

Sloanea merevariensis Pittier ex Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Alto Río Guaña (Merevari) near Brazil frontier, without date, *Felix Cardona 1051* (also numbered *1053, 1055*) (holotype, F; isotypes, US, VEN). Figure 5.

Arbor; ramulis minute pubescentibus; petiolis 2.5–3.3 cm longis, minute adpresso-puberulentibus; foliorum laminis obovatis apice rotundatis basi acutis 8.5–13 cm longis 4–6.5 cm latis, costa media supra dense tomentosa, subtus pilosula pilis laxis munita; nervis lateralibus subtus puberulis pilis patentibus praeditis; nervis lateralibus utroque latere 9–10; inflorescentiis umbellatis vel corymboso-racemosis 3–5-floris; pedunculis 6–7 mm longis moderate adpresso-puberulentibus; pedicellis 7–8 mm longis moderate adpresso-puberulentibus; sepalis quattuor reflexis ovatis acutis 4–4.5 mm longis; antheris 1.5–1.6 mm longis hispidulis lateraliter dehiscentibus, connectivo in acumen late lanceolatum acutum 0.3–0.4 mm longum producto; filamentis 2 mm longis pilosulis; stylis quadripartitis erectis supra medium glabris infra medium minute puberulis. Capsula ignota.

Tree with minutely pubescent branches. Leaves alternate. Petioles 2.5–3.3 cm long, minutely appressed-puberulent except on the more densely pubescent canaliculate upper side; leaf blades obovate, rounded at apex, acute at base, 8.5–13 cm long, 4–6.5 cm wide, glabrous on the upper and lower surfaces except densely tomentose above on the slightly sulcate midrib, this moderately laxly pilose below and laxly puberulous on lower lateral nerves, the nerves 9–10 each side, ascending at 45–50° and anastomosing 3–5 mm from margins; tertiary venation minutely reticulate, elevated both sides, with subparallel obliquely transverse connections with the lateral nerves. Inflorescence lateral and terminal, umbellate or corymbose-racemose with 3–5 flowers. Peduncles 6–7 mm long, moderately appressed-puberulent; pedicels 7–8 mm long, moderately puberulent. Sepals 4, reflexed, dark in drying, subequal, 4–4.5 mm long, 3–3.5 mm wide at base, moderately pubescent without, sparsely appressed pubescent within, the margins pubescent. Anthers lance-elliptic, 1.5–1.6 mm long, hispidulous, laterally dehiscent, the connective prolonged into a short lanceolate, subacute, minutely puberulent awn 0.3–0.4 mm long; filaments 2 mm long, pilosulous. Ovary subglobose, 0.7 mm long; styles 4-parted, erect, 1.5 mm long, minutely puberulous in lower half, glabrous above. Capsule unknown.

This species was distributed by C. E. Smith as *Sloanea laurifolia* (Benth.) Benth. As indicated in another part of the text, *S. laurifolia* is treated by the present author as having less variability than that allowed by Smith. *Sloanea merevariensis* may be differentiated by the obovate, rounded leaf blades having the upper midrib densely tomentose.

Sloanea parvifructa Steyerm., sp. nov. TYPE: Brazil (near Venezuelan border). Serra da Neblina, Rio Negro, Rio Cauaburi, Rio Maturacá, between Missão Salesiana and Serra Pirapucú, 800–1,000 m, 23 Jan. 1966, *Nilo T. Silva & Umbelino Brazão 60865* (holotype, MO; isotype, NY).

Arbor 10 m, ramulis prope apicem dense minuteque pubescentibus; petiolis 1.5–2.7 cm longis minute puberulentibus; foliorum laminis obovato-spathulatis, apice rotundatis vel late obtusis, basi acutis 13–19 cm longis, 4.5–7 cm latis obscure repandis vel integris praeter costam medium sparsim puberulam utrinque glabris; nervis lateralibus utroque latere 7–8; floribus non visis; infructescentiis lateralibus racemosis 4–5-fructus gerentibus 3–3.5 cm longis; pedunculis 5–9 cm longis; pedicellis fructiferis 8–10 mm longis dense puberulis; capsulis parvis, valvulis 9–10 mm longis 7 mm latis, tenuibus, spinis tenuibus 1.5–3 mm longis antrorse pubescentibus.

Tree 10 m tall, the branches minutely pubescent toward the summit. Leaves alternate. Petioles 1.5–2.7 cm long, densely minutely puberulent; leaf blades obovate-spathulate, rounded or broadly obtuse at apex, narrowed at the acute base, 13–19 cm long, 4.5–7 cm wide, obscurely repand or entire, except for the sparsely pubescent upper and lower midribs, glabrous on both surfaces; lateral nerves 7–8 on each side, ascending at 50–60°. Flowers not seen. Infructescence lateral, racemose, bearing 4–5 fruits, the fruiting axes 3–3.5 cm long, 1.5 mm wide, widely spreading from stem, densely puberulous with spreading-ascending trichomes; peduncle 5–9 mm long; fruiting pedicels slender, 8–10 mm long, densely puberulous with spreading-ascending hairs. Capsules relatively small, the valves 9–10 mm long, 7 mm wide; bristles slender, purple, 1.5–3 mm long, antrorsely pubescent. Seeds oblong, 7 mm long, 4.5 mm wide.

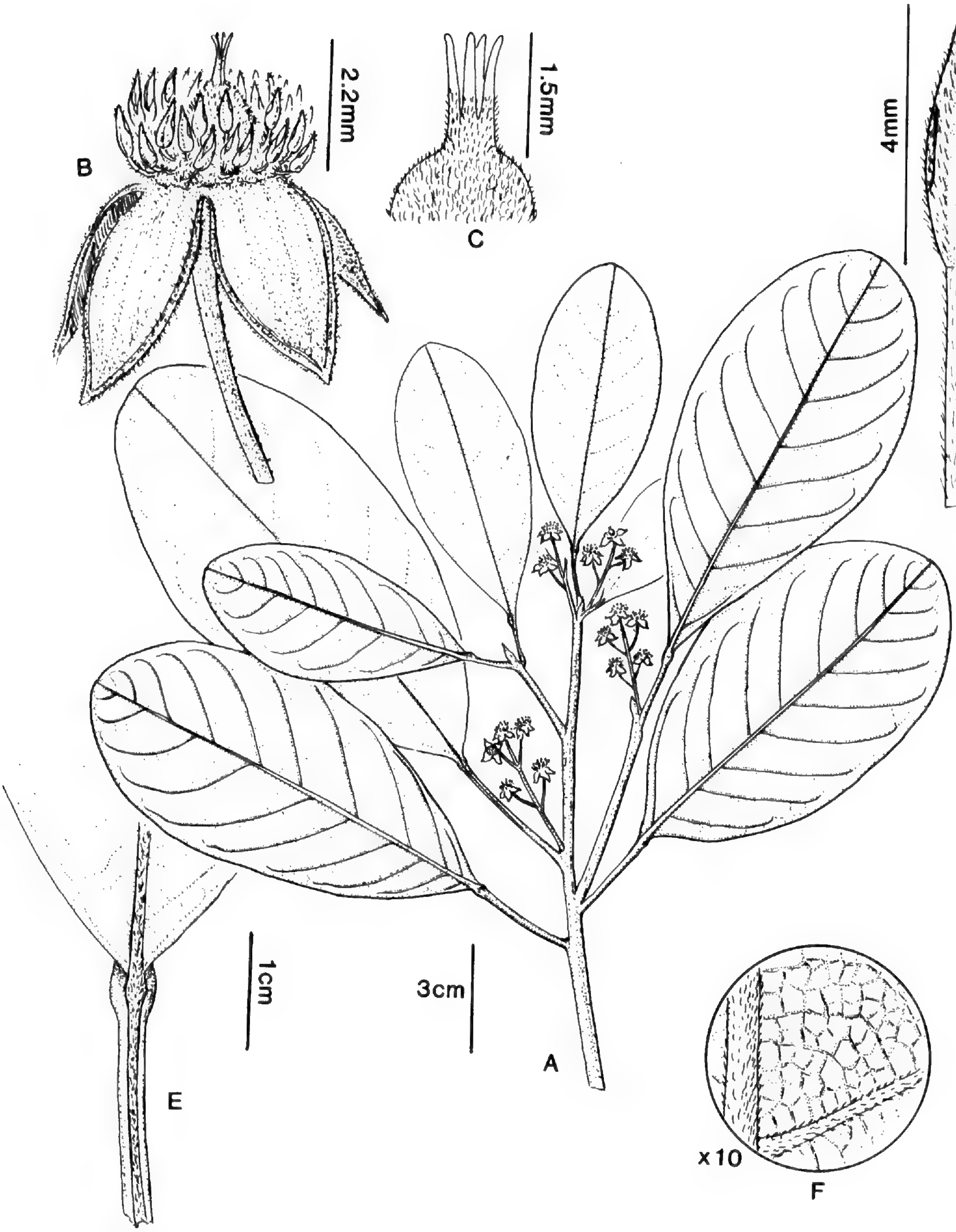

FIGURE 5. Sloanea merevariensis.—*A. Habit.—B. Flower, at anthesis.—C. Pistil.—D. Stamen.—E. Base of leaf blade, adaxial view, with petiole.—F. Lower portion of leaf blade.*

From the related *Sloanea duckei* C. E. Smith of Amazonian Brazil, the new species differs in having densely puberulent petioles, a puberulous lower midrib, and lateral nerves ascending at a greater angle. From *S. spathulata* C. E. Smith of Territorio Acre, Brazil, it differs by having longer infructescences with longer pedicels, much shorter bristles, shorter petioles, more strongly ascending lateral nerves, and obliquely transversely connecting tertiary nerves straighter, less branched, and less prominent.

Sloanea sipapoana Steyerm., sp. nov. TYPE: Venezuela. T. F. Amazonas: Cerro Sipapo (Paráque), Camp Savanna, 1,500 m, 15 Dec. 1948, *Bassett Maguire & Louis Politi 27674* (holotype, MO; isotype, NY). Figure 6.

Arbor ad 15 m alta ubique plerumque glabra, foliis alternis; petiolis 0.9–1.5 cm longis; foliorum laminis coriaceis lanceolatis vel lanceolato-ellipticis apice acutate acuminatis basi obtusis vel subacutis majoribus 8.5–13.5 cm longis 2.5–5 cm latis integerrimis; costa media supra elevata; nervis lateralibus supra vix manifestis subtus paullo elevatis utroque latere 11–13; venatione tertiaria subtus subtiliter reticulata; infructescentia laterali; pedunculo 2.5–3.5 cm longo glabro; pedicellis 1.5–2 cm longis glabris vel sparsim puberulentibus; capsulis inermibus 2–2.5 cm longis minute puberulentibus.

Tree to 15 m tall with glabrous branches. Leaves alternate, glabrous throughout. Petioles 0.9–1.5 cm long; leaf blades coriaceous, lanceolate or lance-elliptic, slenderly acutely acuminate at apex, obtuse to subacute at base, the large ones 8.5–13.5 cm long, 2.5–5 cm wide, entire; midrib elevated above and below; lateral nerves 11–13 each side, ascending at 25–35°, not reaching margin, scarcely evident above, slightly elevated below, anastomosing with tertiary venation 2–7 mm from margin; tertiary venation finely reticulate on lower surface, scarcely evident on upper surface. Infructescence lateral. Peduncle 2.5–3.5 cm long, 1–1.5 mm diam., glabrous. Pedicels 1.5–2 cm long, glabrous to sparsely puberulent. Capsules unarmed, 4-valved, 2–2.5 cm long, the surface densely and minutely puberulent. Seed oblong, 1.1 cm long, 0.8 cm wide.

Paratype. VENEZUELA. T. F. AMAZONAS: Cerro Sipapo (Paráque), upper Caño Negro and right branch (north) of Caño Profundo, 1,455 m, 10 Jan. 1949, *Maguire & Politi 28266-A* (MO, NY).

Apparently a member of section 4, *Corymbo-Racemi* C. E. Smith, most closely related to *Sloanea oppositifolia* Spruce ex Benth. (= *S. laurifolia* (Benth.) Benth.), from which the new species differs in the alternate, coriaceous leaf blades with an elevated midrib, inconspicuous lateral nerves, and finely reticulate tertiary venation of the lower surface.

Sloanea steyermarkii C. E. Smith

Sloanea steyermarkii C. E. Smith, described from a collection taken from the summit of Auyan-tepui, a massive sandstone table mountain of the Venezualan Guayana, appeared to be a distinct, isolated endemic species, characterized by the dense, congested, subsessile inflorescence; coriaceous, rugose leaf blades rounded at the apex; densely buff- or ferruginous-tawny tomentose lower leaf surfaces with the tomentum completely covering the midrib, nerves, and lower surface; and small, densely bristly fruits with bristles 2–4 mm long.

Additional collections obtained from the summits of various other sandstone table mountains throughout the Venezuelan Guayana have similar patterns of leaf size, shape, rounded apex, congested inflorescences, and small fruits with short bristles but differ chiefly in the density of the pubescence on the lower leaf surface. In typical *Sloanea steyermarkii*, known from the mountains situated within the eastern drainage of the Río Caroní and its tributaries (Ptari-tepui, Chimantá-tepui, Auyan-tepui, and Uaipán-tepui of Estado Bolívar), most or all of the leaves retain dense abaxial tomentum. However, a specimen collected from Uaipán-tepui (*Koyama & Agostini 7185*) has only the youngest leaves with a dense buff tomentum completely covering the lower surface, whereas the older ones have lost most of the dense tomentum and retain only mere traces on the lower surface and along the midrib and nerves.

Westward on the summits of the sandstone mountains, beginning with the western drainage of the Río Paragua of Cerro Guaiquinima and the Río Caura of Cerro Guanacoco and the Meseta del Jaua, the indument of the lower surface is less prominent and is manifested only by pale sparse puberulence along the midrib and some of the lateral nerves. This tendency toward glabrity continues westward on the summits of the sandstone mountains of the Territorio Federal Amazonas (Cerro Huachamacari, Yapacana, Aracamuni, Autana, and Sipapo). The taxa that have previously been treated as species, *Sloanea autanae* from Cerro Autana, *S. yapacanae* from Cerro Yapacana, and *S. jauaensis* (including var. *minor*) from the Meseta del Jaua, are best treated by recognizing subspecies with glabrous or glabrate leaf variations of a more widely ranging *S. steyermarkii* geographically isolated in the western portion of the Guayana Highland.

KEY TO THE SUBSPECIES OF *SLOANEA STEYERMARKII*

1a. Lower leaf surface chiefly densely tomentose beneath, at least on the younger leaves, completely covering the surface and nerves with a dense buff- or ferruginous-tawny tomentum; plants of Ptari-tepui westward to Chimantá Massif and Auyan-tepui, Edo. Bolívar .... *S. steyermarkii* subsp. *steyermarkii*

1b. Lower leaf surface glabrous or with a minute scattered pubescence; lower midrib and/or lateral nerves more or less puberulent to glabrous 2

2a. Leaf blades entire, mainly rounded or

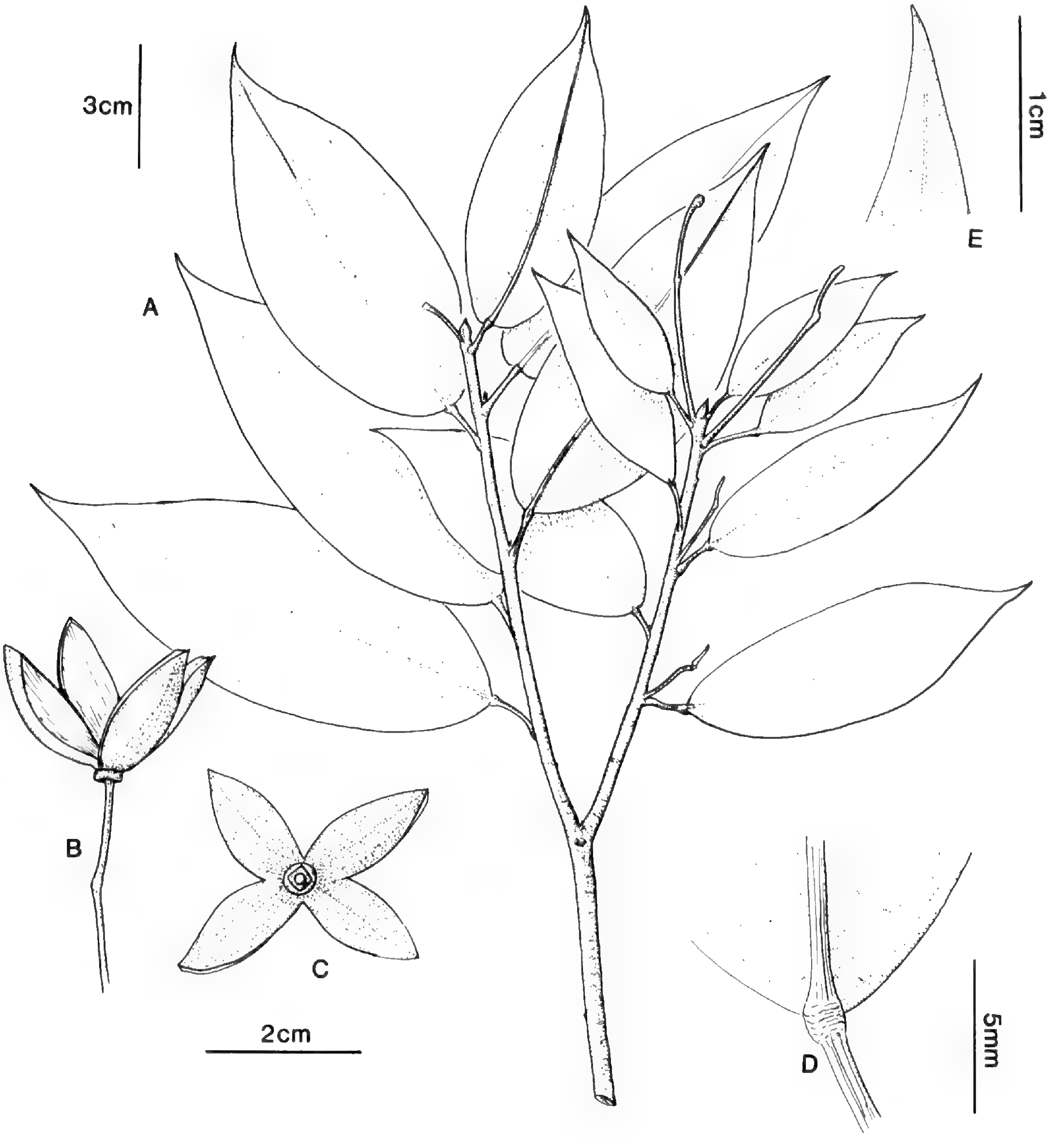

FIGURE 6. Sloanea sipapoana.—*A. Habit.—B. Capsule, lateral view, dehiscing.—C. Capsule, ventral view.—D. Leaf base, with portion of petiole, abaxial view.—E. Leaf blade showing apex, adaxial view.*

broadly obtuse at the apex .... *S. steyermarkii* subsp. *jauaensis*

2b. Leaf blades undulate-repand, often narrowed to a less obtuse apex .... *S. steyermarkii* subsp. *autanae*

Sloanea steyermarkii C. E. Smith subsp. **jauaensis** (Steyerm.) Steyerm., stat. nov. *Sloanea jauaensis* Steyerm., Bol. Soc. Venez. Ci. Nat. 33(132–133): 353. 1976.

Sloanea jauaensis Steyerm. var. *minor*, Bol. Soc. Venez. Ci. Nat. 33(132–133): 354. 1976.
Sloanea yapacanae Steyerm., Pittieria No. 7: 15. 1978.

Specimens examined. VENEZUELA. BOLÍVAR: Meseta del Jaua, Cerro Jaua, 4°48′50″N, 64°34′10″W, porción sur-oeste, 1,810–1,880 m, *Steyermark et al. 109841* (type of *Sloanea jauaensis*, VEN); Meseta del Jaua, Cerro Jaua, 4°48′50″N, 64°34′10″W, porción sur-oeste, 1,810–1,880 m, *Steyermark et al. 109695* (type of *S. jauaensis* var. *minor*, VEN); Cerro Guaiquinima, Río Paragua, below SE escarpment, 1,600–1,700 m, *Maguire 33029* (NY); Cerro Guanacoco, 4°46′30″N, 63°55′5″W, 1,450 m, *Steyermark et al. 109760* (NY, VEN). T. F. AMAZONAS: Cerro Huachamacari, Summit Camp, 1,800 m, *Maguire et al. 30088, 30097* (MO, NY); Cerro Yapacana, 3°45′N, 66°45′W, 1,000–1,200 m, *Steyermark & Bunting 103186* (type of *S. yapacanae*, VEN); Cerro Yapacana, 1,200 m, *Maguire et al. 30737* (NY); Cerro Sipapo, S basin, 1,835 m, *Maguire & Politi 28684* (NY).

A sterile collection from the summit of Cerro Aracamuni (*Liesner & Carnevali 22722*) probably is to be referred to this subspecies.

Sloanea steyermarkii C. E. Smith subsp. **autanae** (Steyerm.) Steyerm., stat. nov. *Sloanea autanae* Steyerm., Pittieria 7: 13. 1978.

Specimens examined. VENEZUELA. T. F. AMAZONAS: Cerro Autana, 4°52'N, 67°27'W, 1,230–1,270 m, *Steyermark 105222* (type of *S. autanae*, VEN).

Sloanea subpsilocarpa Steyerm., sp. nov. TYPE: Venezuela. T. F. Delta Amacuro: bosque pluvial, E de Río Grande, ENE El Palmar, near limits of Edo. Bolívar, 29 Nov.–18 Dec. 1964, *Luis Marcano-Berti 447* (holotype, VEN; isotypes, MO, NY). Figure 7.

Arbor 28–30 m; petiolis 0.6–3 cm longis; foliorum laminis oblongis vel oblongo-ellipticis apice obtuse acutis obtusis vel raro rotundatis basi obtusis vel rotundatis 8–16 cm longis 4–7 cm latis integerrimis ubique glabris; nervis lateralibus utroque latere 4–6(–8); venatione tertiaria supra prominente reticulata; inflorescentia (post anthesim) subpaniculata 2–5-flora; pedunculis 1.5–2 cm longis tomentellis; pedicellis post anthesin 1–2 cm longis fructiferis 2–2.5 cm longis tomentellis; sepalis quattuor coriaceis late ovatis acutis dense fulvo-tomentellis 10–13 cm longis 9 mm latis; antheris 2 mm longis adpresso-pubescentibus prope poros sub apicales lateraliter dehiscentibus, connectivo in acumen lanceolatum obtusum glabrum 1.5 mm longum producto; filamentis 0.5–1 mm longis sparsim adpresso-pubescentibus vel glabris; ovario 5 mm longo dense fulvo-tomentoso; stylis 2 mm longis fulvo-strigillosis; capsulis inermibus vel sparsim breviter tuberculatis subglobosis 4.5 × 4.5 cm.

Trees 28–30 m tall. Leaves alternate. Petioles 0.6–3 cm long; leaf blades oblong or oblong-elliptic, acute or obtuse, rarely rounded at apex, obtuse or rounded at base, 8–16 cm long, 4–7 cm wide, entire, glabrous both sides; midrib sulcate above, elevated below; lateral nerves 4–6(–8) each side, impressed above, elevated below, branching and anastomosing 4–9 mm from the margins, ascending at 50–60°; tertiary venation prominently reticulate and subelevated above, reticulate and subelevated below. Inflorescence (past flowering) subpaniculate, terminal or lateral, 2–5-flowered; peduncles (past flowering) 1.5–2 cm long, 1.5 mm wide, 2–2.5 cm long (fruiting), brown-tomentose; bracts ovate, acute, 4–5 mm long, tomentellous on both sides; pedicels (past flowering) 1–2 cm long, 2–2.5 cm long, 3–3.5 mm wide (fruiting); sepals 4, coriaceous, persistent, broadly ovate, acute, 10–13 mm long, 9 mm wide at base, inner surface blackish, sparsely pubescent basally, densely brown-tomentellous without. Anthers 2 mm long, 0.7–0.8 mm wide, appressed-pubescent, dehiscing laterally by subapical pores, the connective prolonged into a glabrous, lanceolate, obtuse awn 1.5 mm long; filaments shorter than and about width of anther, blackish, 0.5–1 mm long, 0.5 mm wide, sparsely appressed to glabrous. Ovary subglobose-ovoid, 5 mm long, 5 mm wide, obtusely angled, densely brown-tomentose; styles 2 mm long, densely brown strigillose. Fruit unarmed or with a few scattered short, obtuse, glabrous tubercles 0.5–1 mm long on a surface covered with dense brown tomentum intermixed with minute white hairs 0.1–0.2 mm long, subglobose, 4.5 × 4.5 cm; mesocarp ligneous, 6–8 mm thick.

Paratypes. VENEZUELA. T. F. DELTA AMACURO: E de Río Grande, ENE of El Palmar, near limits of Edo. Bolívar, 29 June 1964, *Marcano-Berti 275* (MO, NY, VEN); same locality, *Marcano-Berti 437* (MO, NY, VEN). BOLÍVAR: campamento "El Paraiso" y "La Yagua," a 48 km NE del caserío Los Rosos, este último a 17 km de Upata (sobre la carretera nueva Upata–San Felix), 9 Sep. 1966, *Blanco 578* (VEN).

Common name. Almidon.

This species has been confused with *Sloanea laurifolia* (Benth.) Benth., from which it differs in the larger, thicker sepals, pubescent anthers with a longer, lanceolate awn, subpaniculate inflorescence, larger bracts, and stouter peduncle and pedicels. From *S. latifolia* (Rich.) Schum. (*S. inermis* Ducke) *S. psilocarpa* is distinguished by the shorter stamens with pubescent anthers; larger fruits with shorter, obtuse, glabrous tubercles; broadly ovate sepals broader at the base; and usually obtuse to rounded leaf bases.

Sloanea wurdackii Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Río Parguaza, just below Raudal Maraca (ca. 110 km above river mouth), 115 m, 30 Dec. 1955, *John Wurdack & Joseph Monachino 41017* (holotype, MO; isotype, NY). Figure 8.

Arbor 6–20 m; petiolis 3.5–10 cm longis sparsim puberulentibus admodum glabris; foliorum laminis late oblongo-ovatis apice rotundatis basi subacutis vel rotundatis majoribus 18–25 cm longis 9.5–15 cm latis integerrimis admodum glabris; nervis lateralibus utroque latere 10–12; inflorescentiis elongatis duobus vel tribus simul laxe racemosis vel subpaniculatis 4–8.5 cm longis 2–5-floris, rhachidi glabra vel sparsim puberulenti; pedicellis elongatis apice recurvatis 1–4 cm longis minute puberulentibus; sepalis post anthesim valde reflexis lanceolatis 2.5 mm longis; antheris 0.9–1 mm longis dense adpresso-pubescentibus prope apicem dehiscentibus, connectivo in acumen acutate obtusum pubescentem 0.1–0.2 mm longum producto; filamentis 2 mm longis dense adpresso-pubescentibus; fructu immaturo oblongo 1.5–1.7 cm longo praeter partem basalem 3–4 mm longam inaequaliter spinosis, spinis rigidis 2–3 mm longis.

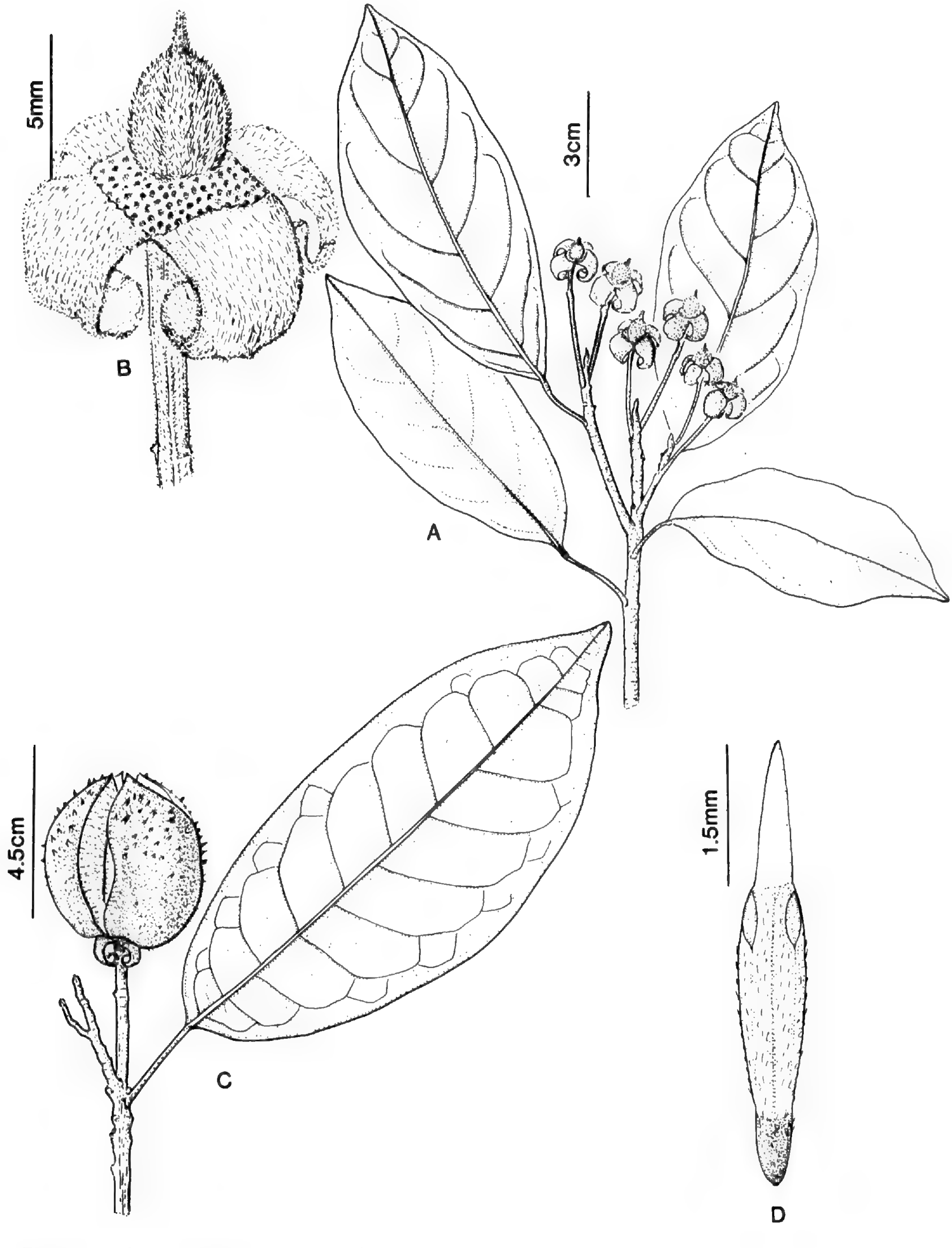

FIGURE 7. Sloanea subpsilocarpa.—*A. Habit.—B. Flower, post anthesis with reflexed sepals.—C. Portion of fruiting branch.—D. Stamen.*

Tree 6–20 m tall. Branches glabrous. Leaves alternate. Petioles 3.5–10 cm long, essentially glabrous but sparsely microscopically puberulent; leaf blades broadly oblong-ovate, rounded at the sometimes mucronate summit, subacute to rounded at base, the larger ones 18–25 cm long, 9.5–15 cm wide, entire or subentire, glabrous both sides; midrib essentially glabrous below but with traces of minute puberulence, prominently elevated; lateral nerves 10–12 each side, ascending at 60–70°,

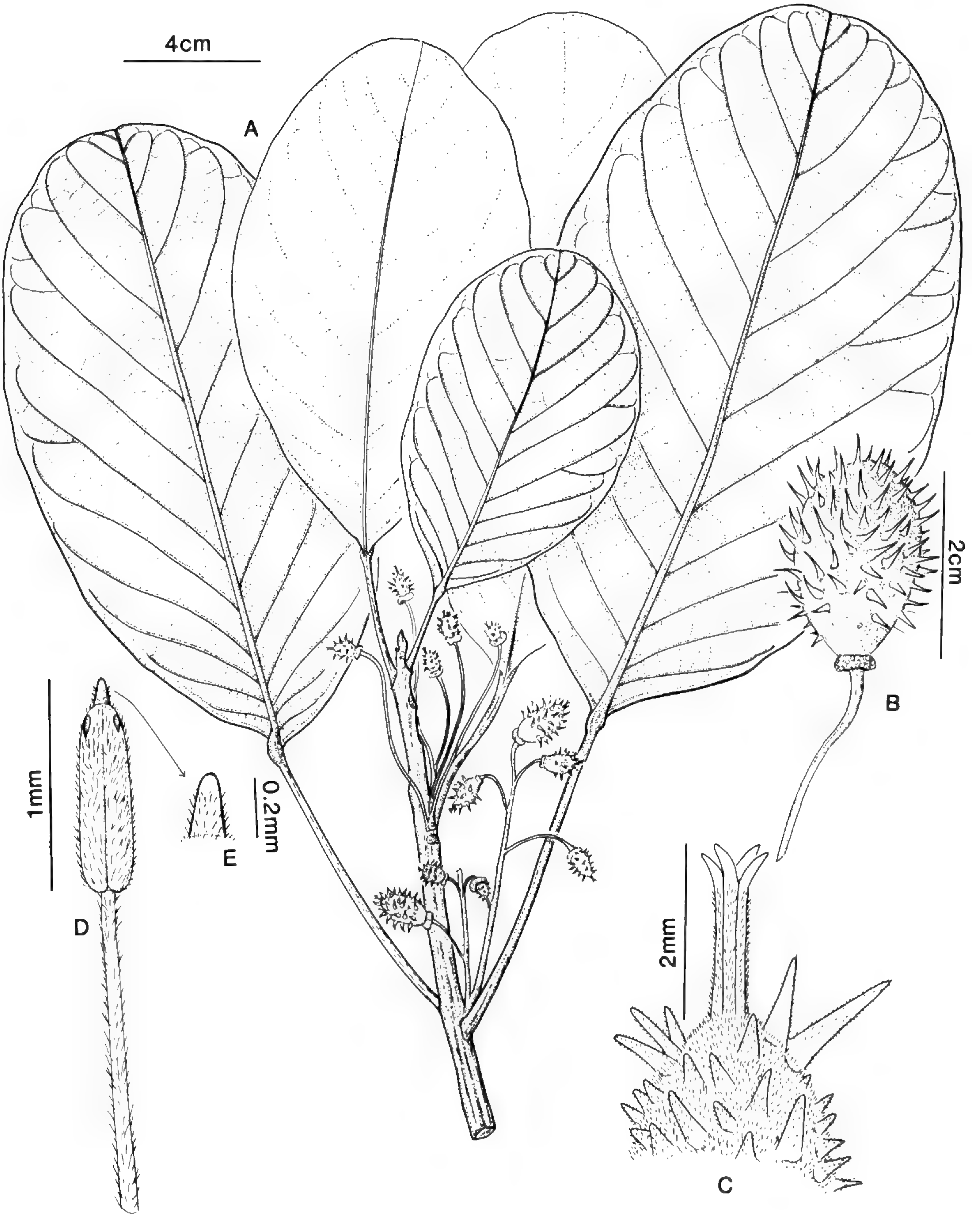

FIGURE 8. Sloanea wurdackii.—*A. Habit.—B. Capsule with pedicel.—C. Pistil.—D. Stamen.—E. Apical connective of anther.*

anastomosing 2–7 mm from the margin, elevated below, impressed above; tertiary venation minutely reticulate, slightly elevated above. Inflorescences elongated, subpaniculate or laxly racemose, 2–3 together, 4–8.5 cm long, 2–5-flowered, the rachis glabrous or minutely sparsely puberulent; pedicels elongated, recurved at apex, 1–4 cm long, the lowest 3.5–4 cm long, minutely puberulent. Sepals strongly reflexed after flowering, lanceolate, 2.5 mm long, 0.7–1 mm wide at base, minutely appressed-pubescent both sides. Anthers linear-lanceolate, 0.9–1 mm long, densely appressed-pubescent, dehiscent near the apex, connective prolonged into a short acutely obtuse pubescent knob 0.1–0.2 mm long; filaments 2 mm long, densely appressed-pubescent. Ovary 3 × 3 mm, densely short pubescent with tubercular processes 0.5–2 mm long; style stout, 2 mm long, appressed pubescent from base to apex. Young fruit oblong, rounded at apex, 1.5–1.7 cm long, 1 cm wide, unequally spinose-tuberculate with rigid stout spines broad at base, 2–3 mm long except absent in the basal 3–4 mm, the tubercles minutely appressed-pubescent; more mature fruit wine purple, 2 cm long, 1.5 cm wide, the spines slender-tipped.

Paratype. VENEZUELA. T. F. AMAZONAS: Dept. Atabapo, Caño Negro, río arriba desde la confluencia con el Río Cunucunuma, 3°40′N, 65°45′W, 200–210 m, 8 Feb. 1982, *Steyermark et al. 126231* (NY, VEN).

This species is characterized by elongated glabrescent pedicels recurved at the apex; elongated, irregularly laxly subpaniculate-racemose inflorescence; short-awned, densely appressed pubescent anthers much shorter than the densely pubescent filaments; stout appressed pubescent style; short, rigid, tubercular spines on a surface lacking tubercules in the basal portion; and general glabrity of stems and leaves. The fruiting structures show similarity to some members of sect. *Paniculi* C. E. Smith, such as *Sloanea caribaea* King & Urban ex Duss. However, the absence of material in full anthesis makes the placing of *S. wurdackii* uncertain. The large leaf blades and elongate petioles somewhat resemble those of *S. schomburgkii* Benth., but that species has longer anthers, which are longer than the filaments.

Although no stamens are present on the paratype, it is referred to the new species because the paratype has the characteristics shortly spinose fruit with rigid slender spines, which are absent in the basal area; the same type of elongated slender, recurved pedicels in an elongated inflorescence; similarly elongated petioles; similar leaf size, shape, and nervation; and general glabrity of the stems, petioles, pedicels, and foliage. The main differences noted in the paratype are the fewer lateral nerves which are farther apart, the lowest ones more spreading at a lesser angle; the leaf bases more rounded or broadly obtuse; and the peculiarly pitted upper surface of the leaf blade.

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BOMBACACEAE

POCHOTA

The following name was inadvertently omitted from the recent publication of this genus by Steyermark & G. W. Stevens (1988):

Pochota robynsii Steyerm. & W. D. Stevens, nom. nov.

Bombacopsis coriacea Robyns, Mem. New York Bot. Gard. 17: 190. 1967, not *Pochota coriacea* (Mart. & Zucc.) Steyerm. & W. D. Stevens.

LITERATURE CITED

STEYERMARK, J. & W. D. STEVENS. 1988. Notes on *Rhodognaphalopsis* and *Bombacopsis* (Bombacaceae) in the Guayanas. Ann. Missouri Bot. Gard. 75: 396–398.

THEACEAE

In the *Flora of the Venezuelan Guayana—III* (Steyermark, 1987b), *Bonnetia bolivarensis* Steyerm., *B. guaiquinimae* Steyerm., *B. ptariensis* Steyerm., and *B. tristyla* subsp. *nervosa* Steyerm. were inadvertently republished. They were published earlier in the same volume and year (Steyermark, 1987a). The holotype specimen remains the same in *B. bolivarensis*, *B. guaiquinimae*, and *B. ptariensis*. In *B. tristyla* subsp. *nervosa*, although the citation of the holotype was changed from *Steyermark & Bunting 103153* to *Maguire et al. 30632*, the original holotype citation of *Steyermark & Bunting 103153* must be retained.

LITERATURE CITED

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TAXONOMIC REVISION OF THE CENTRAL AMERICAN *LISIANTHIUS SKINNERI* SPECIES COMPLEX (GENTIANACEAE)[1]

Kenneth J. Sytsma[2]

ABSTRACT

The Lisianthius skinneri *(Gentianaceae) species complex consists of six closely related species in Panama.* Lisianthius skinneri *is widespread in Central America at low elevations and is morphologically variable. Five mostly cloud-forest species are endemic to central Panama:* L. jefensis, L. peduncularis, L. aurantiacus, L. habuensis, *and* L. weaveri. *The last three species are described as new. Divergence in floral and vegetative morphology among species is compared and contrasted with genetic divergence (DNA and isozymes) previously presented. Morphological divergence within the species complex is not correlated with molecular divergence.*

The *Lisianthius skinneri* (Gentianaceae) species complex is a small, geographically restricted, and interrelated assemblage of taxa. *Lisianthius skinneri* ranges widely throughout Central America but is patchily distributed and shows much ecological and morphological variability. Five endemic species in isolated central Panamanian forests and humid coastal sites exhibit divergence from *L. skinneri* in habit, morphology, breeding system, and ecological tolerance. A taxonomic revision of the *Lisianthius skinneri* species complex based on floral and vegetative morphology is presented here. A biosystematic and evolutionary analysis of the *Lisianthius skinneri* species complex using breeding systems, crossing and cladistic relationships (Sytsma, in prep.), and results of isozyme (Sytsma & Schaal, 1985a) and DNA (Sytsma & Schaal, 1985b) studies is presented elsewhere.

Lisianthius P. Browne is an exclusively neotropical genus in the Gentianaceae. *Lisianthius* and a number of related neotropical shrubby genera form a distinctive but rather diverse group collectively known as the "lisianthioid gentians." *Lisianthius* has been broadly interpreted in the past to include all these lisianthioid genera, usually as *Lisianthus* Linnaeus (1767) or *Lisyanthus* Aublet (1775), orthographic variants of the accepted name *Lisianthius* P. Br. (1756) (Taxon 3: 242. 1954). The most comprehensive and recent taxonomic treatment of the Gentianaceae (Gilg, 1895) places *Lisianthius* and *Macrocarpaea* in the tribe Gentianeae, subtribe Tachiinae. The other lisianthioid genera were relegated to the Helieae. The taxonomy of these lisianthioid gentians is in a state of chaos, with only *Lisianthius* (Weaver, 1972) and *Macrocarpaea* (Ewan, 1948; Nilsson, 1968) adequately monographed. A multidisciplinary study is now beginning on these lisianthioid genera (Nilsson, 1970; Maas et al., 1984; Maas, 1985). Many of these genera are confined to poorly accessible high-elevation peaks, thus explaining the small number of available specimens and the poor or incomplete nature of the few existing ones (Sytsma, 1987).

The genus *Lisianthius* consists of 30 species of woody or semiwoody Gentianaceae almost totally confined to Central America and the Greater Antilles. One species, *L. seemannii* (Griseb.) O. Kuntze, ranges into northwestern Colombia. The center of diversity for the genus is in Guatemala and Mexico, which together have 12 species. The genus exhibits a high degree of endemism. Jamaica has eight species, all endemic. Panama has seven species, five of which are endemic. *Lisianthius* species found

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in Cuba (two species), Hispaniola (one species), and Puerto Rico (one species) are all endemic to each island. Weaver (1972) monographed *Lisianthius* in detail and gave a much needed intrageneric classification scheme. Chromosome numbers for all *Lisianthius* species previously examined (20 out of 30) are identical. Two sections were recognized: *Omphalostigma* and *Lisianthius*. Section *Omphalostigma* (Griseb.) Weaver is composed of only two species, *L. saponarioides* Cham. & Schlecht. and *L. meianthus* Donn. Sm., both exhibiting distinctive salverform corollas and equal filaments inserted near the apex of the corolla tube.

Section *Lisianthius* possesses basically tubular or funnelform corollas and unequal filaments inserted in the lower half of the corolla tube. This section is composed of subsect. *Herbacei* Weaver, annual or perennial suffrutescent herbs with determinate main axes, and subsect. *Fruticosi* Weaver, perennial subshrubs or shrubs with indeterminate main axes. Subsection *Fruticosi* is further divided into three series (*Longifolii* Weaver, *Exserti* Weaver, *Umbellati* Weaver) based on inflorescence architecture, exsertion of stamens and styles, and pollen grain reticulation. With its 18 species, series *Longifolii* is the largest species group in the genus and contains the *Lisianthius skinneri* species complex of Panama.

THE *LISIANTHIUS SKINNERI* SPECIES COMPLEX

BIOGEOGRAPHY AND ECOLOGY

Seven species of *Lisianthius* occur in Panama. Four of these already had been known (Elias & Robyns, 1975) and three are described as new in this paper. Of the seven Panamanian species of *Lisianthius*, six (excluding *L. seemannii* (Griseb.) Kuntze) form an unusual and distinctive interrelated species assemblage, hereafter referred to as the *Lisianthius skinneri* species complex. *Lisianthius seemannii*, ranging from Costa Rica to northwestern Colombia, is not especially closely related to the *L. skinneri* species complex, although it is likewise placed in series *Longifolii* of subsect. *Fruticosi*. *Lisianthius seemannii* has much smaller, usually ovate leaves and vegetatively most closely resembles the Jamaican *L. longifolius* rather than members of the *L. skinneri* species complex. The congested inflorescence in *L. seemannii*, a multicompound dichasium, is unique in series *Longifolii*. The long narrow corolla tube and lobes, paler inside than out, also clearly separate *L. seemannii* from the *L. skinneri* species complex.

Lisianthius skinneri (Hemsley) O. Kuntze is the widest-ranging species in the genus, but with a marked patchy distribution from southeastern Guatemala to the Darién province of Panama. It occurs from sea level to elevations of near 1,500 m in moist to wet tropical forests. The Atlantic Coastal Plain populations in Guatemala, Honduras, and Panama are frequently situated at sea level, while the populations in Costa Rica and the interior of Panama are found at mid elevations or occasionally higher elevations. *Lisianthius skinneri* has not been collected on the Atlantic Coastal region of Nicaragua or Costa Rica. It is not known whether this absence is due to poor collecting in these areas or whether it reflects an unusual geographic disjunction.

The distribution of *Lisianthius skinneri* is clearly correlated with moisture availability. The mid-elevation forests situated on both the Atlantic and Pacific flanks of the Cordillera de Talamanca extending southeastward from Costa Rica into western Panama and the Cordillera de San Blas and Serranía del Darién in eastern Panama receive abundant rainfall. Only on the more humid and wetter Atlantic side has *L. skinneri* been able to occupy lower elevation sites near or at sea level.

The distribution of *Lisianthius skinneri* throughout its range is markedly patchy, with populations usually separated by many kilometers. This is especially evident in central Panama where large portions of the lower to mid elevations have been extensively explored and collected. *Lisianthius skinneri* is very local in occurrence, as seen in the distribution map of all known populations in Panama (Fig. 1). Some gaps in this distribution will be eliminated with more collecting, especially towards high elevations and on the Atlantic watershed, but undoubtedly the patchy distribution of this species will remain.

Most populations occur in disturbed or partially open habitats. Forest edge sites along roads and paths are now more common because of increasing utilization of the lower elevation forest by people. Often populations are seen in more closed habitats such as tree fall gaps. Scattered groups of individuals are also occasionally encountered in undisturbed forests but do not form the larger clumped populations typically seen in the more disturbed habitats. Population size varies from few to about a hundred individuals. Most populations, however, cover less than 50 square meters and are composed of about 50 flowering shrubs.

In contrast to the wide-ranging distribution of *Lisianthius skinneri*, the other members of the *L. skinneri* species complex are all endemic to central Panama. The physiography of the central Panama mountain system is unusual because it is relatively

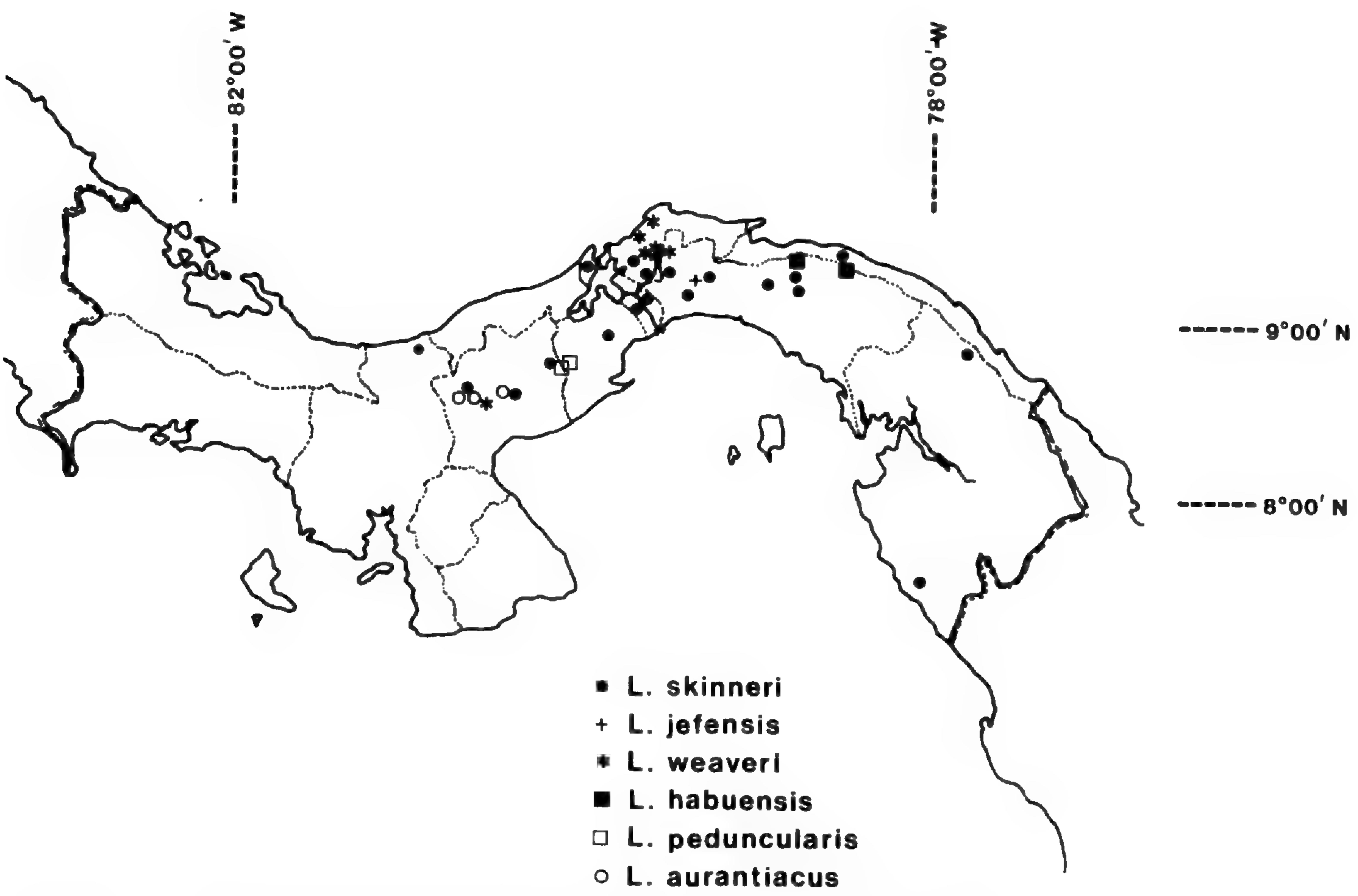

FIGURE 1. *Distribution of the* Lisianthius skinneri *species complex in Panama.*

low in relief, sinuous in nature, and discontinuous in extent. The central Panama region is thus marked by isolated, cloud forest peaks (600–1,500 m) interrupted by more extensive low- to mid-elevation forests. Four of the additional five species in the *L. skinneri* species complex are restricted to separate cloud forest peaks in this region (Fig. 1). These species include *L. jefensis* Robyns & Elias, *L. peduncularis* L. O. Williams, *L. aurantiacus* sp. nov., and *L. habuensis* sp. nov. *Lisianthius weaveri* sp. nov. is unique in the species complex in that several populations occupy forest-edge sites near beaches on the Atlantic side. Like the cloud-forest populations, these populations still occupy a high-rainfall environment. All species except *L. aurantiacus* and *L. weaveri* are comprised of few populations restricted to a small area. *Lisianthius aurantiacus* and *L. weaveri* are more widespread in distribution but are markedly patchy in occurrence.

MORPHOLOGY

Morphological characters used to delimit species in the *Lisianthius skinneri* species complex are almost exclusively confined to features of the inflorescence and flower. Additional vegetative characters are occasionally divergent in the group and will also be presented. Only characters that are variable among members of the species complex, and hence of possible phylogenetic interest, will be presented here. A more formal description of all characters will be given in the next section. Measurements were made primarily on dried specimens. Floral characters of the Panamanian populations were measured directly on FAA-preserved material. Only herbarium specimens were examined for populations of *L. skinneri* occurring outside Panama.

Habit. All species except *Lisianthius aurantiacus* are true shrubs. *Lisianthius aurantiacus* in open sites is typically arboreal and can reach heights over 6 m. These trees are slender-stemmed and evenly branched to the top. In more closed forest environments, *L. aurantiacus* is a 2–3 m branched shrub, as are the remaining taxa. Occasionally, taller individuals of *L. peduncularis* are seen in the elfin forest atop Cerro Carocoral. Like most species of sect. *Lisianthius* subsect. *Fruticosi,* these species are not distinctly woody except at the base, even though they persist for years. They usually have a single main stem that is branched above, but totally unbranched flowering plants are seen in *L. skinneri, L. weaveri,* and *L. jefensis.* The main shoot has an indeterminate growth pattern, and the lateral shoots ("flowering branches") have a determinate growth pattern.

Leaves. Two types of leaves are evident in the *Lisianthius skinneri* species complex, true foliage leaves and lateral shoot leaves, which can be a problem if leaf characteristics are used in a systematic analysis. This is especially so because many herbarium collections contain only lateral shoots without true foliage leaves (Weaver, 1972). The foliage leaves of all species except *L. jefensis* are obovate, membranaceous, glossy green above, and paler beneath. Leaves of *L. habuensis* have somewhat undulating margins. *Lisianthius jefensis* leaves are subcoriaceous and usually smaller than those of the other five species. It is interesting that a number of other endemic species on Cerro Jefe also have subcoriaceous to fully coriaceous leaves (pers. obs.). Leaves on the determinate lateral "flowering branches" are smaller, with the transition from foliage leaves to lateral shoot leaves abrupt. Two collections of higher elevation *L. skinneri* from Volcán Arenal, Costa Rica (*Wilbur & Stone 10257*, *Lent et al. 3321*) appear to have thickened leaves as well, although Weaver (1972) did not mention it in his monograph. Lateral shoot leaves are ovate to lanceolate and merge into the foliaceous inflorescence bracts. Lateral shoot leaves are absent from *L. aurantiacus* because flowering branches are reduced to single or paired axillary flowers. Small floral bracts are present, however.

Inflorescences. The inflorescence of *Lisianthius* is very difficult to interpret but is an important characteristic in determining phylogenetic relationships within the genus. Architecture of the inflorescence varies considerably in *Lisianthius*, and Weaver (1972) set forth a probable evolutionary scheme for the development of the various types. The arrangement of inflorescences in sect. *Lisianthius* subsect. *Fruticosi* is characterized almost entirely by opposite branching with each division terminated by dichasia. The dichasia are axillary or, more often, both terminal and axillary on determinate lateral shoots. Foliaceous leaves are located below the lowest trichotomy and the upper divisions are subtended by bractlike appendages. The various arrangements of inflorescences in the *L. skinneri* species complex are depicted schematically in Figure 2.

Lisianthius skinneri, *L. weaveri*, and *L. jefensis* are characterized by a ternate compound dichasium in each axillary inflorescence (Fig. 2a). This inflorescence type comes closest in the *L. skinneri* complex to the primitive multi-compound dichasium that Weaver (1972) postulated for the genus. Simple reduction to a twice-compound dichasium gives the inflorescence type seen in *L. peduncularis* (Fig. 2b). A further reduction of two lateral dichasia (Fig. 2c), or, alternatively, reduction in the terminal dichasium (Fig. 2d) generates the two reduced inflorescences commonly exhibited by *L. habuensis*. Reductions of the *L. peduncularis* type to a single flower, but retaining the three sets of bracts, gives the three-bracted nodes subtending a one-flowered axillary inflorescence sometimes evident in *L. aurantiacus* (Fig. 2e). *Lisianthius aurantiacus*, however, usually has two levels of bracts and either one or two flowers in each axillary inflorescence (Fig. 2f, g).

Calyx. The calyx is variable not only among the species but also within *Lisianthius skinneri*. Populations of *L. skinneri* near sea level in Guatemala and Honduras exhibit the largest calyces in the species. They range from 6 to 8 mm, with the calyx lobes ranging from 3 to 6 mm long. The smallest calyx is seen in populations in the interior of Costa Rica and Panama. Here the calyx ranges from 5 to 6 mm, with the calyx lobes 2 to 4 mm, and is generally appressed and carinate. The calyces in *L. weaveri* are similar to those in *L. skinneri* but are stouter, spreading, and only somewhat ridged. The calyces in *L. peduncularis* and *L. aurantiacus* are very long, 10–13 mm and 13–15 mm, respectively. The calyx lobes of these two species are exceptionally long, averaging about ¾–⅞ of the total length. *Lisianthius jefensis* also has a longer, more attentuate calyx than *L. skinneri*. The calyx in *L. habuensis* is similar in size to *L. skinneri* (6–8 mm long) but with longer dark green lobes (4–5 mm long) that are strongly carinate and scarious on the margins

Corolla. The structure of the corolla in all species is basically uniform (Fig. 3). The basal portion of the corolla enclosing the ovary is constricted into a narrow tube. The stamens are inserted on the inside of the corolla tube at the distal end of the constriction. Immediately above the insertion of the stamens the corolla flares out, often abruptly. Just below the lobes the corolla tube is again constricted, but usually not to the degree as in the basal region. *Lisianthius skinneri* shows extreme variation in the proportions of the corolla. The Guatemalan plants (including the type specimen) have long (5–5.4 cm), narrow, and membranaceous-textured yellow corollas. The corolla lobes are greenish, broad, and short acuminate. Plants from Honduras, Costa Rica, and the interior of Panama closely resemble the Guatemalan plants but have a broader, more inflated corolla tube,

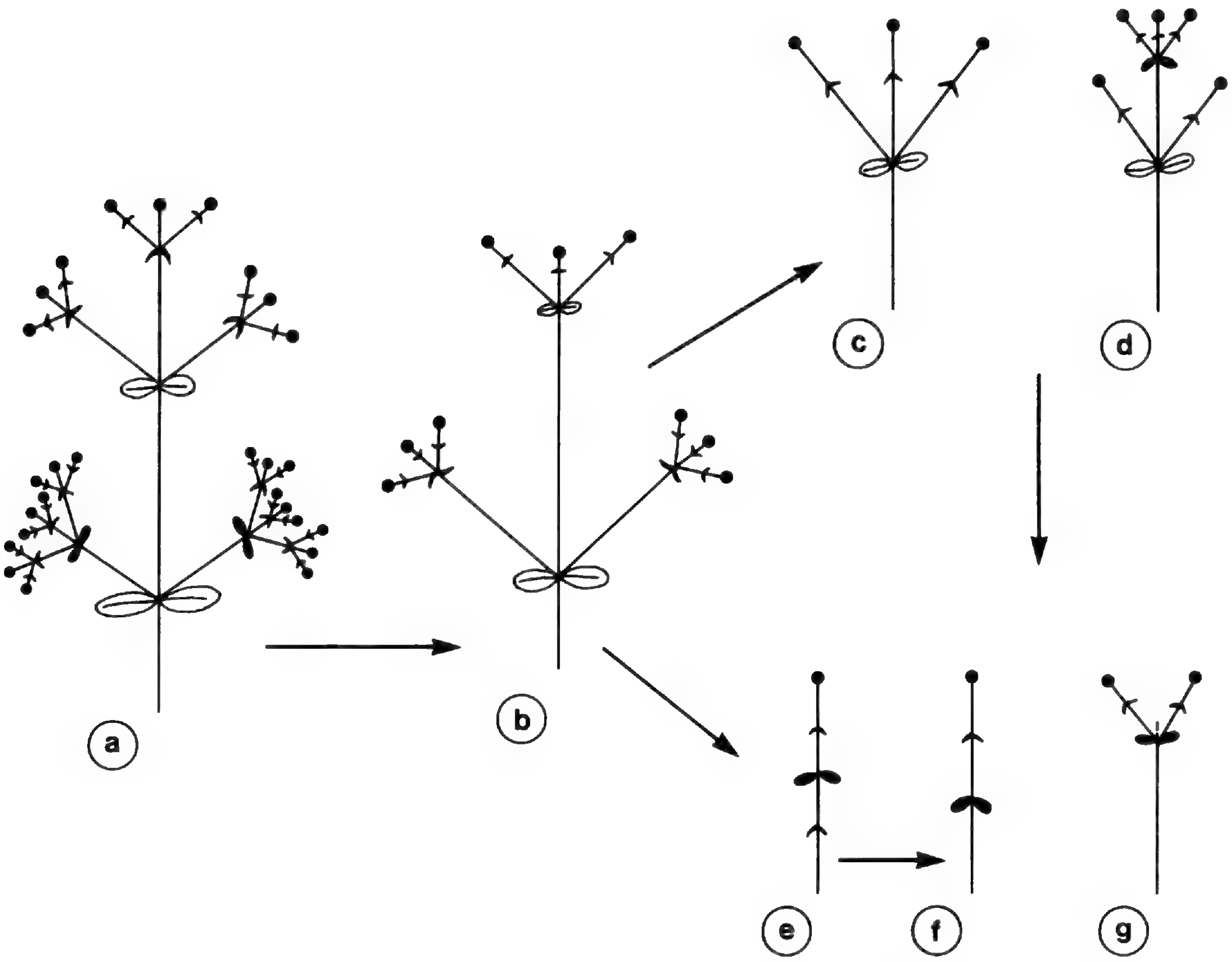

FIGURE 2. *Schematic arrangement of the inflorescences in the* Lisianthius skinneri *species complex. Arrows represent probable evolutionary pathways for inflorescence types and do not imply phylogenetic pathways of the representative species.—a.* L. skinneri, L. jefensis, *and* L. weaveri.—*b.* L. peduncularis.—*c, d.* L. habuensis.—*e–g.* L. aurantiacus.

markedly so in the El Llano–Cartí road populations in Panama. The two previously cited Costa Rican collections from Volcán Arenal (*Wilbur & Stone 10257*, *Lent et al. 3321*) are aberrant in having waxy, thick-textured corollas. The five endemic species in Panama are all characterized by thick-textured, waxy corollas. The correlation of this unique corolla form to wetter higher elevations or to the humid Atlantic Coastal Plain (*Lisianthius weaveri* in part) suggests that this floral character might provide protection against extremely damp conditions and subsequent floral destruction. The high incidence of damaged and rotting, thin-textured flowers on higher-elevation *L. skinneri* plants on Cerro Jefe and the continental divide near Cascajal supports this idea. *Lisianthius jefensis* and *L. weaveri* exhibit the smallest corollas. The corolla of *L. jefensis* is 2.5–4 cm long, with spreading and recurved lobes 4–6.5 mm long, while the corolla of *L. weaveri* is 2.6–4.5 cm long, waxy yellow and green tipped, and surrounds long-exserted styles. The corolla of *L. habuensis* is broad and 4.9–6.1 cm long with the corolla lobes triangular, smallish (3.5–5 mm long and wide at the base), dark green with cream margins, and slightly recurved. The flowers of *L. peduncularis* and *L. aurantiacus* are very similar, both having very long corollas (4.8–6 cm and 5.5–7.8 cm, respectively) and long attentuate lobes (8–10 mm and 9–11 mm, respectively). The pumpkin orange to red corolla color and dark green corolla lobes of *L. aurantiacus* are strikingly different from any Panamanian *Lisianthius*.

Androecium. Weaver (1972) used the placement of stamens as a diagnostic character in separating *Lisianthius skinneri* from *L. jefensis* and *L. peduncularis*. In *L. skinneri* the stamens are inserted well above the apex of the calyx lobes, whereas in the other two species the stamens are inserted at or just above the apex of the lobes. This latter condition also applies to the new cloud-forest species, *L. habuensis* and *L. aurantiacus*. The use of this character as diagnostic is misleading because

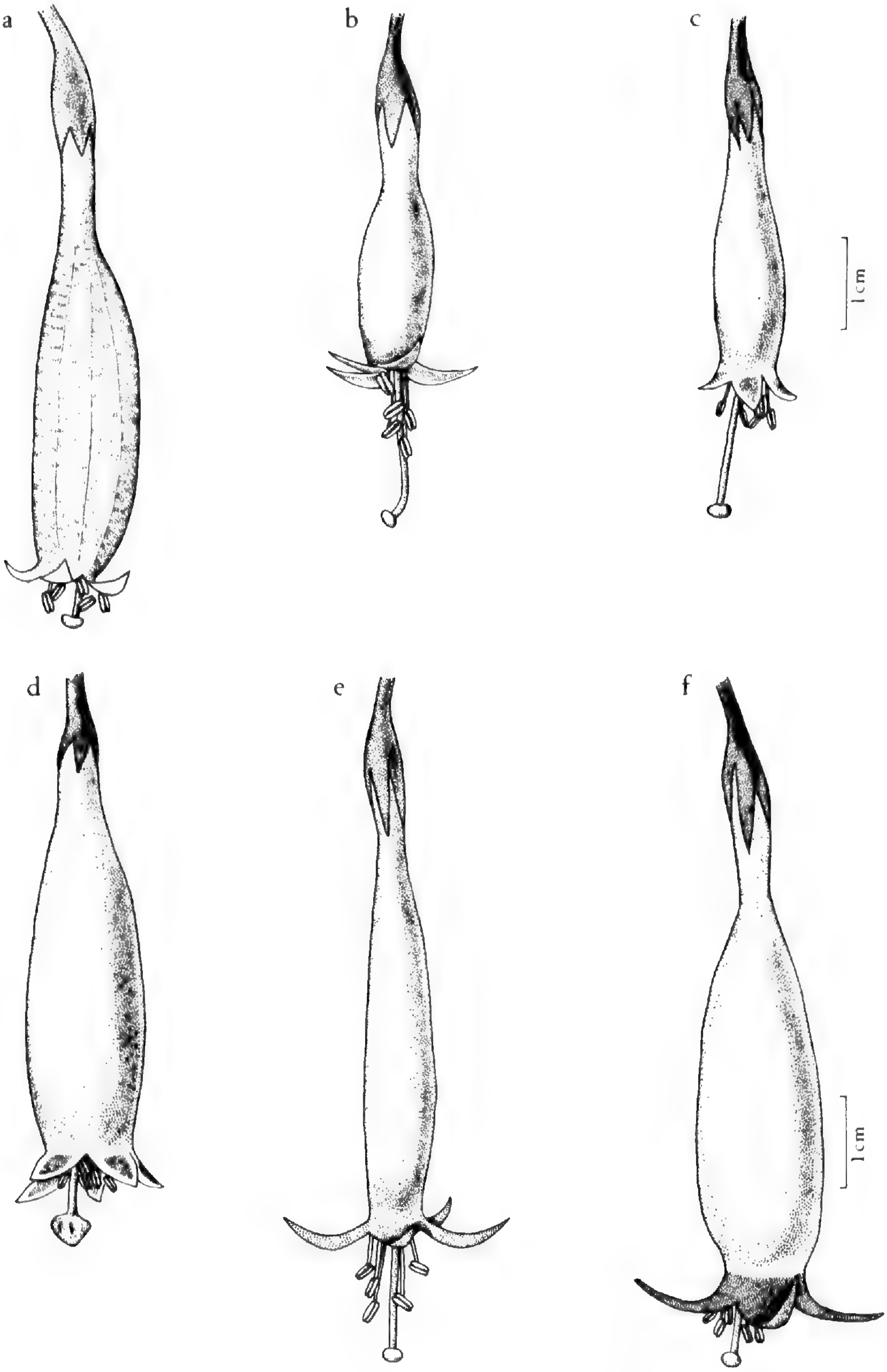

FIGURE 3. *Flowers in the* Lisianthius skinneri *species complex.*—*a.* L. skinneri.—b. L. jefensis—*c.* L. weaveri—*d.* L. habuensis.—*e.* L. peduncularis.—*f.* L. aurantiacus.

it does not reflect a difference in the placement of the stamen, but rather in the length of the calyx. All species in the *L. skinneri* species complex have the stamens attached to the inner corolla tube about the level of the apex of the ovary. Stamen length varies depending on corolla tube length, with most species having stamens protruding slightly from the corolla lobes. The stamens in *L. jefensis* are proportionally longer than in the other species and are conspicuously exserted. Anthers and pollen are whitish yellow in most *L. skinneri* individuals, greenish yellow in some individuals of *L. skinneri* and in the other species, except for *L. aurantiacus*, in which they are bluish green.

Gynoecium. Style, ovary, capsule, and seed size, like the stamens, are correlated with flower size in general. Exceptions include *Lisianthius jefensis* and *L. weaveri*, which both have longer exserted styles. Stigma shape and size are diagnostic characters separating out *L. habuensis*. All other species in the complex exhibit smooth, small stigmas (1–1.5 mm broad). The stigma in *L. habuensis* is unique and divergent in being large (2.5–3 mm broad), conical, and rough textured.

SYSTEMATIC TREATMENT

The grouping of populations into formal taxonomic categories has two underlying purposes. The first and traditionally the primary purpose of such an endeavor is the construction of an information retrieval system that permits effective communication about the populations (Raven, 1979). The taxonomic system constructed should preserve information that enters the system and should minimize its loss once taxonomic decisions have been made. The second purpose is the construction of a taxonomic system that best reflects the phylogenetic or historical relationships of the populations. Often, both goals of taxonomic decision-making cannot be simultaneously satisfied.

In delimiting species in the *Lisianthius skinneri* species complex, problems were encountered in grouping populations into formal categories of "species." As previously indicated, DNA techniques indicated the paraphyletic nature of *L. skinneri* (Sytsma & Schaal, 1985b). Populations of *L. skinneri* examined at the DNA level could be placed in two separate lineages that have been involved in separate speciation events. Cladistic analysis strictly following Hennig's (1966) principles would raise a western Panamanian *L. skinneri* population to the species level to preserve monophyly and to reflect better the apparent phylogeny of the species complex. This separation is unsatisfactory because it violates the first purpose of an effective information retrieval system. Although clearly this western population is *phylogenetically* divergent by DNA analysis, it also clearly falls within the range of morphological variation of the widespread *L. skinneri* as predefined. Because of the broad distribution and ancestral nature of *L. skinneri*, it is very likely that many clusters of populations in *L. skinneri* will be shown by DNA analysis to represent divergent and independent lineages and by similar reasoning would also have to be accorded species status.

In assigning formal names to clusters of populations in the *Lisianthius skinneri* species complex, therefore, additional sources of data were used in addition to genealogical or phylogenetic interpretation. For example, *L. jefensis* is identical to an eastern population of *L. skinneri* by cladistic DNA analysis (Sytsma & Schaal, 1985b) but is maintained as a distinct species derived from *L. skinneri* based on its peculiar morphology, lack of hybridization, and endemic nature. The western Panamanian population of *Lisianthius skinneri*, apparently a member of a lineage that has given rise to other species, is maintained as *L. skinneri* because no changes in morphology, reproductive barriers, or habitat preference are outside the range of variation found in typical members of *L. skinneri*.

KEY TO THE *LISIANTHIUS SKINNERI* SPECIES COMPLEX

1a. Leaves subcoriaceous; anthers and styles conspicuously exserted, and long surpassing the corolla lobes; endemic to Cerro Jefe, Panama .... 3. *Lisianthius jefensis*
1b. Leaves membranaceous; anthers and styles included, or slightly exserted and not conspicuously surpassing the corolla lobes, or only the styles conspicuously exserted.
  2a. Corolla lobes ≥ 7 mm long; calyx lobes ≥ 6 mm long.
    3a. Inflorescence of 1–2 axillary flowers; corolla pumpkin orange to red; plant often treelike .... 6. *Lisianthius aurantiacus*
    3b. Inflorescence of twice compound dichasia; corolla yellow; plants shrubby .... 5. *Lisianthius peduncularis*
  2b. Corolla lobes ≤ 5 mm long; calyx lobes ≤ 6 mm long.
    4a. Calyx lobes 4–5 mm long; inflorescence of simple dichasia, never ternately compound; stigma 2.5–3 mm in diameter, conical, convoluted .... 4. *Lisianthius habuensis*
    4b. Calyx lobes 2–4 (rarely 5) mm long; inflorescence of twice or ternately compound dichasia; stigma 1–1.5 mm in diameter, rounded, smooth.
      5a. Corollas 5–5.4 cm long, thin-textured; styles slightly exserted past anthers .... 1. *Lisianthius skinneri*
      5b. Corollas 2.6–4.5 cm long, thick-textured; styles long exserted past anthers .... 2. *Lisianthius weaveri*

1. Lisianthius skinneri (Hemsley) O. Kuntze, Rev. Gen. Pl. 2: 429. 1891. *Leianthus skinneri* Hemsley, Biol. Centr. Amer. 2: 345. 1882. *L. skinneri* (Hemsley) Perkins, Bot. Jahrb. (Syst.) 31: 492. 1902. TYPE: Guatemala. Locality not given: *Skinner s.n.* (lectotype, K, photographs, F, MO).

Lisianthus arcuatus Perkins, Bot. Jahrb. Syst. 31: 492. 1902. TYPE: none designated.
Lisianthus scopulinus Robyns & Elias, Ann. Missouri

Bot. Gard. 55: 62, fig. 2. 1968. TYPE: Panama. Veraguas: mouth of Río Concepción, *Lewis, Croat & Hawker 2799* (MO).

Shrub or subshrub, 0.5–3 m tall; stem terete, erect, green. Leaves membranaceous, deep to light green, paler below; blades 4–24 cm long and to 7.7 cm wide, obovate to obovate-elliptic, sharply acuminate; the costa prominent, lateral veins 2–3, ascending; petiole amplexicaul, winged. Inflorescences terminal or axillary, composed of ternately compound, laxly flowered dichasia; foliaceous leaved below first division, bracted above; bracts opposite, lanceolate to linear, 2 mm long or longer. Flowers horizontal to nodding; calyx 5–7 mm long, the lobes 3–5 mm long, carinate dorsally, ± scariously margined, stout or attenuate, appressed or spreading; corolla tubular-funnelform, constricted apically and distally, the tube 5–5.4 cm long and to 1 cm broad, bright yellow, occasionally greenish-tipped, membranaceous, the lobes ovate, 2.5–5.5 mm long, 2.5–4 mm wide, yellowish green to dark green, often with cream margins, often recurved at tip, short to long acuminate. Stamens inserted within corolla at apex of ovary; filaments 4.2–4.7 cm long, unequal in length, longest one at least equaling or surpassing corolla lobes; anthers 2–3 mm long and ca. 1 mm wide, bilobate at the base; pollen whitish yellow. Style 4.7–5.1 cm long, usually slightly exserted past anthers; stigma peltate, 1–1.5 mm broad. Capsules fusiform, 1.8–2.2 cm long, beaked by persistent style to 9 mm long; seeds asymmetrical, surface corrugated, to 0.75 mm long. Chromosome number, $n = 18$.

Distribution. From sea level to 1,300 m in moist to wet tropical forests or roadsides, at middle elevations in Costa Rica and the interior of Panama, and along the Atlantic Coastal Plain of Guatemala, Honduras, and Panama.

Lisianthius skinneri as delimited here encompasses all populations of the *L. skinneri* species complex outside Panama and most populations at low to mid elevations in Panama. Based on distribution and DNA analysis, *L. skinneri* is the ancestral species in the complex (Sytsma & Schaal, 1985b). The four endemic cloud-forest species that were examined by DNA analysis arose from at least two lineages within *L. skinneri*. The corolla is longer and thinner in texture (membranaceous) than corollas in the now segregated *L. weaveri*. The latter species has smaller flowers with thickened and waxy corollas like other species in this complex. *Lisianthius skinneri* as defined here is composed of populations showing moderate variability (Weaver, 1972). This is not surprising, considering both the widespread distribution and ancestral nature of the species. This variation, however, presents considerable problems when species circumscription is attempted. *Lisianthus scopulinus* Robyns & Elias from Veraguas Province, Panama, has somewhat large calyx lobes (4–5 mm long) for *L. skinneri*. It resembles *L. skinneri* in all other traits and is here merged with *L. skinneri* as another geographically variable population. One population of *L. skinneri* from Costa Rica is unique in having thickened flowers and in occurring at higher elevations on Volcán Arenal (*Wilbur & Stone 10257*, *Lent et al. 3321*). This population was not visited during the study, so its status as a distinct element in the *L. skinneri* species complex is only tentative.

Representative specimens examined. GUATEMALA. IZABAL: south shore of Lake Izabal, *Proctor et al. 3049* (F). ALTA VERA PAZ: eastern portions of Vera Paz & Chiquimula, *Watson 380a* (G). HONDURAS. ATLANTIDA: 42 km SE of Tela to La Ceiba, *Davidse & Pohl 2194* (MO); San Alejo, *Standley 7829* (F); Cuyamel, *Carleton 584* (F). COSTA RICA. ALAJUELA: 17–22 km beyond San Ramón to Cataratas, *Almeda et al. 4301* (F, MO); middle slopes N side of Volcán Arenal, *Lent 3868* (F, MO); *Lent et al. 3321* (F); Villa Quesada near San Carlos, *Smith 1884* (F, MO); 13.5 mi. E of Arenal, 6.5 mi. W of Fortuna, *Wilbur & Stone 10257* (DUKE, F, MO, NY, US). GUANACASTE: Volcán Miravalles, *Burger & Gentry 9126* (F); Hacienda Santamaria, *Dodge et al. 6320* (F, MO); lower slopes Cerro La Giganta [Cerro Miravalles], 2 km W of Río Naranjo, *Utley & Utley 1899* (DUKE); Tilarán, *Valerio 115* (F); SE lower slopes Volcán Miravalles, *Wilbur & Almeda 16623* (DUKE, F, MO, US). HEREDIA: Finca Hnos. Vargas, Puerto Viejo de Sarapiquí, *Jiménez 3577* (MO); Río La Paz & Cariblanco de Sarapiquí, *Pittier 14159* (US). PANAMA. COCLÉ: La Mesa, N of El Valle de Antón, *Allen 2369* (MO); continental divide past Llano Grande, *Dressler 5627* (MO); Río San Juan below junction with Río Tífe, *Hammel 3436* (MO); 5 mi. past Llano Grande near continental divide, *Sytsma 3872* (MO); 4 mi. past Llano Grande at continental divide, *Sytsma 3939* (MO); 9 km N of Llano Grande, *Hammel 1713* (MO). COMARCA DE SAN BLAS: El Llano–Cartí Rd., 10 km N of Panamerican Hwy., *Folsom 2622* (MO); Nusagandi, along El Llano–Cartí Rd., below (N of) Punta Mamá, 350 m, *de Nevers & Nuñez 3565* (MO); Río Nergala, 100–300 m, *de Nevers & Herrera 4548* (MO); Río Irgandí and Río Cartí Senni, *de Nevers & Herrera 6610* (MO, WIS); Río Cangandí & Río Titamibe, 50–150 m, *de Nevers 4677* (MO); Río Sidro, base of Cerro Habu, *Sytsma et al. 2622* (MO); Cerro Habu, 400–800 ft., *Sytsma et al. 2799* (MO). DARIÉN: upper Río Membrillo on construction road to San Blas, *Duke 10891* (MO). PANAMÁ: Cerro Campana, near FSU Field Station, ca. 800 m, *Kennedy & Williams 233* (WIS); Cerro Jefe region [Cerro Azul & Altos de Pacora], *Antonio 3204* (MO); *Correa et al. 582* (DUKE, MO); *D'Arcy et al. 3955* (MO); *Dwyer 2649, 9445* (MO); *Knapp 927* (MO); *Lewis et al. 2314* (MO); *Maas et al. 1540* (MO); *Sytsma & D'Arcy 3672, 3673* (MO); *Sytsma & Antonio 3828* (MO); *Sytsma & Knapp 4795* (MO); *Sytsma et al. 5006*

FIGURE 4. Lisianthius weaveri (Antonio 3737 *(MO)).—a. Habit.—b. Flower.—c. Dehisced fruit.*

(MO); *Tyson 5320* (DUKE, MO); *Weaver & Foster 1482* (DUKE, MO, NY); *Weaver & Wilbur 2242* (DUKE, NY), *2244* (DUKE, MO, NY); *Webster et al. 16475* (DUKE, MO); *Wilbur et al. 11338, 15540* (DUKE); *Wilbur & Teeri 13606* (DUKE, MO, NY); El Llano–Cartí region, 6–8 mi. from Pan American Highway, *Antonio 1690* (MO); *Croat 49099* (MO); *D'Arcy 10591* (DUKE, MO); *Folsom 1439* (MO); *Gentry 5788* (MO); *Hahn 324* (MO); *Hamilton & Stockwell 1102* (MO); *Hammel 862* (MO); *Kennedy et al. 3148* (MO); *Knapp 930* (MO); *Mori et al. 4719* (MO); *Mori & Kallunki 5565* (MO); *Nee & Dressler 9327* (MO); *Sytsma &*

Sytsma 3099 (MO); *Sytsma 3989* (MO); *Sytsma & Andersson 4432* (MO); *Wilbur & Luteyn 19490* (DUKE, F, MO, NY); 11 km N of Gamboa, *Croat 32937* (MO); Río Boquerón, trail to Río Pequeni, *Dressler 6001* (MO); 10 km N of Magarita on road to Madroño, *Hammel & D'Arcy 5117* (MO); *Hammel 6007* (MO); headwaters Río Arenal, *Johnston 1502* (MO); Gorgas Memorial Labs yellow fever research camp, Río Piedras, *Mori & Kallunki 3364* (MO); Pipeline road, 9 km N of Gamboa, *Nee 7681* (MO, WIS); Pipeline road, 8 km N of Gamboa, *Nee 9580* (MO); Canal Zone, Río Indio, *Steyermark & Allen 17427* (MO). VERAGUAS: mouth of Río Concepción, *Lewis et al. 2799* (DUKE, MO).

2. **Lisianthius weaveri** K. J. Sytsma, sp. nov. TYPE: Panama. Colón: Santa Rita ridge trail along Río Piedras, 8,000 ft., 9 Mar. 1979, *Hammel 6357* (holotype, MO; isotype, WIS). Figure 4.

Frutex ad 2.5 m altus. Folia obovata-elliptica, ad 23 cm longa et 8.5 cm lata. Inflorescentiae axillares et terminales, dichasio biternato vel triternato. Calyx 5–6 mm longis; tubus ad 2 mm longus; lobi 3–4.5 mm longi, scariosescens ad margineum. Corolla aurea, cerea, 2–3.5 cm longa; lobi triangulares, virides, cerescens ad margineum, 2–3 mm longi et lati. Stamina filamentis ± exsertis. Stilus antherae superans 5–10 mm; stigma peltatum, 1–1.5 mm latum. Capsulae fusiformes ad fusiformes late, 1.5–2 cm longa.

Shrub or subshrub, to 2.5 m tall; stem terete, erect, green. Leaves membranaceous, deep green above, paler below; blades to 23 cm long and to 8.5 cm wide; obovate to obovate-elliptic, ± strongly acuminate tipped; the costa prominent, with 2–3 sets of lateral veins, these ascending and becoming parallel with margin; petiole amplexicaul. Inflorescences terminal or axillary in upper nodes; ternately compound dichasia (or only twice compound); foliaceous leaved below, bracted above. Flowers horizontal or nodding; calyx 5–6 mm long, tube to 2 mm long, the lobes 3–4.5 mm long, carinate dorsally, scariously margined, triangular-attenuate, ± appressed; corolla tubular-funnelform, constricted distally and ± apically, the tube 2.2–3.3 cm long and to 8 mm wide, waxy and fleshy, bright yellow; lobes 2–3 mm long and wide, broadly triangular, green but with cream or yellow margins. Stamens inserted within corolla at apex of ovary; filaments to 2.5 cm long, equaling or barely exceeding corolla lobes; anthers 2–2.5 mm long and 0.75–1 mm wide, bilobate at base, pollen yellowish. Style to 3.5 cm long, far exserted (5–10 mm) past anthers; stigma peltate, 1–1.5 mm broad. Capsules fusiform to broadly fusiform, 1.5–2 cm long, beaked by persistent style to 10 mm long.

Distribution. *Lisianthius weaveri* is known from mid- to high-elevation cloud forests in Coclé and Colón provinces and at sea level on the Atlantic Coastal Plain in Colón Province, Panama.

Lisianthius weaveri is the only cloud forest species of *Lisianthius* found on both sides of the the Panama Canal. This species has been collected from a number of sites in the higher ridges leading to Cerro Bruja, so far an inaccessible peak dominating the ridge of mountains paralleling the Atlantic Ocean in eastern Colón Province. Populations of *L. skinneri* collected in the lower reaches of this region are quite distinct from those of *L. weaveri*. *Lisianthius weaveri* is also found near the continental divide above El Cope, Coclé Province, the southeastern edge of the Cordillera de Talamanca extending northwestard towards Costa Rica. Three additional populations occupy high-rainfall, forest-edge sites near the beach on the humid Atlantic side of Panama. *Lisianthius weaveri* resembles *L. jefensis*, also with short and waxy corollas, but lacks the exserted stamens and coriaceous leaves of the latter. The short, fleshy, and waxy corolla and the exserted style readily distinguish *L. weaveri* from lower-elevation *L. skinneri* populations. Weaver (1972) cited the *Weaver & Wilbur 2249* collection as distinctive with its short, fleshy corolla and long exserted style. Although *L. skinneri* is certainly variable in floral features, the collections of *L. weaveri* surpass this level of variability and can be readily distinguishable from all other collections of *L. skinneri*. A possible but as yet untested origin of *L. weaveri* might involve hybridization between *L. skinneri* and *L. jefensis*. In many of its floral characters, *L. weaveri* is strikingly intermediate between these geographically adjacent species. *Lisianthius weaveri* is named in honor for Richard E. Weaver, Jr., monographer of the genus.

Representative specimens examined. PANAMA. COCLÉ: Alto de Calvario, *Folsom & Jaslon 2680* (MO); El Cope, W of sawmill, *Hammel 3545* (MO). COLÓN: Cerro Pilón, *Loften s.n.* (MO); Cerro Santa Rita, *Allen & Allen 5104* (MO); Santa Rita trail to Río Piedras, *Antonio 3737, 3869* (MO, WIS); Río Miguel de La Borda near Guasimo, *Croat 9919* (MO); W of Portobello, *D'Arcy & D'Arcy 6698* (F, MO); Maria Chiquita, *Dwyer & Kirkbride 7771* (DUKE, MO); S approach to Cerro Bruja from Río Escandaloso, *Hammel 3210* (MO); Río Boquerón and Río Escandaloso, *Hammel 3988* (MO, WIS); Santa Rita hills, *Smith & Smith 3434* (F); 3 km SW of Río Guanche, road between Puerto Pilón and Portobelo, *Sytsma & Andersson 4792* (MO); 5–7 mi. SE of Portobelo, *Weaver & Wilbur 2249* (DUKE, F, MO, NY); Santa Rita ridge, *Wilbur et al. 15020* (DUKE).

3. **Lisianthius jefensis** Robyns & Elias, Ann. Missouri Bot. Gard. 55: 60, fig. 1. 1968 (as "*Lisianthus*"). TYPE: Panama. Panamá: Cerro Jefe, *Elias & Hayden 1798* (MO).

Slender shrub or subshrub, 1–2.5 m tall; stem terete, green. Leaves glossy dark green above, paler below; blades to 12 cm long and to 4.5 cm wide, subcoriaceous, oblanceolate to narrowly obovate, apically acuminate, the lateral veins prominent; petioles amplexicaul, winged. Inflorescences terminal or axillary, composed of twice to ternately compound dichasia, rarely reduced, usually loosely arranged; bracts opposite, 2–5 mm long. Flowers horizontal, or more often nodding; calyx 7–13 mm long, lobes long acuminate, 5–9 mm long, scariously margined, weakly carinate; corolla tubular, thickened and waxy, constricted apically and distally, tube 2.1–3.5 cm long, sometimes greenish tipped, lobes 4–6 mm long, triangular, to 3 mm wide. Stamens inserted on corolla at apex of ovary; filaments 1.5–3 cm long, the longest ones long exserted past corolla lobes; anthers 2.5–3.5 mm long, yellow, bilobate at base. Style to 3.5 cm long, conspicuously exserted past anthers; stigma peltate, to 1 mm broad. Capsule shortly fusiform, 1–1.6 cm long, beaked; seeds asymmetrical, corrugated. Chromosome number, $n = 18$.

Distribution. *Lisianthius jefensis* is known only from the Cerro Jefe region of the Province of Panamá, elevation 800–900 m. This species is widespread near the rounded peak but can be found scattered at lower elevations. Cerro Jefe is subjected to alternating periods of wet cloud cover and intense sunlight due to an unusual combination of local topography and climate. *Lisianthius jefensis* is a conspicuous and locally widespread member of the floristically diverse and predominantly shrubby flora of Cerro Jefe that contains numerous other local endemics. This forest is dominated by species of *Clusia* and *Calopothrinax cookii.*

Two populations of *Lisianthius skinneri* are found immediately below the cloud forest zone. The transition between the two life zones is abrupt, with the change readily perceived. In one locality individuals of *L. skinneri* and *L. jefensis* are only meters apart, with no hybrids reported or seen (see also Weaver, 1972). DNA analysis clearly indicates that *L. jefensis* has been derived recently from eastern populations of *L. skinneri. Lisianthius jefensis* is morphologically similar to *L. weaveri* in floral characters and might have been involved in the origin of the latter species by hybridization with *L. skinneri.*

Representative specimens examined. PANAMA. PANAMÁ: Cerro Jefe, 6–8 mi. past Goofy Lake, 3–4 mi. past Cerro Azul, 800–900 m elevation; *Almeda & Nakai 3452* (F, MO); *Antonio et al. 3402* (MO); *Antonio 4699* (MO); *Busey 798* (MO); *Correa & Dressler 1154* (MO, NY); *Correa et al. 1617* (DUKE, MO); *Croat 14435, 17341* (MO); *D'Arcy & Hamilton 14801* (MO); *D'Arcy et al. 15516* (MO); *Duke 8010* (MO), *9413* (MO, US); *Dwyer et al. 5035* (MO); *Dwyer & Hayden 8087* (MO); *Folsom et al. 5655* (MO); *Foster 1164* (DUKE); *Gentry 2115* (DUKE, F, MO), *6771* (F, MO); *Hammel 3716, 4817* (MO); *Hamilton & D'Arcy 602* (MO); *Hayden 1008* (DUKE, MO); *Kirkbride & Crebbs 16* (F, MO); *Knapp 925, 2225, 3509, 3538, 5202* (MO); *Luteyn 3200* (DUKE, F, MO); *Luteyn & Kennedy 3959* (DUKE); *McPherson 6878* (MO); *Miller & Miller 896* (MO, WIS); *Mori & Kallunki 2376* (MO, US); *Mori 7129* (MO); *Nee 11456* (MO); *Robyns 4438* (MO); *Skog et al. 4219* (MO, US); *Stimson 5390* (DUKE); *Sullivan 218* (MO); *Sytsma 1399, 2025* (MO); *Sytsma et al. 2902* (MO); *Sytsma & Antonio 3829* (MO); *Sytsma & D'Arcy 3695, 3696* (MO); *Sytsma & Knapp 4798, 4799* (MO); *Sytsma 4105* (MO); *Tyson et al. 3203* (MO); *van der Werff & van Herdeveld 6972* (MO, WIS); *Weaver & Foster 1481* (DUKE, MO); *Weaver & Wilbur 2241, 2243, 2250* (DUKE, F, MO, NY, US); *Webster et al. 16457* (DUKE, MO); *Wilbur & Teeri 13604* (DUKE, MO, NY); *Wilbur et al. 15524* (DUKE, F, MO, NY, US); *Wilbur 24126* (DUKE, F); *Witherspoon & Witherspoon 8484* (US).

4. **Lisianthius habuensis** K. J. Sytsma, sp. nov. TYPE: Panama. Comarca de San Blas: Cerro Habu, vicinity of peak, cloud forest, 800 m, 78°49′W, 9°23′N, *Sytsma, Antonio & Dressler 2685* (holotype, MO). Figure 5.

Frutex 1–4 m altus. Folia obovata-elliptica, 13–19.5 cm longa, 3.5–5.8 cm lata. Inflorescentiae axillares et terminales, dichasio reducto, 3–7-floribus; pedunculis elongatis. Calyx viridis, tubularis, 6–8 mm longis; lobi 4–5 mm longi. Corolla aurea, cerea, 4.9–6.1 cm longa; lobi triangulares, virides, cerescens ad margineum, 3.5–5 mm longi et lati. Stamina filamentis ± exsertis. Stilus antherae superans 1–3 mm; stigma grande, conicum, corrugatum, ad 3–3.5 mm longa. Capsulae fusiformes, ad 2 cm longa.

Shrub or subshrub, 1–4 m tall; stem terete, erect. Leaves membranaceous, usually pale green to green; petiole 1.3–2.5 cm long, amplexicaul; blade obovate to obovate-elliptic, basally attenuate, apically long acuminate to attenuate, 13–19.5 cm long and 3.5–5.8 cm wide, with 2–4 ascending lateral veins, the costa prominent beneath. Inflorescences of reduced dichasia, usually once compound, or reduced, on long axillary or terminal peduncles, 14–30 cm long; bracts opposite, over 2 mm long. Flowers nodding; calyx tubular, green, 6–8 mm long, the lobes lanceolate, acuminate, scariously margined, strongly carinate, 4–5 mm long; corolla bright yellow, waxy, the tube funnelform, inflated, 4.9–6.1 cm long, the lobes dark green with yellow border, broadly deltoid or triangular ovate, 3.5–5 mm long and broad, recurved slightly. Stamens inserted within corolla tube at apex of ovary; filaments exserted just past corolla lobes; anthers 2–3 mm long, bilobate at base; pollen

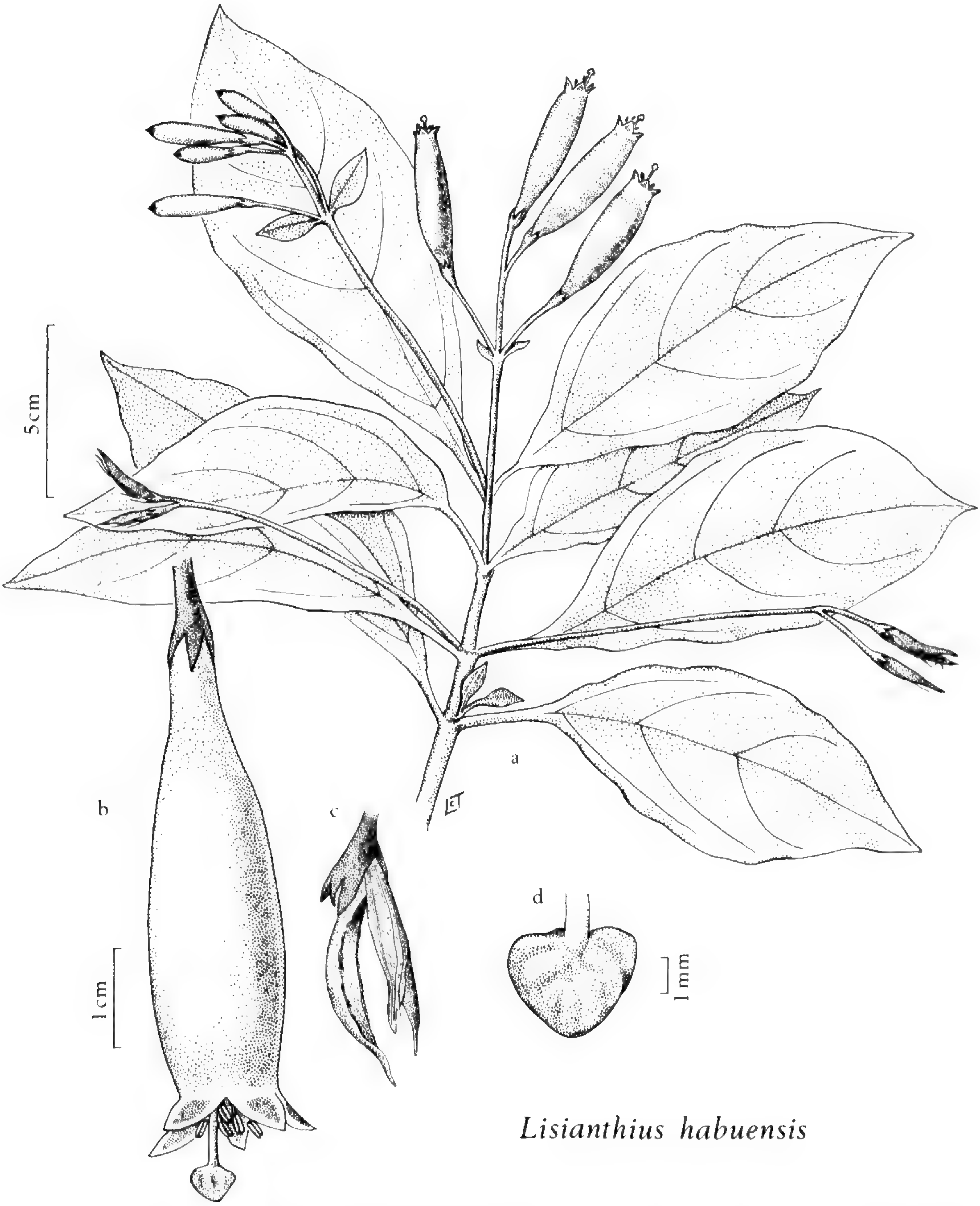

FIGURE 5. Lisianthius habuensis (Sytsma et al. 2685 (MO)).—*a. Habit.—b. Flower.—c. Dehisced fruit.—d. Stigma.*

yellowish. Style surpassing anthers; stigma large, conical, to 3.5 mm long, contorted, almost corrugated. Capsule fusiform, to 2 cm long, with short beak; seeds asymmetrical, seed texture corrugated.

Distribution. *Lisianthius habuensis* occurs near the eastern range of the species complex in the province of Panamá and in the Comarca de San Blas. A large population was discovered at the very top of Cerro Habu (800 m), Comarca de San Blas. This peak is located on the Cordillera de San Blas adjacent to the Atlantic coast and receives extremely abundant rainfall. *Lisianthius habuensis* dominates the shrub layer on the very tip of Cerro Habu but is not found more than 50 m below the summit. A second population was found near the Continental Divide on the the road from El Llano to Cartí, Province of Panamá, approximately 20 km from Cerro Habu. A large portion of this population grows on the roadside, with a few scattered individuals in the forest interior. Several populations of *L. skinneri* are located 3–5 km south of (below) *L. habuensis* along the El Llano–Cartí road. A third population was discovered at the headwaters of three rivers in the Province of Panamá at elevations of 100–400 m.

Lisianthius habuensis is distinct from all other species of *Lisianthius* by having an unusual stigma. The large ovoid stigma is obvious in the field, although not as noticeable on dried herbarium specimens. The unique corolla and lobes further distinguish it from all other species. DNA evidence indicates that this species is most closely related to a lineage giving rise to *L. peduncularis* and *L. aurantiacus.*

Additional specimens examined. PANAMA. PANAMÁ: headwaters of Río Chagres, Río Esperanza and Río Piedras, 79°20′W, 9°20′N, *de Nevers 4086* (MO); 8 mi. along El Llano–Cartí road from Pan American Highway, 300–400 m, *Sytsma 4002* (MO, WIS); *Sytsma et al. 5003* (MO, WIS).

5. **Lisianthius peduncularis** L. O. Williams, Fieldiana, Bot. 31: 408, fig. 1. 1968 (as "*Lisianthus*"). TYPE: Panama. Coclé: El Valle de Antón, *Allen 3410* (MO).

Shrub or subshrub, occasionally large, to 3.5 m tall; stems terete, distinctly woody below, herbaceous above. Leaves petiolate, the petiole amplexicaul; blades dark green above, paler below, 6–20 cm long, to 7.5 cm broad, broadly ovate, abruptly acuminate to acute; the lateral veins prominent, strongly ascending. Inflorescences longly pedunculate, loose and open, once compound dichasia, sometimes reduced; bracts opposite, lanceolate to sublinear. Flowers nodding, the pedicels 6–13 mm long. Calyx 7.5–13 mm long, the lobes lanceolate, carinate, scariously margined, long acuminate at the apex, 5.5–10 mm long. Corolla tube funnelform, 4.5–6 cm long, bright yellow, inflated in the middle; the lobes dark green, 6–10 mm long, long acuminate, usually spreading. Stamens inserted in the corolla tube at the apex of the ovary; filaments 3.2–4 cm long, just surpassing the corolla tube but not the lobes; anthers 2–3 mm long, yellow, bilobed at the base. Style to 5 cm long, just exceeding the corolla lobes, always surpassing the anthers; stigma peltate. Capsule fusiform, to 1.5 cm long, sharply beaked; seeds irregular in shape, corrugated in texture. Chromosome number, $n = 18$.

Distribution. *Lisianthius peduncularis*, endemic to the north rim and adjacent ridges of El Valle de Antón, Coclé Province, is now known to be composed of three small populations. Two populations are restricted to exposed elfin forest ridges (900–1,000 m) and usually are found associated with *Symbolanthus pulcherrimus* Gilg, a lisianthioid shrub characteristic of such habitats. A third population is found on the northern lower flanks of the El Valle crater (800 m). This large population of approximately 80 individuals grows on a soft porous rhyolite bedrock in association with a low *Clusia*-dominated scrubby open forest similar to the vegetation type on Cerro Jefe. *Lisianthius skinneri* has been collected on the road from El Valle leading up to these *L. peduncularis* sites. P. Allen (*2369*) collected it in 1941, but the species has not been collected since from the region despite extensive searches and collecting through the Flora of Panama project.

Morphologically, *Lisianthius peduncularis* most closely resembles the new *L. aurantiacus* with which it shares long corolla tubes and lobes, and reduced inflorescences. They differ strikingly in habit and corolla color. Both occur at the western edge of the species complex in Panama. DNA analysis clearly indicates that these two species form a close pair of "sister species."

Representative specimens examined. PANAMA. COCLÉ: N rim, El Valle de Antón, *Allen 1793* (MO, US); La Mesa, N of El Valle, *Allen 2369* (US); Cerro Pajita, *Allen & Allen 4187* (MO); El Valle, Club Campestre, *Croat 14288* (F, MO); Cerro Pilón, *Croat 22945* (DUKE, F, MO, WIS); Cerro Pilón, *Duke 12192* (MO); Cerro Carocoral, *Duke & Dwyer 15094* (MO); Cerro Carocoral, *Kirkbride 1094* (MO); trail past La Mesa, *Clusia* forest, *Luteyn 4082* (DUKE); Cerro Pilón, *Mori 6631* (MO); Cerro Gaital, *Reveal & Balogh 4945* (MO); Divide SW of La Mesa at end of logging road, *Stein & Hamilton 1002* (MO, WIS); Cerro Carocoral, *Sytsma 3815* (MO); Las Minas, N of El Valle, *Sytsma 4039* (MO); La Mesa, N of El Valle, *Sytsma et al. 4367* (MO); inside crater at El Valle de Antón at La Mesa, *Weaver et al. 2247* (DUKE, F, NY, US); trail to La Mesa, 4.5 mi. past El Valle, *Wilbur & Luteyn 11696* (DUKE, MO, NY); trail past La Mesa, *Clusia* thicket, *Wilbur et al. 15622* (DUKE).

6. **Lisianthius aurantiacus** K. J. Sytsma, sp. nov. TYPE: Panama. Coclé: Mountains between La Pintada and Cascajal, *Dressler 5625* (holotype, MO; isotype, WIS). Figure 6.

Frutex vel arbor, ad 6.5 m alta; truncus ad 7 cm latis, ramosis aequaliter apicem versus. Folia obovata-elliptica, ad 25 cm longa et 6.5 cm lata. Inflorescentiae axillares, dichasio reducto, 1–2-floribus; pedunculis elongatis, ad 12 cm longis. Calyx viridis, tubularis, 10–16 mm longis; lobi 8–13 mm longi, acuminati longe. Corolla aurea, au-

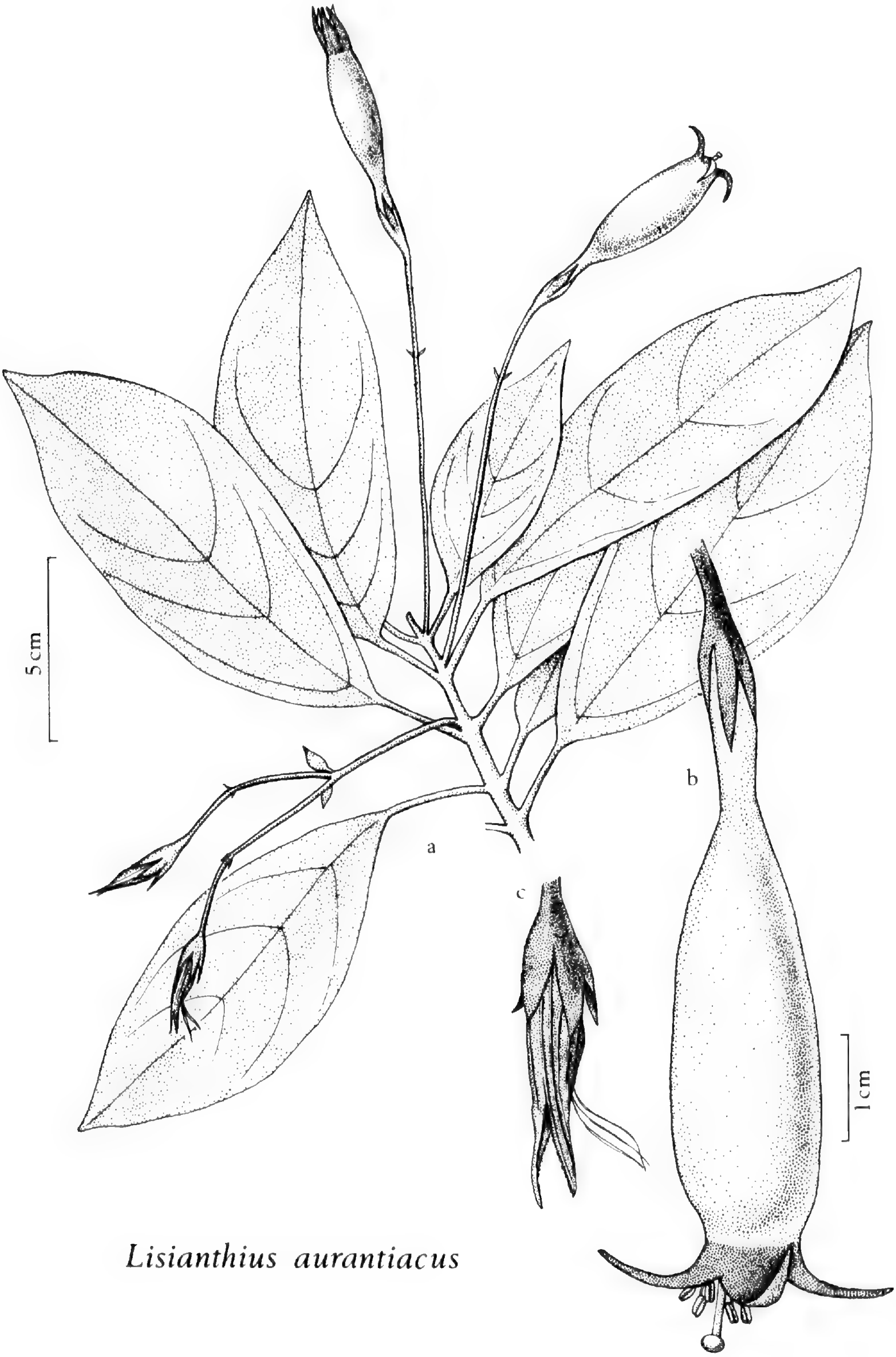

FIGURE 6. Lisianthius aurantiacus (Hammel 2508 *(MO))*.—*a. Habit.—b. Flower.—c. Dehisced fruit.*

rantiacus, 5.5–7.8 cm longa; lobi triangulares, virides, 10–14(–17) mm longi, 3–5 mm lati. Stamina filamentis ± exsertis; antherae 2.5–5 mm longae. Stilus antherae superans 1–3 mm; stigma peltatum, aquamarinum. Capsulae fusiformes, 1.8–2.5 cm longa.

Shrub or slender-trunked tree, to 6.5 m tall. Stem to 7 cm wide, terete, evenly branched to the top. Leaves petiolate, the petiole 5–15 mm long, amplexicaul; blade glossy dark green above, slightly paler below, 2–3 lateral veins conspicuous, strongly ascending, the costa prominent below, membranaceous; to 25 cm long and 6.5 cm broad, obovate to obovate-elliptic, basally cuneate to slightly attenuate, apically acuminate. Inflorescence axillary, opposite, consisting of 1 or 2 flowers; the peduncles to 12 cm long, containing 1–3 sets of foliaceous to linear bracts, the larger bracts to 15 mm long; the pedicels to 2 cm long. Flowers strongly nodding. Calyx tubular, dark green, 10–16 mm long, the lobes lanceolate, long acuminate, scariously margined, carinate at the base only, 8–13 mm long. Corolla 5.5 –7.8 cm long, tubular-funnelform, inflated, the tube bright pumpkin orange, the lower ⅙ narrowly constricted, the lobes dark green, triangular, acuminate and spreading, 10–14(–17) mm long and 3–5 mm wide at the base. Stamens 4.5–6.3 cm long, exserted to the midpoint of the lobes; filaments filiform, inserted on the corolla tube at the apex of the ovary; anthers 2.5–5 mm long, slightly sagittate at base, yellow. Style 4.7–6.7 mm long, slightly exserted past the anthers; stigma blue-green, capitate, slightly bilobed at apex. Capsule fusiform, 1.8–2.5 cm long, 5–7 mm diam., with a beak 4 mm long.

Distribution. *Lisianthius aurantiacus* has the most widespread distribution of the cloud-forest species. It has been collected in three localities: on the continental divide near Cascajal, Coclé Province (650 m); below the continental divide on the Atlantic watershed north of El Cope, Coclé Province (800–900 m); and the Cerro Tífe region 15 km west of El Cope (400–450 m). *Lisianthius aurantiacus* usually occurs sporadically in closed forests, with only a few individuals seen together. Populations in the more disturbed Cascajal area are large and more treelike (to 6 m), effectively forming a canopy. *Lisianthius aurantiacus* is found at lower elevations than the other cloud-forest species. The cloud forests in this region of Coclé Province are lower in elevation than in other areas of central Panama because of local climatic conditions. The forests are floristically more similar to mid-elevation moist forests where *L. skinneri* thrives. Indeed, a population of *L. skinneri* was discovered growing sympatrically with *L. aurantiacus* in the Cascajal area.

Lisianthius aurantiacus is undoubtedly the most spectacular member of the genus. Its arboreal habit, very large pumpkin orange corolla (thus the specific epithet), and highly reduced inflorescence distinguish it from all other *Lisianthius* species. A more northern species, *L. axillaris,* is strikingly similar to *L. aurantiacus.* The only species with red or orange flowers known prior to *L. aurantiacus* was *Lisianthius axillaris,* a common roadside plant in Belize and surrounding regions. It exhibits not only a reddish corolla, but also an axillary inflorescence of a single flower as well. This is a clear case of floral convergence. *Lisianthius aurantiacus* is most closely related to *L. peduncularis,* with which it shares several other floral characters.

Representative specimens examined. PANAMA. COCLÉ: trail from Caño Sucio to Cerro Tífe, base of waterfall, *Antonio 3687* (MO, WIS); area between Caño Blanco del Norte, Caño Sucio and Chorro del Río Tífe, *Davidse & Hamilton 23581* (MO, WIS); Caribbean side of divide at El Cope, *Hamilton & Davidse 2680, 2693* (MO, WIS); 7 km N Llano Grande, road to Coclesito, *Hammel 1970, 2508* (MO, WIS); continental divide N of Penonomé, road to Coclesito, *Hammel 4032* (MO); continental divide N. of Penonomé, between Llano Grande and Cascajal, *Hammel 7221* (MO, WIS); *Hammel & Kress 8509* (DUKE); S of Cascajal, Continental Divide, *Knapp 1954* (MO, WIS); waterfall of Río Tífe, Knapp 3704 (MO, WIS); Los Pedregales, ridge between Río Blanco del Norte and Río Caño Sucio, *Knapp & Dressler 3788* (MO, WIS); Coclecito Rd., Continental Divide, 500 m, *de Nevers et al. 6726* (MO, WIS); between Caño Sucio and Cerro Tífe, *Sytsma et al. 2532* (MO, WIS); 4 mi. past Llano Grande to Cascajal, *Sytsma 3981* (MO, WIS); *Sytsma et al. 4379, 5005* (MO, WIS).

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CHROMOSOME NUMBERS IN *LOTONONIS* AND *BUCHENROEDERA* (FABACEAE—CROTALARIEAE)[1]

Ben-Erik Van Wyk
and Anne Lise Schutte[2]

ABSTRACT

Original chromosome counts for Buchenroedera *(new generic report) and* Lotononis *(44 new specific reports) are presented. The most common somatic number in* Lotononis, *18, was found in 29 species. Three species of* Buchenroedera *and nine species of* Lotononis *have* $2n = 28$. *In* Lotononis *section* Krebsia $2n = 28, 42, 56$, *and 84 were found in a closely related species group. This is the first report of a polyploid series in the Crotalarieae and includes the highest numbers recorded in the tribe. The chromosome numbers indicate anomalies in the existing sectional classification of* Lotononis *and may provide evidence for a more natural generic and infrageneric classification.*

The genera *Lotononis* (DC.) Eckl. & Zeyh. and *Buchenroedera* Eckl. & Zeyh. are poorly known cytologically, with only six species of the former and none of the latter having been investigated previously. As part of an ongoing taxonomic study of these genera, chromosome counts were made for 47 species, representing almost the full range of variation in *Lotononis* (ca. 120 species centered in southern Africa, with a few extending into Asia) and *Buchenroedera* (ca. 16 species restricted to the eastern parts of southern Africa). The results are presented here, and their systematic significance in terms of an improved generic and infrageneric classification is discussed.

MATERIALS AND METHODS

Mitotic counts were made from root tips of germinated seeds. Standard methods of pretreatment in hydroxyquinoline (0.02% mass/volume) and staining in lacto-propionic orcein were used. The duration of hydrolysis (1–8 minutes) and the concentration of HCl (0.2–0.5 N) proved to be important. The chromosomes are small (ca. 1–3 μm long). Voucher specimens (listed in Table 1) are housed at the Rand Afrikaans University Herbarium (JRAU). A list of the species studied and voucher specimen details are given in the Appendix. Our efforts to collect seeds have been rewarded by numerous rediscoveries of rare species and have provided a fairly representative sample of the two genera.

RESULTS AND DISCUSSION

The results listed in Table 1 are arranged according to Duemmer's (1913) sectional classification. Where morphologically heterogenous sections of *Lotononis* have been subdivided into two or more groups, or where species have been moved to more appropriate positions, the reasons for doing so are given in the footnotes. The arrangement of species in Table 1 is aimed at facilitating the discussion that follows and is not intended as a formal infrageneric classification, but it nevertheless reflects major discontinuities and shows basic affinities.

Several morphological characters provide links among the species of *Lotononis* with $2n = 28$ and among those with $2n = 18$. The latter are presently placed in various sections, indicating that Duemmer's infrageneric treatment is artificial; that the same chromosome number has evolved independently in several different groups seems unlikely. Section *Krebsia*, for example, presently comprises three distinct groups, two of which have obvious

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[1] *We thank Dr. Johan Spies (Botanical Research Institute, Pretoria) and Dr. Gerrit Davidse (Missouri Botanical Garden) for useful comments. Taxonomic research on* Lotononis *and* Buchenroedera *by the senior author is registered as a Ph.D. project at the University of Cape Town.*

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TABLE 1. *Chromosome numbers in* Lotononis *and* Buchenroedera. *Species are arranged in sections following the treatment of Duemmer (1913), with some minor modifications that are explained in the footnotes. All known counts are included—those taken from the literature are preceded by an asterisk (*).*

Genera, Groups, and Species	Chromosome Number (2*n*)	Voucher or Reference
Buchenroedera Eckl. & Zeyh.		
B. lotononoides Scott Elliot	28	*BVW 1966*
B. meyeri Presl	28	*BVW 1765*
B. tenuifolia Eckl. & Zeyh. var. *tenuifolia*	28	*BVW 1675*
Lotononis (DC) Eckl. & Zeyh.		
Lotononis section *Aulacinthus* (E. Mey.) Benth.		
L. leucoclada (Schltr.) Duemmer	28	*BVW 2430*
L. gracilis (E. Mey.) Benth.	28	*BVW 2250*
Lotononis section *Krebsia* (Eckl. & Zeyh.) Benth.		
Part 1: *Krebsia* sensu stricto		
L. biflora (H. Bol.) Duemmer	± 84	*BVW 1952*
L. carnosa (Eckl. & Zeyh.) Benth.	84	*BVW 1663*
L. caerulescens (E. Mey.) B-E. van Wyk[1]	56	*BVW 2483*
L. cytisoides (E. Mey.) Benth.	28	*BVW 1721*
L. cytisoides (E. Mey.) Benth. aff.	56	*BVW 1761*
L. divaricata (Eckl. & Zeyh.) Benth.	56	*BVW 2484*
L. divaricata (Eckl. & Zeyh.) Benth. aff.	42	*BVW 1666*
L. trisegmentata Phill. var. *robusta* Phill. forma *robusta*	28	*BVW 1917*
L. trisegmentata Phill. var. *robusta* Phill. forma *sericea* Phill.	28	*BVW 1956, 1958*
Part 2: *L. digitata* group[2]		
L. digitata Harv.	18	*BVW 2341*
L. benthamiana Duemmer	18	*BVW 2538*
"L. magnifica" B-E. van Wyk ined.	18	*BVW 2549*
Part 3: *L. transvaalensis* group[3]		
L. transvaalensis Duemmer	18	*BVW 1860*
L. procumbens H. Bol.[4]	18	*BVW 2504*
Lotononis section *Polylobium* (Eckl. & Zeyh.) Benth.		
Part 1: *Polylobium* sensu stricto		
L. exstipulata L. Bol.	28	*BVW 2280*
**L. involucrata* (Berg.) Benth.	28	(Dahlgren, 1967)
**L. serpens* (E. Mey.) Dahlgr.[5]	18	(Goldblatt, 1981b)
Part 2: *L. angolensis* group[6]		
**L. angolensis* Bak.	18	(Byth, 1964)
**L. listii* Polhill	18	(Byth, 1964)
**L. bainesii* Bak.	36	(Byth, 1964)
Lotononis section *Telina* (E. Mey.) Benth.		
L. acuminata Eckl. & Zeyh.	28	*BVW 2581*
"L. repens" B-E. van Wyk ined.	28	*BVW 2573*
L. pungens Eckl. & Zeyh.[7]	28	*BVW 1725*
L. versicolor (E. Mey.) Benth.[7]	28	*BVW 1386*
Lotononis section *Oxydium* Benth.[8]		
L. rostrata Benth.[9]	18	*BVW 2324*
L. rostrata aff.	18	*BVW 2429*
L. acutiflora Benth.	18	*BVW 2544*
L. oxyptera (E. Mey.) Benth.	18	*BVW 2318*
L. lenticula (E. Mey.) Benth.	18	*BVW 2018*
L. rabenaviana Dinter & Harms	18	*BVW 2057*

TABLE 1. *Continued.*

Genera, Groups, and Species	Chromosome Number ($2n$)	Voucher or Reference
Lotononis section *Lipozygis* (E. Mey.) Benth.		
Part 1: *L. polycephala* group[10]		
L. polycephala (E. Mey.) Benth.	18	*BVW 2408*
L. bolusii Duemmer	18	*BVW 2443*
"L. longicephala" B-E. van Wyk ined.	18	*BVW 2241*
Part 2: *L. eriantha* group[11]		
L. eriantha Benth.	18	*ALS 383*
L. foliosa H. Bol.	18	*BVW 2607*
L. lanceolata (E. Mey.) Benth.	18	*BVW 1884*
Lotononis section *Leobordea* (Del.) Benth.		
**L. platycarpa* (Viv.) Pic.-Serm.	18	(Goldblatt, 1981b)
Lotononis section *Leptis* (Eckl. & Zeyh.) Benth.		
Part 1: *L. laxa* group[12]		
L. laxa Eckl. & Zeyh.	18	*BVW 2015*
L. woodii H. Bol.	18	*BVW 2608*
L. macrosepala Conrath	18	*BVW 2622*
Part 2: *L. brachyloba* group[13]		
L. brachyloba (E. Mey.) Benth.	18	*BVW 2244*
"L. fruticoides" B-E. van Wyk ined.	18	*BVW 2020*
L. leptoloba H. Bol.	18	*ALS 276*
L. maximilianii Schltr. (cleistogamous)	18	*ALS 271*
L. maximilianii (chasmogamous)	18	*ALS 282*
Part 3: *L. calycina* group[14]		
L. calycina (E. Mey.) Benth.	18	*BVW 2621*
L. sericoflora Duemmer	18	*BVW 1899*
L. humifusa Benth.	18	*BVW 1700*
L. mucronata Conrath aff.	18	*BVW 2619*
"L. curvicarpa" B-E. van Wyk ined.	18	*BVW 2725*

[1] Better known as *Lebeckia microphylla* E. Mey.
[2] Species added to section *Krebsia* by Harvey (1862) and Duemmer (1913).
[3] Species added to *Krebsia* by Duemmer (1913).
[4] Position in section *Polylobium* was based on a superficial characterization.
[5] An anomalous species. Dahlgren (1964) suggested similarities with *L. involucrata.*
[6] Species added to section *Polylobium* by Baker (1871) and related species.
[7] Superficially similar to *L. laxa* and previously associated with the section *Leptis.*
[8] This section was referred to the genus *Crotalaria* by Duemmer (1913).
[9] Better known as *L. micrantha* (E. Mey.) Benth.
[10] A distinct group of *Lipozygis* with indehiscent, wind-dispersed fruit.
[11] A distinct group of pyrophytes from grassland areas of the eastern parts of southern Africa.
[12] Perennial herbs with acute keel petals as in section *Oxydium.*
[13] Annuals with acute keel petals as in section *Oxydium.*
[14] Annuals and perennials with obtuse keel petals as in the *L. eriantha* group of section *Lipozygis.*

affinities elsewhere in the genus. The woody habit of *L. digitata* and *L. transvaalensis* was used to place them in *Krebsia,* but both are morphologically very similar to various species of section *Leptis.* Another example is section *Polylobium*; *Lotononis umbellata* and its allies are closely related to section *Aulacinthus* and perhaps not distinct from it at the sectional level. The *L. angolensis* group is quite different from other species of section *Polylobium* and its position in this section is unsatisfactorily artificial.

Two separate phylogenetic lines with base numbers of $x = 9$ and $x = 7$ are suggested, and further research will show if other evidence supports such a dichotomy in the genus. Not a single count of $2n = 16$ or 32 has been made, so that a base number of 8, which is common in some of the other genera, so far appears to be totally absent in *Lotononis*.

At the generic level, the data also give some indications of affinity. *Buchenroedera* is so closely related to *Lotononis* (especially to section *Krebsia*) that its generic status has been questioned (Polhill, 1976, 1981). The shared chromosome number of $2n = 28$ (and presumably a base number of 7) agrees with chemical evidence (Van Wyk & Verdoorn, 1988) that *Buchenroedera* is perhaps best considered a section of *Lotononis*.

The remarkable similarities between species of *Crotalaria* and *Lotononis* have caused confusion in past taxonomic treatments. For example, most species of *Lotononis* section *Oxydium* were transferred to *Crotalaria* by Duemmer (1913). The presence of macrocyclic pyrrolizidine alkaloids in both genera (Van Wyk & Verdoorn, in prep.) indeed indicates that *Lotononis* is more closely related to *Crotalaria* than to other genera of the tribe, all of which seem to contain only quinolizidine alkaloids. *Crotalaria*, however, have $2n = 16$, 32, or rarely 14 (Goldblatt, 1981a), while those species of *Lotononis* that closely resemble *Crotalaria* (section *Oxydium* and some groups of *Leptis*) all have $2n = 18$. The morphological distinction between *Lotononis* and *Crotalaria* (Polhill, 1968) is therefore strongly supported by the data at hand.

Some of the woody species of *Lotononis* (sections *Aulacinthus* and *Krebsia*) are very similar to species of *Lebeckia*. *Lotononis caerulescens* (E. Mey.) B-E. van Wyk, for example, has until recently been known as *Lebeckia microphylla* E. Mey., but morphological and chemical evidence (Van Wyk, 1988; Van Wyk & Verdoorn, 1988) clearly showed it to be misplaced in *Lebeckia*. The sections *Aulacinthus* and *Krebsia* sensu stricto have $2n = 28$, 42, 56, and 84, while four counts of $2n = 18$ are known for *Lebeckia* (Dahlgren, 1967). Here again, the cytological data agree with the morphological distinction between *Lotononis* and *Lebeckia*. *Lotononis angolensis* and related species (section *Polylobium*) are chemically similar to *Lebeckia* and also have the same chromosome number. Morphological characters such as the zygomorphic calyx and dimorphic stipules, however, are typical of *Lotononis*.

Not a single count of $2n = 14$ is known for *Lotononis*; so it seems to be cytologically different from the genus *Pearsonia*. The only available count for the latter genus was by Frahm-Leliveld (1969), who reported $2n = 14$ for *P. flava* (Bak. f.) Polhill. The species of *Pearsonia* are similar to *Lotononis* except for their highly modified flowers (Polhill, 1973), and the shared chromosome base number of $x = 7$ may indeed indicate a common ancestry.

From a phylogenetic point of view, the different base numbers in *Lotononis* suggest interesting questions about generic relationships in the Crotalarieae. The base number of the tribe is almost certainly $x = 9$ (Goldblatt, 1981a), and $2n = 18$ in some species of *Lotononis* is presumably the ancestral condition. The only way to achieve $2n = 28$ (if *Lotononis* is monophyletic) is to postulate descending aneuploidy from $n = 9$ to 8 and 7 and subsequent polyploidy. Since $2n = 16$ and 14 appear to be totally absent in *Lotononis*, it may be argued that *Crotalaria* and *Pearsonia* form part of the lineage that gave rise to the group of species with $2n = 28$, 42, 56, and 84. If *Lotononis* proves to be polyphyletic, this possibility can be seriously considered, but the generic characters of the current concept of *Lotononis* are present in at least some species of each major group. Although there are marked phenetic similarities linking all the major groups, *Lotononis* as a whole is not monothetic. It is defined by combinations of apomorphic tendencies, such as single stipules, suffrutescent or herbaceous habit, absence of bracteoles, fusion of the lateral calyx lobes, verrucose upper suture of the fruit, tuberculate testa, elongated funicles, flower dimorphism associated with cleistogamy, ability to produce HCN, and presence of macrocyclic pyrrolizidine alkaloids. There is not a single apomorphy known to us that would unambiguously support monophyly. A possible solution would be to separate the lineage with $2n = 28$ from the one with $2n = 18$ and to split the latter into several smaller groups. Despite conflicting character information, there are some indications from the morphology that the geographically widespread and generally herbaceous $2n = 18$ lineage is more primitive than the predominantly woody and essentially southern African $2n = 28$ lineage.

In a tribal context, the occurrence of polyploidy in *Lotononis* (section *Krebsia*) is of some interest. Polyploidy and high chromosome numbers are typical of the Genisteae but have never been reported from any genus of the Crotalarieae (Goldblatt, 1981a). It is also noteworthy that polyploidy should occur in an essentially woody group (previously considered to be one of the basal groups of *Lotononis*) and not in the supposedly more derived herbaceous groups. Unlike the situation in the other large genera of the Crotalarieae (*Aspalathus* and to some extent *Crotalaria*), there is no direct evidence of aneuploidy, although it must have played a significant role in the phylogeny of *Lotononis.*

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APPENDIX

List of species, collection data, and voucher specimen details of the material used for chromosome counts. Voucher specimen numbers refer to our own collections (abbreviated as *BVW* and *ALS*) and are all housed in the Rand Afrikaans University Herbarium (JRAU). Authorities for names are given in Table 1.

Buchenroedera lotononoides: Loteni, Natal, *BVW 1966.* ***B. meyeri***: Mhlahlane, Transkei, *BVW 1765.* ***B. tenuifolia*** var. ***tenuifolia***: Queenstown, E Cape, *BVW 1675.*

Lotononis acuminata: Humansdorp district, S Cape, *BVW 2581.* ***L. acutiflora***: Khamiesberg, Cape, *BVW 2544.* ***L. benthamiana***: Springbok district, Cape, *BVW 2538.* ***L. biflora***: Loteni, Natal, *BVW 1952.* ***L. bolusii***: Piquetberg, Cape, *BVW 2443.* ***L. brachyloba***: Ceres, Cape, *BVW 2244.* ***L. caerulescens***: Cradock, E Cape, *BVW 2483.* ***L. calycina***: Bethal, Transvaal, *BVW 2621.* ***L. carnosa***: Queenstown, E Cape, *BVW 1663.* "***L. curvicarpa***" (ined.): Devon, Transvaal, *BVW 2725.* ***L. cytisoides***: Winterberg, E Cape, *BVW 1721.* ***L. cytisoides*** aff.: Mhlahlane, Transkei, *BVW 1761.* ***L. digitata***: Garies, Cape, *BVW 2341.* ***L. divaricata***: Swagershoek Pass, E Cape, *BVW 2484.* ***L. divaricata*** aff.: Queenstown, E Cape, *BVW 1666.* ***L. eriantha***: Roodepoort, Transvaal, *ALS 383.* ***L. exstipulata***: Ceres district, Cape, *BVW 2280.* ***L. foliosa***: Johannesburg, Transvaal, *BVW 2607.* "***L. fruticoides***" (ined.): Graaff Reinet district, Cape, *BVW 2020.* ***L. gracilis***: Ceres, Cape, *BVW 2250.* ***L. humifusa***: Grahamstown district, E Cape, *BVW 1700.* ***L. lanceolata***: Dullstroom, Transvaal, *BVW 1884.* ***L. laxa***: Colesberg, Cape, *BVW 2015.* ***L. lenticula***: Colesberg, Cape, *BVW 2018.* ***L. leptoloba***: Nieuwoudtville, Cape, *ALS 276.* **L. leucoclada**: Clanwilliam, Cape, *BVW 2430.* "***L. longicephala***" (ined.): Touw's River, Cape, *BVW 2241.* ***L. macrosepala***: Bethal district, Transvaal, *BVW 2622.* "***L. magnifica***" (ined.): Khamiesberg, Cape, *BVW 2549.* ***L. maximiliani***: Nieuwoudtville, Cape, *ALS 271* (cleistogamous form), *ALS 282* (chasmogamous form). ***L. mucronata*** aff.: Ermelo district, Transvaal, *BVW 2619.* ***L. oxyptera***: Citrusdal, Cape, *BVW 2318.* ***L. polycephala***: Khamiesberg, Cape, *BVW 2408.* ***L. procumbens***: Volksrust district, Natal, *BVW 2504.* ***L. pungens***: Tarkastad district, E Cape, *BVW 1725.* ***L. rabenaviana***: Beaufort West district, Cape, *BVW 2057.* "***L. repens***" (ined.): Outeniqua Pass, S Cape, *BVW 2573.* ***L. rostrata***: Citrusdal, Cape, *BVW 2324.* ***L. rostrata*** aff.: Klawer, Cape, *BVW 2429.* ***L. sericoflora***: Harrismith, Orange Free State, *BVW 1899.* ***L. transvaalensis***: Nelspruit, E Transvaal, *BVW 1860.* ***L. trisegmentata*** var. ***robusta*** forma ***robusta***: Clarens, Orange Free State, *BVW 1917.* ***L. trisegmentata*** var. ***robusta*** forma ***sericea***: Loteni, Natal, *BVW 1956*; Sani Pass, Natal, *BVW 1958.* ***L. versicolor***: Beaufort West district, Cape, *BVW 1386.* ***L. woodii***: Wakkerstroom district, Natal, *BVW 2608.*

GEORGE ENGELMANN TYPE SPECIMENS IN THE HERBARIUM OF THE MISSOURI BOTANICAL GARDEN[1]

Steven J. Wolf[2]

ABSTRACT

Eight hundred ninety-two type specimens (in 62 families) representing 589 taxa described by George Engelmann have been located in the herbarium of the Missouri Botanical Garden. For each specimen the following are given: literature citation, kind of type, locality and date of collection, collector, and name it is currently filed under in the herbarium.

Asa Gray once remarked that George Engelmann had the potential to become the "gatekeeper for all scientists going into the wilderness" (Dupree, 1959). Engelmann, a well-trained botanist and physician, on the edge of the American frontier in mid-19th century St. Louis, the gateway to the West, was indeed the right man in the right place at the right time. Some of the first botanical expeditions to the American West were organized, outfitted, and coordinated by Engelmann, who then received and processed the incoming plant specimens and sent them on to Gray (Timberlake, 1984). Among these early expeditions were Geyer's to Illinois, Missouri, and Iowa; Lindheimer's to Texas; Wislizenus's to the New Mexico Territory and northern Mexico, and Fendler's to the southern Rocky Mountains. By the 1850s most expeditions to the West were government supported; however, the plant specimens from them continued to be funneled through Engelmann in St. Louis (Timberlake, 1984). As a result, his herbarium, which consisted of about 97,000 specimens at his death, contained collections from more than 30 collecting expeditions. Although largely from the American West and Mexico, collections also came from South America and Asia.

Engelmann, a prolific and industrious scientist, was much more than a gatekeeper. In addition to maintaining a full-time medical practice, he published more than 100 botanical papers (Sargent, 1884; Timberlake, 1984), described more than 600 new taxa of plants (Trelease & Gray, 1887), founded the Academy of Science of St. Louis, and was largely responsible for the foundation of what later became the herbarium of the Missouri Botanical Garden. It was Engelmann who convinced Henry Shaw, a wealthy St. Louis businessman planning a botanical garden, that to be scientifically credible his garden must have a library and herbarium (Timberlake, 1984). In fact it was Engelmann who purchased the Bernhardi Herbarium for Shaw, which comprised the first specimens of this herbarium. After Engelmann's death in 1884, his entire herbarium was added to Shaw's herbarium which, upon Shaw's death, became known as the herbarium of the Missouri Botanical Garden.

On the 100th anniversary of the death of George Engelmann, it seemed appropriate to re-examine his herbarium, particularly with respect to possible type specimens it might contain. Complete lists of Engelmann's publications, including his contributions to the works of others, are provided in Sargent (1884) and Timberlake (1984), and references to and reprints of most of his newly described taxa are included in Trelease & Gray (1887). The only major omissions in the latter are Engelmann's contributions to Coulter's (1894, 1896) revision of North American cacti. In the present study, a search for type specimens of Engelmann's more than 600 described taxa was conducted. An un-

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derstanding of some of Engelmann's habits was most helpful in locating types. He sometimes wrote "n. sp." on newly named specimens or wrote the descriptions on the sheet itself. Although he sometimes did not mention a specific collection or collector, it is often apparent which ones he had seen and used for his descriptions. For example, if his protologue stated "Battlefields of Buena Vista, near Saltillo, Flowers May," there is often a specimen with this exact wording on the label, collected in May by one of the collectors of that particular expedition. Additionally, if in describing a new taxon he had stated that it resembled or was related to taxon "X," the type would often have been initially labeled taxon "X," but this epithet would later have been crossed out and the new epithet penciled in by Engelmann.

The purpose of the present paper is to provide a list of types or possible type material contained in Engelmann's herbarium. Since many of the collections examined by Engelmann were widely distributed, and since only specialists should designate lectotypes, I have adopted a conservative type terminology. The only exception is that I have adopted Rollins's (1972) view that "the existence of a holotype in the institution where the author worked is assumed until proven otherwise." If Engelmann cited only one specimen and that specimen has been located in his herbarium, it is considered a holotype and supersedes previously designated lectotypes. Annotations by specialists on the sheets themselves, as well as known lectotypifications in the monographs listed below, have been accepted unless a holotype has been located. I have adopted the term "type material" in cases in which it is not clear what kind of type the specimen is but in which it is apparent that Engelmann did see it and may have used it in making his descriptions. This term is especially useful in dealing with Lindheimer's collections from Texas because they were apparently widely distributed and the exsiccatae numbers often consisted of mixed material collected in different locales, in different years, and sometimes even after the date of publication of Engelmann & Gray (1845). It is therefore suggested that specialists examine these specimens, some of which bear Lindheimer's original collection label and number, in order to determine if they are heterogeneous material and/or what kind of types they are.

In the present paper a total of 892 types, representing 589 taxa in 62 families, described by or attributed to George Engelmann are presented. In the following list the name of the taxon, its authorship, and place of publication are given, followed by the kind of type, location and date of collection, and the collector(s) and collection number if known. Also given is the current name under which it is filed in the herbarium. Taxa for which works containing numerous lectotypifications have been consulted, and for which synonymies have been followed, include: *Agave* (Gentry, 1982), *Arceuthobium* (Hawksworth & Weins, 1972), *Asclepias* (Woodson, 1954), Cactaceae (Benson, 1982), *Cuscuta* (Yuncker, 1932), *Euphorbia* (Wheeler, 1941), *Isoetes* (Pfeiffer, 1922), *Phoradendron* (Trelease, 1916), *Quercus* (Trelease, 1924), *Sagittaria* (Bogin, 1955), *Vitis* (Bailey, 1934), and *Yucca* (McKelvey, 1938, 1947). The taxa are arranged by family according to Kartesz & Kartesz (1980).

ACANTHACEAE

Dianthera humilis Engelm. & Gray, Boston J. Nat. Hist. 5: 55. 1845. SYNTYPE: west of Houston, Texas, 1845, *F. Lindheimer 159.* = *Justicia ovata* (Walt.) Lindau.

Dipteracanthus nudiflorus Engelm. & Gray, Boston J. Nat. Hist. 5: 229. 1845. HOLOTYPE: Sim's Bayou, near Houston, Texas, 1842, *F. Lindheimer s.n.*

AGAVACEAE

Agave angustissima Engelm., Trans. Acad. Sci. St. Louis 3: 306. 1876. HOLOTYPE: Octillo, Mexico, 1849, *J. Gregg 959.*

Agave couessii Engelm. in Trelease, Annual Rep. Missouri Bot. Gard. 22: 94. 1911. HOLOTYPE: Ft. Whipple, Arizona, 1865, *E. Coues & E. Palmer 253,* "couessi" added by Engelm. = *A. Parryi* Engelm. var. *couessii* (Engelm. ex Trel.) Kearny & Peables.

Agave desertii Engelm., Trans. Acad. Sci. St. Louis 3: 310. 1875. HOLOTYPE?: San Felipe, California, 1875, *E. Palmer & G. Hitchcock s.n.,* annotated "n. sp." by Engelm.

Agave falcata Engelm., Trans. Acad. Sci. St. Louis 3: 304. 1875. LECTOTYPE: Saltillo, Mexico, 1847, *A. Wislizenus 312* (2 sheets). = *A. striata* Zucc. subsp. *falcata* (Engelm.) Gentry.

Agave maculata Engelm. in Torr., Bot. Mex. Bound. Surv. 214. 1859. HOLOTYPE: Rio Grande, 1847, *A. Wislizenus 373* (3 sheets). = *Manfreda maculosa* (Hook.) Rose.

Agave maculosa Hook. var. *brevituba* Engelm., Trans. Acad. Sci. St. Louis 3: 301. 1875. LECTOTYPE: below El Paso, Texas, 1851–1852,

C. *Wright 1905.* = *Manfreda maculosa* (Hook.) Rose.

Agave newberryi Engelm., Trans. Acad. Sci. St. Louis 3: 309. 1879. HOLOTYPE: northwestern Arizona, 1858, *J. S. Newberry s.n.* = *A. utahensis* Engelm.

Agave palmeri Engelm., Trans. Acad. Sci. St. Louis 3: 319. 1875. SYNTYPE: southern Arizona, 1869, *E. Palmer s.n.* (3 sheets).

Agave parryi Engelm., Trans. Acad. Sci. St. Louis 3: 312. 1875. SYNTYPES: Arizona Territory, 1871, *F. Bischoff s.n.*; 1846, *Emory s.n.*; 1874, *J. T. Rothrock 274* (3 sheets).

Agave schottii Engelm., Trans. Acad. Sci. St. Louis 3: 306. 1875. HOLOTYPE: Sierra del Pajarito, Arizona, 1855, *A. Schott s.n.*

Agave shawii Engelm., Trans. Acad. Sci. St. Louis 3: 314. 1875. SYNTYPE: San Diego, California, *s.d., G. N. Hitchcock s.n.* (2 sheets).

Agave utahensis Engelm. in Watson, Bot. King's Expl. 497. 1871. LECTOTYPE: St. George, Utah, 1870, *E. Palmer s.n.* (2 sheets). Syntype: *J. E. Johnson s.n.*

Agave virginica L. var. *tigrina* Engelm., Trans. Acad. Sci. St. Louis 3: 302. 1875. HOLOTYPE: South Carolina, 1873, *Mellichamp s.n.* = *Manfreda virginica* (L.) Rose.

Agave wislizenii Engelm., Trans. Acad. Sci. St. Louis 3: 320. 1875. HOLOTYPE: San Sebastino, Mexico, 1847, *A. Wislizenus 280* (2 sheets). = *A. parrasana* Berger.

Asyliron leiophyllum Engelm. ex Trelease, Proc. Am. Phil. Soc. 50: 433. 1911. HOLOTYPE: Presidio del Norte, Texas, 1880, *D. Harvard s.n.*

Yucca angustifolia Pursh var. *radiosa* Engelm. in Watson, Bot. King's Expl. 496. 1871. LECTOTYPE: Arizona, 1867, *E. Palmer 201.* = *Y. elata* Engelm.

Yucca angustissima Engelm. ex Trelease, Annual Rep. Missouri Bot. Gard. 13: 58. 1902. LECTOTYPE: deserts of the Colorado River, 1853 & 1854, *J. M. Bigelow s.n.* (2 sheets).

Yucca brevifolia Engelm. in Watson, Bot. King's Expl. 496. 1871. LECTOTYPE: Date Creek, *s.d., E. Palmer?*, MO Nos. 135643 & 135646.

Yucca elata Engelm., Bot. Gaz. 7: 17. 1882. LECTOTYPE: Camp Grant, Arizona, *s.d., J. T. Rothrock 382.*

Yucca macrocarpa Engelm., Bot. Gaz. 6: 244. 1881. LECTOTYPE: Santa Rita Mts., Arizona, 1880, *G. Engelmann s.n.* = *Y. schottii* Engelm.

Yucca schottii Engelm., Trans. Acad. Sci. St. Louis 3: 46. 1873. LECTOTYPE: Santa Cruz River, Arizona, 1855, *A. Schott s.n.*

Yucca yucatana Engelm., Trans. Acad. Sci. St. Louis 3: 37. 1873. HOLOTYPE: Nohpat, Yucatán, Mexico, 1865, *A. Schott s.n.* = *Y. aloifolia* L.

ALISMATACEAE

Sagittaria calycina Engelm. in Torr., Bot. Mex. Bound. Surv. 212. 1859. LECTOTYPE: Alexandria, Louisiana, *s.d., J. Hale s.n.* Syntypes: banks of Missouri, 1856, *G. Engelmann s.n.*; Kimms Salt Pond, Missouri, 1856, *G. Engelmann s.n.* = *S. montevidensis* Cham. & Schlecht. subsp. *calycina* (Engelm.) Bogin.

Sagittaria calycina Engelm. var. *fluitans* Engelm. in Torr., Bot. Mex. Bound. Surv. 212. 1859. HOLOTYPE: western Texas, 1851–1852, *C. Wright 1899.* = *S. montevidensis* Cham. & Schlecht. subsp. *calycina* (Engelm.) Bogin.

Sagittaria calycina Engelm. var. *spongiosa* Engelm. in Gray, Man. Bot. 5: 493. 1868. HOLOTYPE: Wilmington, Delaware, 1860, *Tatnall s.n.* = *S. montevidensis* Cham. & Schlecht. subsp. *spongiosa* (Engelm.) Bogin.

Sagittaria cristata Engelm. in Arthur, Contr. Flor. Iowa 5: 3. 1882. LECTOTYPE & 2 ISOLECTOTYPES: Armstrong, Iowa, 1881, *Cratty s.n.* = *S. graminea* Michx. subsp. *cristata* (Englem.) Bogin.

Sagittaria graminea Michx. var. *platyphylla* Engelm. in Gray, Man. Bot. 5: 494. 1868. LECTOTYPE & ISOLECTOTYPE: Texas, *s.d., F. Lindheimer 713.* Syntype?: Mississippi, 1860, "ex herb *A. Wood.*"

Sagittaria heterophylla Pursh var. *angustifolia* Engelm. in Gray, Man. Bot. 5: 494. 1868. TYPE MATERIAL?: Lakes, American Bottom (in Illinois, near St. Louis), 1846, *N. Riehl s.n.* = *S. rigida* Pursh.

Sagittaria recurva Engelm. ex Patterson, Checklist 130. 1887. LECTOTYPE & ISOLECTOTYPE: Texas, *s.d., F. Lindheimer 713.* = *S. graminea* Engelm. var. *platyphylla* Engelm.

Sagittaria trachysepala Engelm. ex Michelin in DC., Monogr. Phan. 3: 74. 1881. ISOTYPE: Texas, *s.d., Drummond 423.*

Sagittaria variabilis Engelm. in Gray, Man. Bot. 1: 461. 1848. LECTOTYPE: St. Louis, Missouri, 1846, *G. Engelmann s.n.* = *S. latifolia* Willd.

ANACARDIACEAE

Rhus microphylla Engelm. ex Gray, Pl. Wrightiana 1: 31. 1852. SYNTYPE: Texas, 1850, *F. Lindheimer 734.*

APIACEAE

Apium butleri Engelm. in Watson, Proc. Amer. Acad. Arts 21: 453. 1887. ISOLECTOTYPE: eastern Texas, *s.d.*, *E. Hall 244*. = *Ammoselinum butleri* (Engelm.) Coult. & Rose.

Cynosciadium pinnatum var. *pumilum* Engelm. & Gray, Boston J. Nat. Hist. 5: 218. 1845. TYPE MATERIAL: no locale but collected by *F. Lindheimer s.n.*, 1843; prairie west of the Brazos, Texas, *F. Lindheimer s.n.* Annotated "n. sp." by Engelmann.

Daucosma laciniata Englem. & Gray in Gray, Boston J. Nat. Hist. 6: 211. 1850. TYPE MATERIAL: upper Guadalupe, Texas, 1846, *F. Lindheimer s.n.*

Eryngium heterophyllum Engelm. in Wisliz., Mem. Tour. No. Mex. 107. 1848. HOLOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus 176.*

ARISTOLOCHIACEAE

Aristolochia longiflora Engelm. & Gray, Boston J. Nat. Hist. 5: 259. 1845. HOLOTYPE: Texas, 1844, *F. Lindheimer s.n.*

ASCLEPIADACEAE

Asclepias brachystephana Engelm. in Torr., Bot. Mex. Bound. Surv. 163. 1859. LECTOTYPE: New Mexico, 1851–1852, *C. Wright 1692.*

Asclepias euphorbiifolia Engelm. ex Gray, Proc. Amer. Acad. Arts 16: 104. 1881. LECTOTYPE: San Luis Potosí, Mexico, *s.d.*, *Schaffner 55.*

Asclepias involucrata Englem. in Torr., Bot. Mex. Bound. Surv. 163. 1859. LECTOTYPE: Copper Mines, New Mexico, 1851–1852, *C. Wright 1690.*

Asclepias leucophylla Engelm. in Parry, Amer. Naturalist 9: 348. 1875. HOLOTYPE: southern Utah, 1874, *C. C. Parry 207*. = *A. erosa* Torr.

Asclepias lindheimeri Engelm. & Gray, Boston J. Nat. Hist. 5: 250. 1845. SYNTYPE: Industry, Texas, 1844, *F. Lindheimer 272*. = *A. oenotheroides* Cham. & Schlecht.

Asclepias sullivantii Engelm. ex Gray, Man. Bot. 1: 366. 1848. SYNTYPE: St. Louis, Missouri, 1834, *G. Engelmann 451.*

Astephanus utahensis Englem in Parry, Amer. Naturalist 9: 347. 1875. PROBABLE HOLOTYPE: southern Utah, 1874, *C. C. Parry 209*. Engelmann wrote "spec. nov." on it.

Gonolobus curtisii Engelm. in Parry, apparently not published, but annotated "n. sp." by Engelm. TYPE MATERIAL: North Carolina, 1844, *Curtis s.n.* = *Matelea gonocarpa* (Walt.) Shinners.

Gonolobus cynanchoides Engelm. & Gray, Boston J. Nat. Hist. 5: 251. 1845. TYPE MATERIAL: Industry, Texas, 1844, *F. Lindheimer 273.* = *Matelea cynanchoides* (Engelm.) Woods.

Gonolobus reticulatus Engelm. ex Gray, Proc. Amer. Acad. Arts 12: 75. 1877. TYPE MATERIAL: Guadalupe, Texas, 1846, *F. Lindheimer 461*. = *Matelea reticulatus* (Engelm.) Woods.

Mellichampia filifolia Engelm., apparently not published, but annotated "n. sp." by Engelm. TYPE MATERIAL: St. George, Utah, July 1874, *Parry s.n.*

Sarcostemma heterophyllum Engelm. in Torr., Bot. Mex. Bound. Surv. 362. 1859. HOLOTYPE: New Mexico, 1851–1852, *C. Wright 1681.*

ASTERACEAE

Agassiza suavis Gray & Engelm., Proc. Amer. Acad. Arts 1: 46. 1847. SYNTYPE: San Antonio, Texas, 1845, *F. Lindheimer 351* distributed as No. 437 for 1846 (2 sheets). = *Gaillardia suavis* (Gray & Englem.) Britton & Rusby.

Aster anomalus Engelm. in Torrey & Gray, Fl. N. Amer. 2: 503. 1843. TYPE MATERIAL: Rockspring near Prairie du Pont, Sept. 1842, *G. Engelmann s.n.* The only prepublication dated specimen.

Aster azureus Lindl. ex Hook. var. *vernalis* Engelm. ex Small, Fl. S.E. U.S. 1215. 1903. HOLOTYPE: prairies west of Houston, Texas, 1842, *F. Lindheimer s.n* (2 sheets).

Keerlia bellidifolia Gray & Engelm., Proc. Amer. Acad. Arts 1: 47. 1846. SYNTYPE: Guadalupe, Texas, 1845, *F. Lindheimer 415.*

Liatris acidota Engelm. & Gray, Boston J. Nat. Hist. 5: 218. 1845. ISOTYPES: Texas, 1843, *F. Lindheimer 72, 73.*

Lindheimera texana Gray & Engelm., Proc. Amer. Acad. Arts 1: 47. 1847. SYNTYPES: New Braunfels, Texas, 1846, *F. Lindheimer 424* (2 sheets); New Braunfels, Texas, 1847, *F. Lindheimer 638.*

Porophyllum amplexicaule Engelm. ex Gray, Pl. Wrightiana 1: 120. 1852. HOLOTYPE?: near Messillas, Mexico, *s.d.*, *J. Gregg s.n.*, annotated "n. sp." by Engelm.

Rudbeckia missouriensis Engelm. ex Boynton & Beadle, Biltmore Bot. Stud. 1: 17. 1901. TYPE MATERIAL: Meramec Station, Missouri, July 1879, *H. Eggert s.n.*; Allentown, Missouri, Sept. 1879, *G. Letterman s.n;* Allentown, Missouri, July 1879, *G. Letterman s.n.*

Sanvitalia angustifolia Engelm. ex Gray, Pl.

Wrightiana 1: 112. 1852. HOLOTYPE?: Buena Vista, Mexico, *s.d.*, *J. Gregg 274*, annotated "n. sp." by Engelm.

Vernonia lettermanii Engelm. ex Gray, Proc. Amer. Acad. Arts 16: 78. 1881. LECTOTYPE: Washita, Arkansas, 1879, *G. W. Letterman s.n.* Syntypes: Arkansas, 1879 & 1880, *G. W. Letterman s.n.* (2 sheets).

Vernonia lindheimeri Gray & Engelm., Proc. Amer. Acad. Arts 1: 46. 1848. HOLOTYPE: New Braunfels, Texas, 1846, *F. Lindheimer 408.*

Zinnia intermedia Engelm. in Wisliz., Mem. Tour. No. Mex. 107. 1848. HOLOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus 182.* = *Z. peruviana* (L.) L.

BORAGINACEAE

Lithospermum breviflorum Engelm., Trans. Amer. Philos. Soc. 12: 203. 1861. HOLOTYPE?: 200 miles above Fort Pierre, 1853–1854, *F. V. Hayden s.n.*, only Hayden specimen and "breviflorum" added by Engelm.

Myosotis inflexa Engelm., Amer. J. Sci. 46: 98. 1844. HOLOTYPE?: no locale, 1842, *C. A. Geyer s.n.*, annotated "n. sp." by Engelm.

Myosotis macrosperma Engelm., Amer. J. Sci. 46: 98. 1844. HOLOTYPE: Prairies, Texas, 1839, *F. Lindheimer s.n.*, annotated "n. sp." by Engelm.

BRASSICACEAE

Dithyrea wislizenii Englem. in Wisliz., Mem. Tour. No. Mex. 97. 1848. TYPE MATERIAL: Mexico, 1846, *A. Wislizenus 63* (2 sheets).

Nasturtium calycinum Engelm., Trans. Amer. Philos. Soc. 12: 184. 1859. LECTOTYPE: Yellowstone River, 1853–1854, *F. V. Hayden 93.* Syntype: Ft. Union, mouth of Yellowstone, 1855?, *F. V. Hayden s.n.* = *Rorippa calycinum* (Engelm.) Rydb.

Sisymbrium incisum Engelm. ex Gray, Mem. Amer. Acad. Arts. II. 4: 8. 1849. SYNTYPES: Santa Fe Creek, New Mexico, 1847, *A. Fendler 30 & 31*; Moro, New Mexico, 1847, *A. Fendler 29.* = *Descuriana richardsonii* (Sweet) O. E. Schulz. subsp. *incisa* (Engelm.) Delting.

Vesicaria auriculata Englem. & Gray, Boston J. Nat. Hist. 5: 240. 1845. ISOTYPE: Brazos, Texas, 1844, *F. Lindheimer 271* (2 sheets). = *Lesquerella auriculata* (Englem. & Gray) S. Wats.

Vesicaria recurvata Englem. ex Gray, Boston J. Nat. Hist. 6: 240. 1850. ISOLECTOTYPE: New Braunfels, Texas, 1846, *F. Lindheimer 8.* Syntype: New Braunfels, Texas, 1846, *F. Lindheimer 330.* = *Lesquerella recurvata* (Englem. ex Gray) S. Wats.

CACTACEAE

Cactus gabbii Englem. in Coult., Contr. U.S. Natl. Herb. 3: 109. 1894. HOLOTYPE: Peninsula of California, Mexico, 1867, *W. Gabb 19.* = *Mammillaria brandegeei* (Coult.) K. Brandegee.

Cereus berlandieri Englem., Proc. Amer. Acad. Arts 3: 286. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 38. 1859. LECTOTYPE: southern Texas, 1834, *Berlandier 2433.* = *Echinocereus berlandieri* (Englem.) Engelm. ex Rumpler.

Cereus caespitosus Engelm. in Engelm. & Gray, Boston J. Nat. Hist. 5: 247. 1845. LECTOTYPE: cult. from Industry, Texas, 1845, *F. Lindheimer s.n.* = *Echinocereus reichenbachii* (Tenscheck) Haage, f., ex Britt. & Rose.

Cereus caespitosus Engelm. var. *castaneus* Engelm. in Gray, Boston J. Nat. Hist. 6: 202. 1850. LECTOTYPE: Liano, Texas, 1847, *F. Lindheimer s.n.* = *Echinocereus reichenbachii* (Tenscheck) Haage, f., ex Britt. & Rose.

Cereus caespitosus Engelm. var. *major* Engelm., Proc. Amer. Acad. Arts 3: 280. 1856. LECTOTYPE: Texas, 1851, *F. Lindheimer s.n.* = *Echinocereus reichenbachii* (Tenscheck) Haage, f., ex Britt. & Rose.

Cereus calvus Engelm. in Coult., Contr. U.S. Natl. Herb. 3: 409. 1896. HOLOTYPE: Peninsula of California, Mexico, 1867, *W. Gabb 2.*

Cereus chloranthus Engelm., Proc. Amer. Acad. Arts 3: 278. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 29. 1859. LECTOTYPE: El Paso and Stony Hills at Frontera, Texas, 1852, *C. Wright 95* (3 sheets, 1 box). = *Echinocereus chloranthus* Engelm.

Cereus coccineus Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 51. 1849. LECTOTYPE: Wolf Creek, Mexico, 1846, *A. Wislizenus s.n.* (2 sheets). Syntype: Santa Fe, New Mexico, *s.d.*, *A. Fendler 272.* = *Echinocereus triglochidiatus* Engelm. var. *melanacanthus* (Engelm.) L. Benson.

Cereus coccineus Engelm. var. *cylindricus* Engelm. in Gray, Mem. Amer. Acad. Arts. II.

4: 51. 1849. LECTOTYPE: Santa Fe, New Mexico, 1846, *A. Fendler s.n.* = *Echinocereus triglochidiatus* Engelm. var. *melanacanthus* (Engelm.) L. Benson.

Cereus coccineus Englem. var. *melanacanthus* Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 51. 1849. LECTOTYPE: Santa Fe, New Mexico, 1846, *A. Fendler 4.* = *Echinocereus triglochidiatus* Engelm. var. *melanacanthus* (Engelm.) L. Benson.

Cereus conoides Engelm. & Bigelow, Proc. Amer. Acad. Arts 3: 284. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 35. 1857. LECTOTYPE: Anton Chico, New Mexico, 1853, *J. M. Bigelow s.n.* Syntype: 1853, *J. M. Bigelow s.n.* = *Echinocereus triglochidiatus* Englem. var. *melanacanthus* (Engelm.) L. Benson.

Cereus ctenoides Engelm., Proc. Amer. Acad. Arts 3: 279. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 31. 1859. LECTOTYPE: Santa Rosa, Mexico, 1853, *J. M. Bigelow s.n.* (2 sheets). Syntypes: Pecos, 1851, *C. Wright s.n.*; Rio Grande, 1853, *J. M. Bigelow s.n.* = *Echinocereus pectinatus* (Scheidw.) Engelm.

Cereus dasycanthus Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 50. 1849. NEOTYPE: between San Antonio and El Paso, Texas, 1849, *C. Wright s.n.* = *Echinocereus pectinatus* (Scheidw.) Engelm. var. *neomexicanus* (Standl.) L. Benson.

Cereus dasycanthus Engelm. var. *minor* Engelm., Proc. Amer. Acad. Arts 3: 279. 1856. LECTOTYPE: Frontera, Texas, 1851, *C. Wright s.n.* (2 sheets). Syntype: Chihuahua, Mexico, 1852, *J. M. Bigelow s.n.* = *Echinocereus pectinatus* (Scheidw.) Englem. var. *minor* (Engelm.) L. Benson.

Cereus dubius Engelm., Proc. Amer. Acad. Arts 3: 282. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 36. 1859. LECTOTYPE: Rio Grande, Texas, 1852, *C. Wright 410.* = *Echinocereus enneancanthus* Engelm. var. *dubia* (Engelm.) L. Benson.

Cereus emoryi Engelm., Amer. J. Sci. 14: 338. 1852. LECTOTYPE: San Diego, California, 1850, *C. C. Parry s.n.*

Cereus engelmannii Parry var. *chrysocentrus* Engelm. & Bigelow, in Engelm., Proc. Amer. Acad. Arts 3: 283. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 35. 1857. LECTOTYPE: Bill Williams River, California, 1854, *J. M. Bigelow s.n.* = *Echinocereus engelmannii* Parry var. *chrysocentrus* (Engelm. & Bigelow) Engelm. ex Rumpler.

Cereus engelmannii Parry var. *variegatus* Engelm. & Bigelow, in Engelm., Proc. Amer. Acad. Arts 3: 283. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 35. 1857. LECTOTYPE: Bill Williams Fork, California, 1854, *J. M. Bigelow s.n.* = *Echinocereus engelmannii* Parry var. *variegatus* (Engelm. & Bigelow) Engelm. ex Rumpler.

Cereus fendleri Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 51. 1849. HOLOTYPE: Santa Fe, New Mexico, 1846, *A. Fendler 3.* = *Echinocereus fendleri* (Engelm.) Engelm. ex Rumpler.

Cereus fendleri Engelm. var. *pauperculus* Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 51. 1849. HOLOTYPE: Santa Fe, New Mexico, 1846, *A. Fendler s.n.* = *Echinocereus fendleri* (Engelm.) Engelm. ex Rumpler.

Cereus flaviflorus Engelm. ex Coult., Contr. U.S. Natl. Herb. 3: 391. 1896. HOLOTYPE: Santa Borga, Mexico, 1867, *W. Gabb 10.* = *Echinocereus maritimus* (Jones) Schumann.

Cereus flexuosus Engelm. ex Coult., Contr. U.S. Natl. Herb. 3: 411. 1896. HOLOTYPE: Peninsula of California, Mexico, 1867, *W. Gabb 5.* = *Machaerocereus gummosus* (Engelm.) Britt. & Rose.

Cereus gonacanthus Engelm. & Bigelow, in Engelm., Proc. Amer. Acad. Arts 3: 285. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 33. 1857. LECTOTYPE: Cedar Woods, west of Zuni, New Mexico, 1853, *J. M. Bigelow s.n.* = *Echinocereus triglochidiatus* Engelm. var. *gonacanthus* (Engelm. & Bigelow) L. Benson.

Cereus greggii Engelm. var. *cismontanus* Engelm. in Wisliz., Mem. Tour. No. Mex. 102. 1848. LECTOTYPE: Cadena, Mexico, 1847, *J. Gregg s.n.* Syntype: Paso del Norte, Mexico, 1846, *A. Wislizenus 222.*

Cereus hexaedrus Engelm., Proc. Amer. Acad. Arts 3: 285. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 34. 1857. LECTOTYPE: near Zuni, New Mexico, 1853, *J. M. Bigelow s.n.* = *Echinocereus triglochidiatus* Engelm. var. *mojavensis* (Engelm. & Bigelow) L. Benson.

Cereus longisetus Engelm., Proc. Amer. Acad. Arts 3: 280. 1856. HOLOTYPE: Santa Rosa, Mexico, 1853, *J. M. Bigelow s.n.* = *Echinocereus longisetus* (Engelm.) Engelm.

Cereus mamillatus Engelm. ex Coult., Contr. U. S. Natl. Herb. 3: 405. 1896. HOLOTYPE: Peninsula of California, Mexico, 1867, *W. Gabb 16.* = *Echinocereus mamillatus* (Engelm. ex Coult.) Britt. & Rose.

Cereus mojavensis Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 281. 1857 (preprint, 1956); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 33. 1857. HOLOTYPE: Mojave Creek, California?, 1854, *J. M. Bigelow s.n.* = *Echinocereus triglochidiatus* Engelm. var. *mojavensis* (Engelm. & Bigelow) L. Benson.

Cereus mojavensis Engelm. var. *zuniensis* Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 281. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 33. 1857. LECTOTYPE: Colorado Chiquito, Arizona, 1853, *J. M. Bigelow s.n.* = *Echinocereus triglochidiatus* Engelm. var. *melanacanthus* (Engelm. & Bigelow) L. Benson.

Cereus paucispinus Engelm., Proc. Amer. Acad. Arts 3: 285. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 37. 1859. LECTOTYPE: cultivated from *C. Wright & J. M. Bigelow s.n.* = *Echinocereus triglochidiatus* Engelm. var. *paucispinus* (Engelm.) Engelm. ex W. T. Marshall.

Cereus pectinatus Scheidw. var. *rigidissimus* Engelm., Proc. Amer. Acad. Arts 3: 279. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 31. 1859. LECTOTYPE: Sonora, Mexico, 1855, *A. Schott s.n.* = *Echinocereus pectinatus* (Scheidw.) Engelm. var. *rigidissimus* (Engelm.) Engelm. ex Rumpler.

Cereus procumbens Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 50. 1849. LECTOTYPE: near the mouth of the Rio Grande below Matamoras by the Missouri Volunteers, 1846, and cult. St. Louis May 1848. = *Echinocereus pentalophus* (DC.) Rumpler.

Cereus roemeri Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 51. 1849. LECTOTYPE: Liano River, Texas, 1847, *F. Lindheimer s.n.* (2 sheets). = *Echinocereus triglochidiatus* Engelm. var. *melanacanthus* (Engelm. & Bigelow) L. Benson.

Cereus schottii Engelm., Proc. Amer. Acad. Arts 3: 288. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 44. 1859. HOLOTYPE: Sierra de Sonoyita, Mexico, *s.d.*, *A. Schott 3.*

Cereus stramineus Engelm., Proc. Amer. Acad. Arts 3: 282. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 35: 1859. LECTOTYPE: near El Paso, Texas, 1851, *C. Wright s.n.* Syntype: *J. M. Bigelow s.n.* = *Echinocereus enneacanthus* Engelm.

Cereus thurberi Engelm., Amer. J. Sci. II. 17: 234. 1854. LECTOTYPE: Sonora, Mexico, 1851, *G. Thurber s.n.*

Cereus titan Engelm. in Coult., Contr. U. S. Natl. Herb. 3: 409. 1896. HOLOTYPE: Cape San Lucas to San Quentin, Mexico, 1867, *W. Gabb 1.* = *Pachycereus pringlei* (S. Wats.) Britt. & Rose.

Cereus viridiflorus Engelm. var. *cylindricus* Engelm., Proc. Amer. Acad. Arts 3: 278. 1856. LECTOTYPE: New Mexico, 1851, *C. Wright s.n.*

Echinocactus bicolor Galeotti var. *schottii* Engelm., Proc. Amer. Acad. Arts 3: 277. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 27. 1859. HOLOTYPE: Cretaceous hills, near Mier, Mexico, 1853, *A. Schott s.n.* = *Thelocactus bicolor* Galeotti var. *schottii* (Engelm.) Krainz.

Echinocactus dasycanthus Engelm., Proc. Amer. Acad. Arts 3: 277. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 28. 1859. LECTOTYPE: El Paso, Texas, 1852, *C. Wright s.n.* (2 sheets). Syntype: Frontera, 1852, *C. Wright 86?* = *Neolloydia intertexta* (Engelm.) L. Benson var. *dasycanthus* (Engelm.) L. Benson.

Echinocactus emoryi Engelm. var. *rectispinus* Engelm. ex Coult., Contr. U.S. Natl. Herb. 3: 362. 1896. HOLOTYPE: Peninsula of California, Mexico, 1867, *W. Gabb 12.* = *Ferocactus wislizenii* Engelm.

Echinocactus flexispinus Engelm. in Wisliz., Mem. Tour. No. Mex. 112. 1848. HOLOTYPE: Pelayo, between Chihuahua and Parras, Mexico, 1847, *A. Wislizenus s.n.* = *Ferocactus hamatacanthus* Muhlenpfordt var. *crassispinus* (Engelm.) L. Benson. On same sheet as *E. hamatacanthus* (Muhlenpfordt) Britt. & Rose var. *crassispinus* Engelm.

Echinocactus hamatacanthus Muhlenpfordt var. *crassispinus* Engelm., Proc. Amer. Acad. Arts 3: 273. 1856. HOLOTYPE: Pelayo, between Chihuahua and Parras, Mexico, 1847, *A. Wislizenus s.n.* On same sheet as *E. flexispinus* Engelm. = *Ferocactus hamatacanthus* (Muhlenpfordt) Britt. & Rose var. *crassispinus* Engelm.

Echinocactus horizonthalonius Lem. var. *centrispinus* Engelm., Proc. Amer. Acad. Arts 3:

276. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 26. 1859. LECTOTYPE: Frontera, New Mexico Territory, 1851–1852, *C. Wright s.n.* (2 sheets) = *Echinocactus horizonthalonius* Lem.

Echinocactus intertextus Engelm., Proc. Amer. Acad. Arts 3: 277. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 27. 1859. LECTOTYPE: El Paso, Texas, *s.d.*, *C. Wright* or *J. M. Bigelow* (no coll.), *s.n.* (2 sheets). Syntype: Chihuahua, 1846, *A. Wislizenus s.n.* = *Neolloydia intertextus* (Engelm.) L. Benson.

Echinocactus lecontei Engelm., Proc. Amer. Acad. Arts 3: 274. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 29. 1857. LECTOTYPE: Bill Williams Fork, Arizona, 1854, *J. M. Bigelow s.n.* Syntype: Gilia, *Leconte s.n.* = *Ferocactus acanthodes* (Lemaire) Britt. & Rose var. *lecontei* (Engelm.) Lindsay.

Echinocactus limitus Engelm. in Coult., Contr. U.S. Natl. Herb. 3: 374. 1896. LECTOTYPE: south of San Diego, 1878, *Parker & Hitchcock s.n.* (2 sheets). = *Ferocactus viridescens* (Nutt.) Britt. & Rose.

Echinocactus longehamatus Galeotti var. *brevispinus* Engelm., Proc. Amer. Acad. Arts 3: 273. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 22. 1859. LECTOTYPE: rocky mountains of the Limpia, Texas, 1852, *J. M. Bigelow s.n.* = *Ferocactus hamatacanthus* (Muhlenpfordt) Britt. & Rose.

Echinocactus orcuttii Engelm., West. Amer. Sci. 2: 46. 1886. HOLOTYPE: Palm Valley, northern Lower California, 1883, *C. R. Orcutt 641* (2 sheets). = *Ferocactus orcuttii* (Engelm.) Britt. & Rose.

Echinocactus peninsulae Engelm. ex Coult., Contr. U.S. Natl. Herb. 3: 361. 1896. HOLOTYPE: Cape San Lucas to San Diego, 1867, *W. Gabb 11*.

Echinocactus polyancistrus Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 272. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 29. 1857. HOLOTYPE: head of the Mojave, California?, 1854, *J. M. Bigelow s.n.* = *Sclerocactus polyancistrus* (Engelm. & Bigelow) Britt. & Rose.

Echinocactus polycephalus Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 276. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 31. 1857. LECTOTYPE: on Mojave River and Mojave Valley, California?, 1854, *J. M. Bigelow s.n.* (3 sheets).

Echinocactus polycephalus Engelm. & Bigelow var. *xeranthemoides* Engelm. in Coult., Contr. U.S. Natl. Herb. 3: 358. 1859. LECTOTYPE: northern Arizona, 1881, *A. L. Siler s.n.*

Echinocactus pubispinus Engelm., Trans. Acad. Sci. St. Louis 2: 199. 1863. HOLOTYPE: Utah, 1851, *H. Engelmann 1.* = *Sclerocactus pubispinus* (Engelm.) L. Benson.

Echinocactus setispinus Engelm. in Engelm. & Gray, Boston J. Nat. Hist. 5: 246. 1845. LECTOTYPE: Colorado River, 1844, *F. Lindheimer s.n.* = *Ferocactus setispinus* (Engelm.) L. Benson.

Echinocactus sileri Engelm. ex Coult., Contr. U.S. Natl. Herb. 3: 376. 1896. HOLOTYPE: Cottonwood Springs and Pipe Springs, Arizona, 1883, *A. L. Siler s.n.* (2 sheets). = *Pediocactus sileri* (Engelm.) L. Benson.

Echinocactus simpsonii Engelm., Trans. Acad. Sci. St. Louis 2: 197. 1863. LECTOTYPE: Kobe Valley, Nevada, 1859, *H. Engelmann s.n.* Syntype: Utah Desert, *s.d.*, *H. Engelmann s.n.* = *Pediocactus simpsonii* (Engelm.) Britt. & Rose.

Echinocactus simpsonii Engelm. var. *minor* Engelm., Trans. Acad. Sci. St. Louis. 2: 197. 1863. LECTOTYPE: Mt. Vernon, *Parry, Hall & Harbour s.n.* = *Pediocactus simpsonii* Engelm. var. *minor* (Engelm.) Cockerell.

Echinocactus uncinatus Hopf. ex Foerst. var. *wrightii* Engelm., Proc. Amer. Acad. Arts 3: 272. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 20. 1859. LECTOTYPE: Frontera, Texas, 1852, *C. Wright 88*. Syntype: Frontera, Texas, 1852, *J. M. Bigelow s.n.* = *Ancistrocactus uncinatus* (Galeotti) Benson var. *wrightii* (Engelm.) L. Benson.

Echinocactus unquispinus Engelm. in Wisliz., Mem. Tour. No. Mex. 12. 1848. LECTOTYPE: Pelayo, Mexico, *s.d.*, *A. Wislizenus s.n.* = *Echinomastus unquispinus* (Engelm.) Britt. & Rose.

Echinocactus viridescens Nutt. var. *cylindraceus* Engelm., Amer. J. Sci. II. 14: 338. 1852. HOLOTYPE: San Felipe, California, 1850, *C. C. Parry s.n.* = *Ferocactus acanthodes* (Lemaire) Britt. & Rose.

Echinocactus whipplei Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 271. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 28. 1857. HOLOTYPE: Colorado Chiquito, Arizona, 1853, *J. M. Bigelow s.n.* = *Sclero-*

cactus whipplei (Engelm. & Bigelow) Britt. & Rose.

Echinocactus whipplei Engelm. var. *spinosior* Engelm., Trans. Acad. Sci. St. Louis 2: 199. 1863. LECTOTYPE: Camp Floyd, Utah, 1859, *H. Engelmann s.n.* (2 sheets). = *Sclerocactus spinosior* (Engelm.) Woodruff & L. Benson.

Echinocactus wislizenii Engelm. in Wisliz., Mem. Tour. No. Mex. 96. 1848. LECTOTYPE: Doñana, Mexico, 1846, *A. Wislizenus s.n.* (3 sheets). = *Ferocactus wislizenii* Engelm.

Echinocactus wislizenii Engelm. var. *decipiens* Engelm. in Rothr., Bot. Wheeler's Surv. 128. 1878. HOLOTYPE: Camp Bowie, Arizona, 1874, *J. T. Rothrock 492.* = *Ferocactus wislizenii* Engelm.

Echinocereus adustus Engelm. in Wisliz., Mem. Tour. No. Mex. 104. 1848. HOLOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus s.n.* (2 sheets).

Echinocereus chloranthus Engelm. ex Rumpler in Forster, Handb. Cact. 2nd edition: 812. 1885. SYNTYPE: Texas, 1852, *J. M. Bigelow s.n.*

Echinocereus coccineus Engelm. in Wisliz., Mem. Tour. No. Mex. 100. 1848. HOLOTYPE: Wolf Creek, Santa Fe, New Mexico, 1846, *A. Wislizenus s.n.* (2 sheets). = *E. triglochidiatus* Engelm. var. *melanacanthus* (Engelm.) L. Benson.

Echinocereus dasyacanthus Engelm. in Wisliz., Mem. Tour. No. Mex. 100. 1848. NEOTYPE: San Antonio to El Paso, Texas, 1849, *C. Wright s.n.* = *E. pectinatus* Scheidw. var. *neomexicanus* (Coult.) L. Benson.

Echinocereus enneacanthus Engelm. in Wisliz., Mem. Tour. No. Mex. 112. 1848. HOLOTYPE: south of Chihuahua, Mexico, 1847, *A. Wislizenus 244.*

Echinocereus polyacanthus Engelm. in Wisliz., Mem. Tour. No. Mex. 104. 1848. LECTOTYPE: Cosihuiriachi, Mexico, 1847, *A. Wislizenus s.n.* (2 sheets + 1 box). = *E. triglochidiatus* Engelm. var. *neomexicanus* (Standley) Benson.

Echinocereus radians Engelm. in Wisliz., Mem. Tour. No. Mex. 104. 1848. HOLOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus s.n.* = *E. adustus* Engelm.

Echinocereus rufispinus Engelm. in Wisliz., Mem. Tour. No. Mex. 106. 1848. HOLOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus s.n.*

Echinocereus triglochidiatus Engelm. in Wisliz., Mem. Tour. No. Mex. 93. 1848. LECTOTYPE: Wolf Creek, New Mexico, 1846, *A. Wislizenus s.n.* (2 sheets + 1 box).

Echinocereus viridiflorus Engelm. in Wisliz., Mem. Tour. No. Mex. 91. 1848. LECTOTYPE: Wolf Creek, New Mexico, 1846, *A. Wislizenus 514* (2 sheets).

Mammillaria applanata Engelm. in Wisliz., Mem. Tour. No. Mex. 105. 1848. LECTOTYPE: western Texas, 1845, *F. Lindheimer s.n.* = *M. gummifera* Engelm. var. *applanata* (Engelm.) L. Benson.

Mammillaria arizonica Engelm. in Brewer & Watson, Bot. Calif. 1: 244. 1876. LECTOTYPE: Arizona, *s.d.*, *Coues & E. Palmer s.n.* Syntype: Arizona, 1871, *Bischoff s.n.* = *Coryphantha vivipara* (Nutt.) Britt. & Rose var. *arizonica* (Engelm.) W. T. Marshall.

Mammillaria barbata Engelm. in Wisliz., Mem. Tour. No. Mex. 105. 1848. HOLOTYPE: Cosihuiriachi, Mexico, *s.d.*, *A. Wislizenus s.n.* = *Neomammillaria barbata* (Engelm.) Britt. & Rose.

Mammillaria chlorantha Engelm. in Rothr., Bot. Wheeler's Surv. 128. 1878. LECTOTYPE: St. George, Utah, 1874, *C. C. Parry s.n.* = *Coryphantha vivipara* (Nutt.) Britt. & Rose var. *desertii* (Engelm.) W. T. Marshall.

Mammillaria compacta Engelm. in Wisliz., Mem. Tour. No. Mex. 105. 1848. Cosihuiriachi, Mexico, 1846, *A. Wislizenus s.n.*

Mammillaria dasyacantha Engelm., Proc. Amer. Acad. Arts 3: 269. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 15. 1859. LECTOTYPE & PROBABLE ISOLECTOTYPE: El Paso, Texas, *C. Wright s.n.* = *Coryphantha dasyacantha* (Engelm.) Orcutt.

Mammillaria desertii Engelm. in Watson, Bot. Calif. 2: 449. 1880. LECTOTYPE: "Ivanpah," 1880, *S. B. & W. F. Parish 455* (3 sheets). = *Coryphantha vivipara* (Nutt.) Britt. & Rose var. *desertii* (Engelm.) W. T. Marshall.

Mammillaria echinus Engelm., Proc. Amer. Acad. Arts 3: 267. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 13. 1859. LECTOTYPE: western Texas, 1849, *C. Wright s.n.* (2 sheets). Syntypes: Presidio del Norte, 1852, *J. M. Bigelow s.n.* (2 sheets); western Texas, 1852, *C. Wright s.n.*; east of El Paso, Texas, *s.d.*, *C. Wright s.n.* = *Coryphantha cornifera* DC. var. *echinus* (Engelm.) L. Benson.

Mammillaria fissurata Engelm., Proc. Amer. Acad. Arts 3: 270. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 18. 1859. LECTOTYPE: Rio Bravo del Norte, Texas, 1852, *A. Schott s.n.* Syntype: Pecos, 1852, *J. M. Bigelow s.n.* = *Ariocarpus fissurata* (Engelm.) K. Schumann.

Mammillaria grahamii Engelm., Proc. Amer. Acad. Arts 3: 262. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 7. 1859. LECTOTYPE: El Paso, Texas, 1852, *C. Wright s.n.* (2 sheets). Syntypes: Colorado Basin, 1855, *A. Schott s.n.*; Gila, *C. C. Parry s.n.*

Mammillaria gummifera Engelm. in Wisliz., Mem. Tour. No. Mex. 106. 1848. LECTOTYPE: Cosihuiriachi, Mexico, 1848, *A. Wislizenus s.n.* = *M. heyderi* Muhlenpfordt var. *gummifera* (Engelm.) L. Benson.

Mammillaria hemisphaerica Engelm. in Wisliz., Mem. Tour. No. Mex. 106. 1848. LECTOTYPE: cult. in St. Louis, Missouri from Matamoras, 1846, *St. Louis Volunteers.* = *M. heyderi* Muhlenpfordt var. *hemisphaerica* Engelm.

Mammillaria lasiacantha Engelm. var. *denuta* Engelm., Proc. Amer. Acad. Arts 3: 261. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 5. 1859. LECTOTYPE: west of the Pecos, 1852, *C. Wright s.n.* = *M. lasiacantha* Engelm.

Mammillaria lasiacantha Engelm. var. *minor* Engelm., Proc. Amer. Acad. Arts 3: 261. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 5. 1859. LECTOTYPE: west of the Pecos, *s.d.*, *C. Wright s.n.* = *M. lasiacantha* Engelm.

Mammillaria macromeris Engelm. in Wisliz., Mem. Tour. No. Mex. 98. 1848. LECTOTYPE: Donana, New Mexico, 1846, *A. Wislizenus s.n.* (2 sheets). = *Coryphantha macromeris* (Engelm.) Orcutt.

Mammillaria meiacantha Engelm., Proc. Amer. Acad. Arts 3: 263. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 27. 1857. LECTOTYPE: east of the Pecos, 1853, *J. M. Bigelow s.n.* = *M. gummifera* Engelm. var. *meiacantha* (Engelm.) L. Benson.

Mammillaria micromeris Engelm., Proc. Amer. Acad. Arts 3: 260. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 3. 1859. LECTOTYPE: San Filipe to the Pecos, Texas, 1851, *C. Wright s.n.* Syntypes: western Texas, 1852, *C. Wright s.n.* (2 sheets) & 1849, *C. Wright s.n.* = *Epithelantha micromeris* (Engelm.) Weber.

Mammillaria micromeris Engelm. var. *greggii* Engelm., Proc. Amer. Acad. Arts 3: 261. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 4. 1859. LECTOTYPE: Saltillo, Mexico, 1848, *J. Gregg 508.* = *Epithelantha micromeris* L. Benson.

Mammillaria nuttallii Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 49. 1849. LECTOTYPE & PROBABLE ISOLECTOTYPE: Ft. Pierre, South Dakota, 1847, *F. V. Hayden s.n.* = *Coryphantha missouriensis* (Sweet) Britt. & Rose.

Mammillaria papyracanthus Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 49. 1849. LECTOTYPE: Santa Fe, New Mexico, 1857, *A. Fendler s.n.* = *Pediocactus papyracanthus* (Engelm.) L. Benson.

Mammillaria pectinata Engelm., Proc. Amer. Acad. Arts 3: 266. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 12. 1859. LECTOTYPE: on the Pecos, Texas, 1849, *C. Wright* (3 sheets). = *Coryphantha cornifera* (DC.) L. Benson.

Mammillaria phellosperma Engelm., Proc. Amer. Acad. Arts 3: 262. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 6. 1859. LECTOTYPE: Mojave Creek, 1854, *J. M. Bigelow s.n.* Syntypes: Gila, *s.d.*, *LeConti s.n.*; Bill Williams Fork, 1854, *J. M. Bigelow s.n.* = *M. tetrancistra* Engelm.

Mammillaria pusilla Sweet var. *texana* Engelm., Proc. Amer. Acad. Arts 3: 261. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 5. 1859. SYNTYPES: Eagle Pass to Santa Rosa, *s.d.*, *J. M. Bigelow s.n.*; Rio Grande, *s.d.*, *Poselger s.n.* = *M. prolifera* (Miller) Haw. var. *texana* (Engelm.) Borg.

Mammillaria radiosa Engelm. in Gray, Boston J. Nat. Hist. 6: 196. 1850. LECTOTYPE: western Texas, 1846, cult. St. Louis, Missouri, *F. Lindheimer s.n.* (2 sheets). = *Coryphantha vivipara* (Nutt.) Britt. & Rose var. *radiosa* (Engelm.) Backeberg.

Mammillaria recurvispina Engelm., Proc. Amer. Acad. Arts 3: 266. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 12. 1859. LECTOTYPE: Sierra del Pajarito, Mexico, 1855, *A. Schott s.n.* = *Coryphantha recurvata* (Engelm.) Britt. & Rose.

Mammillaria scheeri Muhlenpfordt var. *valida* Engelm., Proc. Amer. Acad. Arts 3: 265. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 10. 1859. LECTOTYPE: Limpio, Mexico, 1852, *C. Wright s.n.* Syntype: El Paso, *s.d.*, *C. Wright s.n.* (2 sheets). = *Coryphantha scheeri* Muhlenpfordt.

Mammillaria similis Engelm. & Gray. var. *caespitosa* Engelm. in Engelm. & Gray, Boston

J. Nat. Hist. 5: 246. 1845. LECTOTYPE: cultivated St. Louis, from Industry, Texas, 1846, *F. Lindheimer s.n.* (2 sheets). = *Coryphantha missouriensis* (Sweet) Britt. & Rose var. *similis* (Engelm.) L. Benson.

Mammillaria similis Engelm. & Gray var. *robustior* Engelm. in Gray, Boston J. Nat. Hist. 6: 200. 1850. LECTOTYPE: cult. St. Louis from Pierdenales River, Texas, *F. Lindheimer s.n.* = *Coryphantha missouriensis* (Sweet) Britt. & Rose var. *robustior* (Engelm.) L. Benson.

Mammillaria strobiliformis Engelm. in Wisliz., Mem. Tour. No. Mex. 115. 1848. HOLOTYPE: Rinconda, on rocks, 1847, *A. Wislizenus s.n.* = *Neolloydia conoidea* (DC.) Britt. & Rose.

Mammillaria sulcata Engelm. in Engelm. & Gray, Boston J. Nat. Hist. 5: 246. 1845. LECTOTYPE: Industry, Texas, 1844, *F. Lindheimer s.n.* = *Coryphantha sulcata* (Engelm.) Britt. & Rose.

Mammillaria tuberculosa Engelm., Proc. Amer. Acad. Arts 3: 268. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 14. 1859. LECTOTYPE: Flounce Mts., Chihuahua, Mexico, 1852, *J. M. Bigelow s.n.* (2 sheets). Syntypes: El Paso, 1851 & 1852, *C. Wright & J. M. Bigelow s.n.* (2 sheets). = *Coryphantha strobiliformis* (Poselger) Moran.

Mammillaria vivipara Haw. var. *radiosa* Engelm. subvar. *borealis* Engelm., Proc. Amer. Acad. Arts 3: 269. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 15. 1859. LECTOTYPE: Santa Fe, New Mexico, 1847, *A. Fendler 271* (2 sheets). Syntype: New Mexico, 1846, *A. Wislizenus s.n.* = *Coryphantha vivipara* (Nutt.) Britt. & Rose.

Mammillaria vivipara Haw. var. *radiosa* Engelm. subvar. *neomexicana* Engelm., Proc. Amer. Acad. Arts 3: 269. 1857 (preprint 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 15. 1859. LECTOTYPE: southern New Mexico, 1849, *C. Wright s.n.* Syntypes: San Pedro, on the Pecos, *s.d.*, *C. Wright & J. M. Bigelow s.n.* (5 sheets); Sonora, 1855?, *A. Schott s.n.* = *Coryphantha vivipara* (Nutt.) Britt. & Rose. var. *radiosa* (Engelm.) Backeberg.

Mammillaria vivipara Haw. var. *radiosa* Engelm. subvar. *texana* Engelm., Proc. Amer. Acad. Arts 3: 269. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 15. 1859. LECTOTYPE: Pierdenales, in sterile sandy plains in western Texas, cult. St. Louis, 1846, *F. Lindheimer s.n.* = *Coryphantha vivipara* (Nutt.) Britt. & Rose var. *radiosa* (Engelm.) Backeberg.

Mammillaria wrightii Engelm., Proc. Amer. Acad. Arts 3: 262. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 27. 1857. LECTOTYPE: Copper Mines, New Mexico, 1851, *C. Wright s.n.* = *M. barbata* Engelm.

Opuntia angustata Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 292. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 39. 1857. LECTOTYPE: Bill Williams Fork, 1854, *J. M. Bigelow s.n.* Syntypes: Inscription Rock, 1853, *J. M. Bigelow s.n.*; Cajon Pass, 1854, *J. M. Bigelow s.n.* = *O. phaeacantha* Engelm. var. *major* Engelm.

Opuntia arborescens Engelm. in Wisliz., Mem. Tour. No. Mex. 90. 1848. LECTOTYPE: Santa Fe, New Mexico, 1847, *A. Fendler 277.* Syntype: no locale, *A. Wislizenus s.n.* = *O. imbricata* Haw.

Opuntia arbuscula Engelm., Proc. Amer. Acad. Arts 3: 309. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 60. 1859. LECTOTYPE: Gilia, Arizona, *s.d.*, *A. Schott s.n.*

Opuntia arenaria Engelm. & Bigelow, Proc. Amer. Acad. Arts 3: 301. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 52. 1859. LECTOTYPE: Frontera, near El Paso, Texas, 1852, *C. Wright 311.*

Opuntia basilaris Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 298. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 43. 1857. LECTOTYPE: Cactus Pass, Bill Williams Fork, 1854, *J. M. Bigelow s.n.*

Opuntia bernardina Engelm. ex Parish, Bull. Torrey Bot. Club 19: 92. 1892. LECTOTYPE: San Bernardino, California, 1880, *G. Engelmann s.n.* = *O. parryi* Engelm.

Opuntia brachyathra Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 302. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 47. 1857. HOLOTYPE: Zuni, New Mexico, 1853, *J. M. Bigelow s.n.* = *O. fragilis* (Nutt.) Haw. var. *brachyathra* (Engelm. & Bigelow) Coult.

Opuntia bulbispina Engelm., Proc. Amer. Acad. Arts 3: 304. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 55. 1859. HOLOTYPE: near Perros Bravos, Mexico, 1848, *J. Gregg probably 669.* Photo only, type has not been located.

Opuntia californica Engelm. in Emory, Notes Mil. Reconn. Ft. Leavenworth to San Diego, App. 2: 158. 1848. LECTOTYPE: Arizona, 1846?, *Emory? s.n.* = *O. kleiniae* Englem. var. *tetracantha* (Toumey) W. T. Marshall.

Opuntia camanchica Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 293. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 40. 1857. LECTOTYPE: plains, Tucumcari, New Mexico, 1853, *J. M. Bigelow s.n.* = *O. phaeacantha* Engelm. var. *camanchica* (Engelm. & Bigelow) L. Benson.

Opuntia chlorotica Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 291. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 38. 1857. LECTOTYPE: Bill Williams Mt., Arizona, 1853, *J. M. Bigelow s.n.* Syntype: Mojave Creek, 1854, *J. M. Bigelow s.n.*

Opuntia clavata Engelm. in Wisliz., Mem. Tour. No. Mex. 95. 1848. LECTOTYPE: Santa Fe, New Mexico, 1846, *A. Fendler s.n.*

Opuntia clavellina Engelm. in Coult., Contr. U.S. Natl. Herb. 3: 444. 1896. LECTOTYPE: Peninsula of California, 1867, *W. Gabb 23.*

Opuntia cymochila Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 295. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 42. 1857. LECTOTYPE: Tucumcari Hills, New Mexico, 1853, *J. M. Bigelow s.n.* Syntype: Camanche Springs, 1853, *J. M. Bigelow s.n.* = *O. macrorhiza* Engelm.

Opuntia cymochila Engelm. & Bigelow var. *montana* Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 296. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 42. 1857. LECTOTYPE: Sandia Mts., New Mexico, 1853, *J. M. Bigelow s.n.* = *O. macrorhiza* Engelm.

Opuntia dulcis Engelm., Proc. Amer. Acad. Arts 3: 291. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 48. 1859. LECTOTYPE: El Paso, Texas, 1852, *C. Wright s.n.* = *O. phaeacantha* Engelm.

Opuntia emoryi Engelm., Proc. Amer. Acad. Arts 3: 303. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 53. 1859. LECTOTYPE: seeds from Chihuahua, 1852, *A. Schott s.n.* = *O. stanlyi* Engelm.

Opuntia engelmannii Salm-Dyck var. *cyclodes* Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 291. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 37. 1857. LECTOTYPE: Hunah Creek near the Pecos, 1853, *J. M. Bigelow s.n.* = *O. phaeacantha* Engelm. var. *major* Engelm.

Opuntia engelmannii Salm-Dyck var. *littoralis* Engelm. in Brewer & Watson, Bot. Calif. 1: 248. 1876. LECTOTYPE: Santa Barbara, California, 1874, *O. Tittmann s.n.* Syntype: Santa Cruz Island, California, 1874, *O. Tittman s.n.* = *O. littoralis* Engelm.

Opuntia erinacea Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 301. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 47. 1857. HOLOTYPE: Mojave Creek, 1854, *J. M. Bigelow s.n.*

Opuntia filipendula Engelm., Proc. Amer. Acad. Arts 3: 294. 1857. LECTOTYPE: near San Elizario, 1852, *C. Wright s.n.* = *O. macrorhiza* Engelm. var. *pottsii* (Salm-Dyck) L. Benson.

Opuntia fragilis Haw. var. *frutescens* Engelm. in Engelm. & Gray, Boston J. Nat. Hist. 5: 245. 1845. LECTOTYPE: Colorado bottom prairie, 1844, *F. Lindheimer 244.* = *O. leptocaulis* DC.

Opuntia frutescens Engelm. in Engelm. & Gray, Boston J. Nat. Hist. 5: 245. 1845. LECTOTYPE: Colorado bottom prairie, 1844, *F. Lindheimer 244.* = *O. leptocaulis* DC.

Opuntia frutescens Engelm. var. *brevispina* Engelm., Proc. Amer. Acad. Arts 3: 309. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 53. 1857. LECTOTYPE: Texas, 1845, *F. Lindheimer s.n.* = *O. leptocaulis* DC.

Opuntia frutescens Engelm. var. *longispina* Engelm., Proc. Amer. Acad. Arts 3: 309. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 53. 1857. LECTOTYPE: Laguna, Colorado, 1853, *J. M. Bigelow s.n.* = *O. leptocaulis* DC.

Opuntia fulgida Engelm., Proc. Amer. Acad. Arts 3: 306. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 57. 1859. LECTOTYPE: western Sonora, Mexico, *s.d.*, *A. Schott 8.*

Opuntia fusco-atra Engelm., Proc. Amer. Acad. Arts 3: 297. 1856. LECTOTYPE: prairies west of Houston, Texas, 1842, *F. Lindheimer 33.*

Opuntia fusiformis Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 297. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 43. 1857. LECTOTYPE: Deer Creek, Missouri?, 1853, *J. M. Bigelow s.n.* Syntype: Cow Creek, 1846, *A. Wislizenus 417.* = *O. macrorhiza* Engelm.

Opuntia grahamii Engelm., Proc. Amer. Acad. Arts 3: 304. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 55. 1859. LECTOTYPE: Rio Grande, near El Paso, Texas, 1851, *C. Wright s.n.* = *O. schottii* Engelm. var. *grahamii* (Engelm.) L. Benson.

Opuntia grandiflora Engelm., Proc. Amer. Acad. 3: 295. 1857 (preprint, 1856). LECTOTYPE: cultivated St. Louis, Missouri from Industry, Texas, 1847, *F. Lindheimer s.n.* = *O. macrorhiza* Engelm.

Opuntia hystricina Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 299. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 44. 1857. LECTOTYPE: Colorado Chiquito, Arizona, 1853, *J. M. Bigelow s.n.* = *O. erinacea* Engelm. & Bigelow var. *hystricina* (Engelm. & Bigelow) L. Benson.

Opuntia lindheimeri Engelm. in Gray, Boston J. Nat. Hist. 6: 207. 1850. LECTOTYPE: New Braunfels, Texas, 1845, *F. Lindheimer s.n.*

Opuntia macrocentra Engelm., Proc. Amer. Acad. Arts 3: 292. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 49. 1859. LECTOTYPE: Rio Grande, near El Paso, Texas, 1852, *C. Wright s.n.* (2 sheets). = *O. violacea* Engelm. var. *macrocentra* (Engelm.) L. Benson.

Opuntia macrorhiza Engelm. in Gray, Boston J. Nat. Hist. 6: 206. 1850. LECTOTYPE: between the Picardinales & Guadalupe, 1847, *F. Lindheimer 1251.*

Opuntia missouriensis DC. var. *albispina* Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 300. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 46. 1857. LECTOTYPE: Canadian River, Texas?, 1853, *J. M. Bigelow s.n.* = *O. polyacantha* Haw.

Opuntia missouriensis DC. var. *microsperma* Engelm., Proc. Amer. Acad. Arts 3: 300. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 46. 1857. LECTOTYPE: specimens from Ft. Pierre, South Dakota, cult. St. Louis, Missouri in 1854, no collector (2 sheets). = *O. polyacantha* Haw.

Opuntia missouriensis DC. var. *platycarpa* Engelm., Proc. Amer. Acad. Arts 3: 300. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 45. 1857. LECTOTYPE: Yellowstone River, 1854, *F. V. Hayden s.n.* = *O. polyacantha* Haw.

Opuntia missouriensis DC. var. *rufispina* Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 300. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 45. 1857. LECTOTYPE: Pecos, New Mexico, 1853, *J. M. Bigelow s.n.* = *O. polyacantha* Haw. var. *rufispina* (Engelm. & Bigelow) L. Benson.

Opuntia missouriensis DC. var. *subinermis* Engelm., Proc. Amer. Acad. Arts 3: 300. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 46. 1857. LECTOTYPE: Ft. Pierre, South Dakota, 1853, *F. V. Hayden s.n.* = *O. polyacantha* Haw.

Opuntia missouriensis DC. var. *trichophora* Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 300. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 46. 1857. LECTOTYPE: Santa Fe Creek, New Mexico, 1853, *J. M. Bigelow s.n.* = *O. polyacantha* Haw. var. *trichophora* (Engelm. & Bigelow) Coult.

Opuntia mojavensis Engelm., Proc. Amer. Acad. Arts 3: 293. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 40. 1857. LECTOTYPE: Mojave Creek, 1854, *J. M. Bigelow s.n.* = *O. phaeacantha* Haw. var. *mojavensis* (Engelm.) Fosberg.

Opuntia occidentalis Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 279. 1857 (preprint, 1856); U.S. Senate Rept. Expl & Surv. R.R. Route Pacific Ocean. Botany 4: 38. 1857. LECTOTYPE: Los Angeles, California, 1852, *J. M. Bigelow s.n.* Syntype: southern California, 1855, *A. Schott s.n.* = *O. ficus-indica* (L.) Miller.

Opuntia parkeri Engelm. in Coult., Contr. U.S. Natl. Herb. 3: 446. 1896. HOLOTYPE: San Diego, California, 1879, *C. F. Parker s.n.* = *O. parryi* Engelm.

Opuntia phaeacantha Engelm. var. *brunnea* Engelm., Proc. Amer. Acad. Arts 3: 293. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 50. 1859. LECTOTYPE: Rio Grande, near El Paso, Texas, 1852, *C. Wright s.n.* = *O. phaeacantha* Engelm. var. *major* Engelm.

Opuntia phaeacantha Engelm. var. *major* Engelm., Proc. Amer. Acad. Arts 3: 293. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 50. 1857. LECTOTYPE: Santa Fe, New Mexico, 1846, *A. Fendler s.n.*

Opuntia phaeacantha Engelm. var. *nigricans* Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 52. 1849. LECTOTYPE: Santa Fe, New Mexico, *A. Fendler 8.* = *O. phaeacantha* Engelm.

Opuntia procumbens Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 292. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 39. 1857. LECTOTYPE: Aztec Pass, Arizona, 1853, *J. M. Bigelow s.n.* Syntypes: San Francisco Mts., Arizona, 1853, *J. M. Bigelow s.n.*; Cactus Pass, 1854, *J. M. Bigelow s.n.* = *O. phaeacantha* Engelm. var. *discata* (Griffiths) L. Benson & Walkington.

Opuntia prolifera Engelm., Amer. J. Sci. II. 14: 338. 1852. NEOTYPE: Mission Hills, San Diego, California, 1903, *Leroy Abrams 3394.*

Opuntia pulchella Engelm., Trans. Acad. Sci. St. Louis 2: 201. 1863. LECTOTYPE: Walker River, Nevada, 1859, *H. Engelmann s.n.*

Opuntia rafinesquei Engelm., Proc. Amer. Acad. Arts 3: 295. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 41. 1857. LECTOTYPE: St. Louis, Missouri, no collector. = *O. humifusa* (Raf.) Raf.

Opuntia rafinesquei Engelm. var. *arkansana* Engelm. ex Rumpler in Forster, Handb. Cact. 2nd edition: 922. 1885. LECTOTYPE: Fort Smith, 1853, *J. M. Bigelow s.n.* = *O. humifusa* (Raf.) Raf.

Opuntia rafinesquei Engelm. var. *microsperma* Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 295. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 41. 1857. LECTOTYPE: cultivated St. Louis, Missouri, April 1854, no collector. = *O. humifusa* (Raf.) Raf.

Opuntia rafinesquei Engelm. var. *minor* Engelm., U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany. 4: 55. 1857. LECTOTYPE: naked sandstone ledges at Mine la Motte, Missouri, 1845, *G. Engelmann s.n.* = *Opuntia humifusa* (Raf.) Raf.

Opuntia ramosissima Engelm., Amer. J. Sci. II. 14: 339. 1852. NEOTYPE: Sonora, Mexico, 1855, *A. Schott 2.*

Opuntia rufida Engelm., Proc. Amer. Acad. Arts 3: 298. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 51. 1859. LECTOTYPE: Presidio del Norte, Mexico, 1852, *J. M. Bigelow s.n.*

Opuntia schottii Engelm., Proc. Amer. Acad. Arts 3: 304. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 54. 1859. LECTOTYPE: near mouth of Pecos and San Pedro, 1853, *A. Schott s.n.*

Opuntia setispina Engelm. in Salm-Dyck, Cact. Hort. Dyck. 1849: 239. 1850. LECTOTYPE & SYNTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus s.n.* = *O. macrorhiza* Engelm. var. *pottsii* (Salm-Dyck) L. Benson.

Opuntia sphaerocarpa Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 300. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 47. 1857. LECTOTYPE: near Albuquerque, New Mexico, 1853, *J. M. Bigelow s.n.* = *O. polyacantha* Haw. var. *junipera* (Engelm. & Bigelow) L. Benson.

Opuntia sphaerocarpa Engelm. var. *utahensis* Engelm., Trans. Acad. Sci. St. Louis 11: 199. 1863. HOLOTYPE: Steptoe Valley, Utah, 1859, *H. Engelmann s.n.* = *O. erinacea* Engelm. & Bigelow var. *utahensis* (Engelm. & Bigelow) L. Benson.

Opuntia stenochila Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 296. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 43. 1857. LECTOTYPE: Cañon de Zuñi, 1853, *J. M. Bigelow s.n.* = *O. macrorhiza* Engelm.

Opuntia stenopetala Engelm., Proc. Amer. Acad. Arts 3: 289. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 46. 1859. HOLOTYPE: Buena Vista, Mexico, 1848, *J. Gregg 295* (2 sheets).

Opuntia strigil Engelm., Proc. Amer. Acad. Arts 3: 290. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 47. 1859. LECTOTYPE: 6 mi. west of the Pecos, Texas, 1851, *C. Wright s.n.*

Opuntia tapona Engelm. in Coult., Contr. U.S. Natl. Herb. 3: 423. 1896. HOLOTYPE: Peninsula of California, 1867, *W. Gabb 20a.*

Opuntia tenuispina Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 294. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 50. 1859. LECTOTYPE: below El Paso, 1852, *C. Wright 332.* = *O. macrorhiza* Engelm. var. *pottsii* (Salm-Dyck) L. Benson.

Opuntia thurberi Engelm., Proc. Amer. Acad. Arts 3: 308. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae

59. 1859. HOLOTYPE: near Bacuachi, Sonora, 1851, *G. Thurber s.n.*

Opuntia tortispina Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 293. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 41. 1859. LECTOTYPE: Camanche Plains, 1853, *J. M. Bigelow s.n.*

Opuntia vaginata Engelm. in Wisliz., Mem. Tour. No. Mex. 100. 1848. LECTOTYPE: mountains near El Paso, 1846, *A. Wislizenus s.n.* Syntype: between Albuquerque and El Paso, 1846, *A. Wislizenus s.n.* = *O. leptocaulis* DC.

Opuntia versicolor Engelm. in Coult, Contr. U.S. Natl. Herb. 3: 452. 1896. LECTOTYPE: mesas and foothills, near Tucson, Arizona, 1881, *C. G. Pringle s.n.* Syntype: same locale, 1881, *C. G. Pringle 13712.*

Opuntia whipplei Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 307. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 50. 1857. LECTOTYPE: Zuñi, New Mexico, 1853, *J. M. Bigelow s.n.*

Opuntia whipplei Engelm. var. *spinosior* Engelm. & Bigelow in Engelm., Proc. Amer. Acad. Arts 3: 307. 1857 (preprint, 1856); U.S. Senate Rept. Expl. & Surv. R.R. Route Pacific Ocean. Botany 4: 51. 1857. LECTOTYPE: Santa Cruz River Valley, *s.d.*, *A. Schott 5.* = *O. spinosior* (Engelm.) Toumey.

Opuntia wrightii Engelm., Proc. Amer. Acad. Arts 3: 308. 1857 (preprint, 1856); in Emory, Rept. U.S. & Mex. Bound. Surv. 2: Cactaceae 59. 1859. LECTOTYPE: Presidio del Norte, Texas, 1851–1852, *C. Wright s.n.* Syntypes: Presidio del Norte, 1852, *C. C. Parry s.n.*; mountain sides of the Limpia, 1852, *C. Wright 490.* = *O. kleiniae* DC.

CALLITRICHACEAE

Callitriche antarctica Engelm. ex Hegelm., Verh. Bot. Ver. Brandenburg 9: 20. 1867. SYNTYPE: Kerguelen's Land, 1839–1843, *J. D. Hooker s.n.*

Callitriche austinii Engelm. in Gray, Man. Bot. 5: 428. 1868. TYPE MATERIAL: New Jersey, *s.d.*, *Austin s.n.* = *C. terrestris* Raf.

Callitriche heteropoda Engelm. ex Hegelm., Verh. Bot. Ver. Brandenburg 9: 40. 1867. SYNTYPES: Bolivia, *s.d.*, *G. Mandon 1456 & 1496.*

Callitriche japonica Engelm. ex Hegelm., Verh. Bot. Ver. Brandenburg 10: 113. 1868. TYPE MATERIAL: Hakodadi, Japan, 1853–1856, *C. Whipple s.n.*

CAMPANULACEAE

Campanula planifolia Engelm. in Coult., Bot. Gaz. 7: 5. 1882. SYNTYPES: Empire, Colorado, 1881, *G. Engelmann s.n.* (6 sheets); Clear Creek, Colorado, 1881, *G. Engelmann s.n.* (2 sheets); Middle Park, Colorado, 1881, *G. Engelmann s.n.*

Campanula scabella Engelm. in Coult., Bot. Gaz. 6: 237. 1881. LECTOTYPE: Scotts Mountain, California, 1880, *G. Engelmann s.n.*

Lobelia mucronata Engelm. in Wisliz., Mem. Tour. No. Mex. 108. 1848. HOLOTYPE & ISOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus 177.* = *L. fulgens* Willd.

Lobelia pectinata Engelm. in Wisliz., Mem. Tour. No. Mex. 108. 1848. HOLOTYPE & ISOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus 192.* = *L. fenestralis* Car.

Lobelia phyllostachya Engelm. in Wisliz., Mem. Tour. No. Mex. 108. 1848. HOLOTYPE & ISOTYPE: between Monterey and Cerralbo, Mexico, 1847, *A. Wislizenus 337.* = *L. fulgens* Willd.

CAPPARACEAE

Wislizenia refracta Engelm. in Wisliz., Mem. Tour. No. Mex. 99. 1848. HOLOTYPE: Rio Grande, near El Paso, Texas, 1846, *C. Wright 88.*

CAPRIFOLIACEAE

Symphoricarpos spicatus Engelm. ex Gray, Boston J. Nat. Hist. 6: 215. 1850. SYNTYPE: Texas, 1849, *F. Lindheimer 846.* = *S. orbiculatus* Moench.

CARYOPHYLLACEAE

Cerastium nutans Raf. var. *brachypodum* Engelm., Proc. Amer. Acad. Arts 29: 277. 1894. SYNTYPE: banks of Chouteair's Pond, *s.d.*, *G. Engelmann s.n.*

Drymaria nodosa Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 12. 1849. HOLOTYPE: cult. St. Louis, Missouri from Cosihuiriachi, Mexico, 1848. = *D. leptophylla* (Cham. & Schlecht.) Fenzl ex Rohrb. var. *nodosa* (Engelm.) J. Duke.

Paronychia lindheimeri Engelm. in Gray, Boston J. Nat. Hist. 6: 152. 1850. TYPE MATERIAL:

Texas, 1845 and 1846, *F. Lindheimer 335* (2 sheets).

CLUSIACEAE

Hypericum gymnanthum Engelm. & Gray, Boston J. Nat. Hist. 5: 212. 1845. TYPE MATERIAL: Texas, 1844, *F. Lindheimer 17.* = *H. multilum* L.

CONVOLVULACEAE

Cuscuta acuta Engelm., Trans. Acad. Sci. St. Louis 1: 497. 1859. HOLOTYPE: Chatham Island, Galapagos, Ecuador, 1852, *Andersson s.n.*

Cuscuta angulata Engelm., Trans. Acad. Sci. St. Louis 1: 474. 1859. LECTOTYPE: Dutuitskloff, South Africa, *Drege s.n.*

Cuscuta applanata Engelm., Trans. Acad. Sci. St. Louis 1: 479. 1859. LECTOTYPE: Arizona Territory, *s.d., C. Wright Mexican Boundary Survey 1623–541.*

Cuscuta arvensis Bayrich ex Hook. var. *pubescens* Engelm., Trans. Acad. Sci. St. Louis 1: 495. 1859. LECTOTYPE: western Texas, 1847, *F. Lindheimer s.n.* = *C. glabrior* Engelm. var. *pubescens* (Engelm.) Yuncker.

Cuscuta bracteata Engelm., Trans. Acad. Sci. St. Louis 1: 509. 1859. ISOTYPE: Goyaz, Brazil, *s.d., Gardner 3348.*

Cuscuta californica Choisy var. *apiculata* Engelm., Trans. Acad. Sci. St. Louis 1: 499. 1859. HOLOTYPE: Colorado River, California, 1854, *J. M. Bigelow s.n.*

Cuscuta californica Choisy var. *squamigera* Engelm., Trans. Acad. Sci. St. Louis 1: 499. 1859. HOLOTYPE: Rio Virgen, Utah, *s.d., Remy s.n.*

Cuscuta cephalanthi Engelm., Amer. J. Sci. 43: 336. 1842. LECTOTYPE: near St. Louis, Missouri, *s.d., G. Engelmann s.n.*

Cuscuta chinensis Lam. var. *ciliaris* Engelm., Trans. Acad. Sci. St. Louis 1: 480. 1859. LECTOTYPE: Mosul, Kurdistan, *s.d., Kotschy 431* (3 sheets).

Cuscuta corniculata Engelm. var. *sphaerocyma* Engelm., Trans. Acad. Sci. St. Louis 1: 504. 1859. LECTOTYPE: Goyaz Province, *s.d.*, Brazil, *Weddell s.n.* Syntype: Rio Meta, *s.d., Karsten s.n.*

Cuscuta coryli Engelm., Amer. J. Sci. 43: 337. 1842. LECTOTYPE: American Bottom, St. Louis, Missouri, 1841, *G. Engelmann s.n.*

Cuscuta corymbosa Choisy var. *grandiflora* Engelm., Trans. Acad. Sci. St. Louis 1: 483. 1859. LECTOTYPE: Popayán, Columbia, *s.d., Humboldt s.n.*

Cuscuta corymbosa Choisy var. *stylosa* Engelm., Trans. Acad. Sci. St. Louis 1: 484. 1859. ISOLECTOTYPE: Mexico, 1846, *Berlandier 822.*

Cuscuta cristata Engelm., Trans. Acad. Sci. St. Louis 1: 507. 1859. ISOTYPE: Argentina, *s.d., Tweedy 1191.*

Cuscuta cuspidata Engelm. & Gray var. *pratensis* Engelm. in Engelm. & Gray, Boston J. Nat. Hist. 5: 224. 1845. LECTOTYPE: west of the Brazos, Texas, 1843, *F. Lindheimer 125.*

Cuscuta decora Choisy ex Engelm. var. *integriuscula* Engelm., Trans. Acad. Sci. St. Louis 1: 502. 1859. HOLOTYPE: Mendoza, Argentina, *Gilles s.n.* = *C. indecora* Choisy var. *integriuscula* (Engelm.) Yuncker.

Cuscuta denticulata Engelm., Amer. Naturalist 9: 348. 1875. HOLOTYPE: St. George, Utah, *C. C. Parry 205.*

Cuscuta epithymum Murr. var. *angustata* Engelm. subvar. *angustissima* Engelm., Trans. Acad. Sci. St. Louis 1: 463. 1859. HOLOTYPE: Padua, Italy, *s.d., Visiani s.n.* = *C. epithymum* Murr. var. *angustissima* Engelm.

Cuscuta epithymum Murr. var. *kotschyi* Engelm. subvar. *scabrella* Engelm., Trans. Acad. Sci. St. Louis 1: 464. 1859. LECTOTYPE: Sicily, *s.d., Gussone s.n.* = *C. epithymum* Murr. var. *scabrella* (Engelm.) Yuncker.

Cuscuta epithymum Murr. var. *obtusata* Engelm. subvar. *apoda* Engelm., Trans. Acad. Sci. St. Louis 1: 462. 1859. HOLOTYPE: Koniah, Asia Minor, 1845, *Heldreich s.n.* = *C. obtusata* (Engelm.) Traub.

Cuscuta epithymum Murr. var. *obtusata* Engelm., subvar. *macropoda* Engelm., Trans. Acad. Sci. St. Louis 1: 462. 1859. HOLOTYPE: Sierra Nevada, Spain, *s.d., Funk s.n.* = *C. triumvirati* Lange.

Cuscuta epithymum Murr. var. *sagittanthera* Engelm., Trans. Acad. Sci. St. Louis 1: 462. 1859. HOLOTYPE: Tunis, *s.d., Kralik s.n.*

Cuscuta exaltata Engelm., Trans. Acad. Sci. St. Louis 1: 513. 1859. LECTOTYPE: New Braunfels, Texas, *s.d., F. Lindheimer 472* (3 sheets).

Cuscuta globiflora Engelm., Trans. Acad. Sci. St. Louis 1: 520. 1859. ISOTYPE: Cuzo, Brazil, *s.d., Pentland s.n.*

Cuscuta gracillima Engelm., Trans. Acad. Sci. St. Louis 1: 488. 1859. ISOLECTOTYPE: Mexico, *s.d., Mornay s.n.*

Cuscuta gracillima Engelm. var. *saccharata* Engelm., Trans. Acad. Sci. St. Louis 1: 489. 1859. ISOLECTOTYPE: Oaxaca, Mexico, *s.d.*, *Liebman s.n.* = *C. saccharata* (Engelm.) Yuncker.

Cuscuta gronovii Willd. var. *calyptrata* Engelm., Trans. Acad. Sci. St. Louis 1: 508. 1859. LECTOTYPE: western Louisiana, *s.d.*, *J. Gregg s.n.*

Cuscuta gronovii Willd. var. *curta* Engelm., Trans. Acad. Sci. St. Louis 1: 508. 1859. ISOLECTOTYPE: northwest America, *s.d.*, *Douglas s.n.* = *C. curta* (Engelm.) Rydb.

Cuscuta japonica Choisy var. *fissistyla* Engelm., Trans. Acad. Sci. St. Louis 1: 517. 1859. HOLOTYPE: Hong Kong, China, *s.d.*, *Wright 486.*

Cuscuta japonica Choisy var. *paniculata* Engelm., Trans. Acad. Sci. St. Louis 1: 517. 1859. LECTOTYPE: Pekin (sic), China, *s.d.*, *Kirilow s.n.*

Cuscuta japonica Choisy var. *thyrsoidea* Engelm., Trans. Acad. Sci. St. Louis 1: 517. 1859. ISOTYPE: Japan, *s.d.*, *Zollinger 355.*

Cuscuta kurdica Engelm., Trans. Acad. Sci. St. Louis 1: 470. 1859. HOLOTYPE?: Gara Mts., Kurdistan, *Kotschy 388b.*

Cuscuta lehmanniana Bunge var. *esquamata* Engelm., Trans. Acad. Sci. St. Louis 1: 515. 1859. HOLOTYPE: Mont Sipyle, Persia, *s.d.*, *Balansa 411.*

Cuscuta leptantha Engelm., Trans. Acad. Sci. St. Louis 1: 489. 1859. LECTOTYPE: western Texas to El Paso, Texas, 1849, *C. Wright 522.*

Cuscuta lupuliformis Krock var. *asiatica* Engelm., Trans. Acad. Sci. St. Louis 1: 516. 1859. LECTOTYPE: Volga River, Russia, *s.d.*, *Fischer s.n.*

Cuscuta micrantha Choisy var. *latiflora* Engelm., Trans. Acad. Sci. St. Louis 1: 501. 1859. LECTOTYPE: Concon, Chile, *s.d.*, *Poeppig 89.* Syntype: 1827, *Poeppig 159.*

Cuscuta mitraeformis Engelm. in Hemsley, Diag. Pl. Nov. 54. 1880. HOLOTYPE: San Luis Potosí to Tampico, Mexico, 1878–1879, *E. Palmer s.n.*

Cuscuta neuropetala Engelm., Amer. J. Sci. 45: 75. 1843. LECTOTYPE: near Houston, Texas, 1843, *F. Lindheimer 124.* = *C. indecora* Choisy var. *neuropetala* (Engelm.) Hitchcock.

Cuscuta obtusiflora H.B.K. var. *australis* Engelm., Trans. Acad. Sci. St. Louis 1: 492. 1859. LECTOTYPE: New Holland, Australia, *s.d.*, *R. Brown s.n.* = *C. australis* R. Br.

Cuscuta obtusiflora H.B.K. var. *cesatiana* Engelm., Trans. Acad. Sci. St. Louis 1: 493. 1859. LECTOTYPE: Vercelli, Italy, *s.d.*, *Cesati 83?.* = *C. australis* R. Br. var. *cesatiana* (Bertoloni) Yuncker.

Cuscuta obtusiflora H.B.K. var. *cordofana* Engelm., Trans. Acad. Sci. St. Louis 1: 493. 1859. HOLOTYPE: Kordofan, Africa, 1844, *Figari s.n.* = *C. cordofana* (Engelm.) Yuncker.

Cuscuta obtusiflora H.B.K. var. *glandulosa* Engelm., Trans. Acad. Sci. St. Louis 1: 492. 1859. LECTOTYPE: Columbus, Georgia, 1838, *Boykin s.n.*

Cuscuta obtusiflora H.B.K. var. *vera* Engelm., Trans. Acad. Sci. St. Louis 1: 493. 1859. LECTOTYPE: Andes, Peru, *s.d.*, *Humboldt s.n.* = *C. obtusiflora* H.B.K.

Cuscuta odontolepis Engelm., Trans. Acad. Sci. St. Louis 1: 486. 1859. HOLOTYPE: Arizona, 1851–1852, C. Wright 1642.

Cuscuta parviflora Engelm., Trans. Acad. Sci. St. Louis 1: 506. 1859. LECTOTYPE: Minas Geraes, Brazil, *s.d.*, *Ackerman s.n.* Syntype: Villa Rica, Brazil, *s.d.*, *Pohl 5726.*

Cuscuta parviflora Engelm. var. *elongata* Engelm., Trans. Acad. Sci. St. Louis 1: 506. 1859. HOLOTYPE: Goyaz, Brazil, *s.d.*, *Weddell 2125.*

Cuscuta pentagona Engelm., Amer. J. Sci. 43: 340. 1842. HOLOTYPE: Norfolk, Virginia, 1841, *Rugel s.n.*

Cuscuta pentagona Engelm. var. *calycina* Engelm., Amer. J. Sci. 45: 76. 1845. SYNTYPE: Texas, *F. Lindheimer 126.* = *C. campestris* Yuncker.

Cuscuta planiflora Tenore var. *tenorii* Engelm., Trans. Acad. Sci. St. Louis 1: 466. 1859. LECTOTYPE: Naples, Italy, *s.d.*, *Tenore s.n.* = *C. planiflora* Tenore.

Cuscuta planiflora Tenore var. *papillosa* Engelm., Trans. Acad. Sci. St. Louis 1: 467. 1859. LECTOTYPE: Djebel Zaghouan, Tunis, 1854, *Kralik 410a.*

Cuscuta polygonorum Engelm., Amer. J. Sci. 43: 342. LECTOTYPE: west of St. Louis, Missouri, *s.d.*, *G. Engelmann s.n.* Syntype: west of St. Louis, Missouri, *F. Lindheimer s.n.*

Cuscuta racemosa Mart. var. *brasiliana* Engelm., Trans. Acad. Sci. St. Louis 1: 505. 1859. SYNTYPE: Rio de Janeiro, Brazil, 1817, *Martius s.n.*

Cuscuta racemosa Mart. var. *miniata* Engelm., Trans. Acad. Sci. St. Louis 1: 505. 1859. SYNTYPE: Brazil, 1857, *Martius 1292.*

Cuscuta racemosa Mart. var. *nuda* Engelm., Trans.

Acad. Sci. St. Louis 1: 505. 1859. SYNTYPE: near Rio, Brazil, *s.d.*, *Sellow s.n.*

Cuscuta reflexa Roxb. var. *brachystigma* Engelm., Trans. Acad. Sci. St. Louis 1: 519. 1859. LECTOTYPE: Calcutta, India, *s.d.*, *Gaudichaud 129.* = *C. reflexa* Wallich var. *anguina* (Edgeworth) Yuncker.

Cuscuta saururi Engelm., Amer. J. Sci. 43: 339. 1842. LECTOTYPE: St. Louis, Missouri, 1841, *C. A. Geyer s.n.* = *C. gronovii* Willd. var. *saururi* (Engelm.) MacMillan.

Cuscuta squamata Engelm., Trans. Acad. Sci. St. Louis 1: 510. 1859. LECTOTYPE: western Texas to El Paso, Texas, 1849, *C. Wright 518.*

Cuscuta stenolepis Engelm., Trans. Acad. Sci. St. Louis 1: 500. 1859. HOLOTYPE: Mare Island, San Francisco, California, 1855, *C. Wright s.n.*

Cuscuta trichostyla Engelm., Trans. Acad. Sci. St. Louis 1: 495. 1859. ISOTYPE: Parana, *s.d.*, *Tweedie s.n.* Syntype: Santatem, Brazil, *s.d.*, Spruce 854.

Cuscuta umbellata H.B.K. var. *desertorum* Engelm., Trans. Acad. Sci. St. Louis 1: 488. 1859. LECTOTYPE: Piauhy Province, Brazil, 1847, *Martius s.n.*

Cuscuta verrucosa Engelm. var. *glabrior* Engelm., Amer. J. Sci. 43: 341. 1842. LECTOTYPE: west of Houston, Texas, *s.d.*, *F. Lindheimer s.n.* Syntype: Texas, 1833, *Drummond 247.* = *C. glabrior* (Engelm.) Yuncker.

Lepidanche compositarum Engelm., Amer. J. Sci. 43: 344. 1842. LECTOTYPE: American Bottom, St. Louis, Missouri, 1841, *G. Engelmann s.n.*

CUPRESSACEAE

Juniperus occidentalis Hook. var. *monosperma* Engelm., Trans. Acad. Sci. St. Louis 3: 590. 1877. SYNTYPES: Cañon City & Manitou, Colorado, 1874, *G. Engelmann s.n.* (5 sheets).

CYPERACEAE

Cyperus refractus Engelm. in Boeckl., Linnaea 36: 369. 1870. HOLOTYPE: Merimac, *s.d.*, *N. Riel Herbarium 496.*

EPHEDRACEAE

Ephedra aspera Engelm. ex Watson, Proc. Amer. Acad. Arts 18: 157. 1883. TYPE MATERIAL: Sierra Madre, west of Saltillo, Mexico, 1880, *E. Palmer 1288.*

Ephedra pedunculata Engelm. ex Watson, Proc. Amer. Acad. Arts 18: 157. 1883. TYPE MATERIAL: Nvalde, west of San Antonio, Texas, 1880, *E. Palmer 1291.*

EQUISETACEAE

Equisetum laevigatum A. Braun var. *elatum* Engelm. in A. Braun, Amer. J. Sci. 46: 87. 1843. TYPE MATERIAL: banks of Mississippi, below Jefferson Barracks, St. Louis, Missouri, 1843, *G. Engelmann s.n.* (7 sheets).

Equisetum laevigatum A. Braun var. *scabrellum* Engelm. in A. Braun, Amer. J. Sci. 46: 87. 1843. LECTOTYPE: Jefferson Barracks, St. Louis, Missouri, 1843, *G. Engelmann s.n.*

Equisetum robustum A. Braun var. *affine* Engelm. in A. Braun, Amer. J. Sci. 46: 88. 1843. LECTOTYPE: below Jefferson Barracks, St. Louis, Missouri, 1843, *G. Engelmann s.n.* = *E. hyemale* L. var. *affine* (Engelm.) A. A. Eaton.

Equisetum robustum A. Braun var. *minus* Engelm. in A. Braun, Amer. J. Sci. 46: 88. 1843. LECTOTYPE: banks of Mississippi, below St. Louis, Missouri, 1843, *G. Engelmann s.n.* = *E. hyemale* L. var. *affine* (Engelm.) A. A. Eaton.

EUPHORBIACEAE

Aphora humilis Engelm. & Gray, Boston J. Nat. Hist. 5: 54. 1845. ISOTYPE: west of Brazos, Texas, 1844, *F. Lindheimer 306.* = *Argythamnia humilis* (Engelm. & Gray) Muell.-Arg.

Croton corymbulosus Engelm. in Rothr., Bot. Wheeler's Surv. 242. 1878. SYNTYPES: Camp Bowie, New Mexico, 1874, *J. T. Rothrock 506*; Buena Vista, Mexico, 1848, *J. Gregg 71 & 288*; west Texas, 1849, *C. Wright 641*, and 1851–1852, *C. Wright 1805.* = *C. pottsii* (Klotzsch) Muell.-Arg.

Croton fruticulosus Engelm. in Torr., Bot. Mex. Bound. Surv. 194. 1859. SYNTYPES: Texas, 1849, *F. Lindheimer 134* (2 sheets), *176, 177, 297a.* Published as *C. fruticulosum.*

Euphorbia acuta Engelm. in Torr., Bot. Mex. Bound. Surv. 189. 1859. LECTOTYPE: "N. Mex.," 1851, *C. Wright 1839.*

Euphorbia angusta Engelm. in Torr., Bot. Mex. Bound. Surv. 189. 1859. LECTOTYPE: San Pedro River, Texas, 1851, *C. Wright 1828.*

Euphorbia arizonica Engelm. in Torr., Bot. Mex. Bound. Surv. 186. 1859. LECTOTYPE: Arizona, 1856, *A. Schott s.n.*

Euphorbia arkansas Engelm. & Gray, Boston J. Nat. Hist. 5: 261. 1845. SYNTYPES: near

Houston, Texas, 1843 and 1845, *F. Lindheimer s.n.* (2 sheets).

Euphorbia astyla Engelm. ex Boiss. in DC., Prod. 15(2): 40. 1862. HOLOTYPE: Nazas River, Mexico, 1847, *J. Gregg 457. = Chamaesyce albomarginata* (Torr. & Gray) Small.

Euphorbia barbellata Engelm. in Torr., Bot. Mex. Bound. Surv. 190. 1859. LECTOTYPE: Rio Grande, 1848, *C. Wright s.n.*

Euphorbia baueri Engelm. ex Boiss. in DC., Prod. 15(2): 27. 1862. TYPE MATERIAL: "Nov. Holland," *s.d., Bauer s.n.*

Euphorbia bicolor var. *bicolor* Engelm. & Gray, Boston J. Nat. Hist. 5: 233. 1845. SYNTYPE: west of Houston, Texas, 1841, *F. Lindheimer 174.*

Euphorbia bicolor Engelm. & Gray var. *concolor* Engelm. & Gray, Boston J. Nat. Hist. 5: 233. 1845. TYPE MATERIAL: Lynchburg, Texas, 1842, *F. Lindheimer s.n.*

Euphorbia bifurcata Engelm. in Torr., Bot. Mex. Bound. Surv. 190. 1859. HOLOTYPE OR ISOTYPE: valley of the Limpio, 1852, *J. M. Bigelow s.n.*

Euphorbia bilobata Engelm. in Torr., Bot. Mex. Bound. Surv. 190. 1859. LECTOTYPE: Santa Cruz, Sonora, Mexico, 1851–1852, *C. Wright 1831.*

Euphorbia blodgettii Engelm. ex Hitchcock, Annual Rep. Missouri Bot. Gard. 4: 126. 1893. LECTOTYPE: Key West, Florida, *s.d., Blodgett s.n. = Chamaesye blodgettii* (Engelm. ex Hitchcock) Small.

Euphorbia brachycera Engelm. in Torr., Bot. Mex. Bound. Surv. 192. 1859. HOLOTYPE: Donana, above El Paso, Texas, 1851, *C. Wright 1821.*

Euphorbia capitellata Engelm. in Torr., Bot. Mex. Bound. Surv. 188. 1859. HOLOTYPE: San Bernardino, Arizona, 1851, *C. Wright 1849.*

Euphorbia cinerascens Engelm. in Torr., Bot. Mex. Bound. Surv. 186. 1859. LECTOTYPE: Monterrey, Mexico, 1847, *J. Gregg 215.* Syntype: western Texas to El Paso, 1849. *C. Wright 559.*

Euphorbia cinerascens Engelm. var. *appendiculata* Engelm. in Torr., Bot. Mex. Bound. Surv. 186. 1859. LECTOTYPE: San Felipe, California, 1852, *G. Thurber 628. = E. melanadenia* Torr.

Euphorbia commutata Engelm. in Gray, Man. Bot. 2: 389. 1856. TYPE MATERIAL: "Gasconade," May 1835, number 35, illegible but "commutata" added to label by Engelm.

Euphorbia crenulata Engelm. in Torr., Bot. Mex. Bound. Surv. 192. 1859. TYPE MATERIAL: no locale, *s.d., Hartweg 1950.*

Euphorbia curtisii Engelm. in Chapman, Fl. S. U.S. 401. 1860. LECTOTYPE: North Carolina, *s.d., Curtiss s.n.*

Euphorbia deltoidea Engelm. in Chapman, Fl. S. U.S. 2nd edition. 647. 1883. LECTOTYPE: Florida, 1880, *Curtiss 162.*

Euphorbia dentata Michx. var. *cuphosperma* Engelm. in Torr., Bot. Mex. Bound. Surv. 190. 1859. LECTOTYPE: Copper Mines, New Mexico, 1851–1852, *C. Wright 1834.*

Euphorbia dentata Michx. var. *rigida* Engelm. in Torr., Bot. Mex. Bound. Surv. 190. 1859. LECTOTYPE: San Pedro River, New Mexico, 1851–1852, *C. Wright 1837.*

Euphorbia dictyosperma Fisch. & Mey. var. *leiococca* Engelm. in Torr., Bot. Mex. Bound. Surv. 191. 1859. LECTOTYPE: Texas, 1835, *Drummond 327.*

Euphorbia dictyosperma Fisch. & Mey. var. *mexicana* Engelm. in Torr., Bot. Mex. Bound. Surv. 191. 1859. LECTOTYPE: Balson de Mapimi, 1847, *J. Gregg 456. = E. mexicana* (Norton) Engelm.

Euphorbia dioeca H.B.K. var. *indivisa* Engelm. in Torr., Bot. Mex. Bound. Surv. 187. 1859. ISOTYPE: near the Copper Mines, New Mexico, 1851, *C. Wright 1845. = E. indivisa* (Engelm.) Tidstrom.

Euphorbia exstipulata Engelm. in Torr., Bot. Mex. Bound. Surv. 189. 1859. LECTOTYPE: Santa Fe, New Mexico, 1847, *A. Fendler 790.* Syntypes: eastern Sonora, *C. Wright 1833 & 1838.*

Euphorbia floribunda Engelm. ex Boiss. in DC., Prod. 15(2): 39. 1862. LECTOTYPE: east of Guadalahara, Mexico, 1849, *J. Gregg 856a.*

Euphorbia florida Engelm. in Torr., Bot. Mex. Bound. Surv. 189. 1859. LECTOTYPE: west of Chiricahua Mountains, Arizona, 1851, *C. Wright 1829.*

Euphorbia fruticulosa Englem. ex Boiss. in DC., Proc. 15(2): 38. 1862. ISOTYPE: Coahuila, Mexico, *s.d., J. Gregg 506.*

Euphorbia garberi Engelm. ex Chapman, Fl. S. U.S. 2nd edition. 646. 1883. LECTOTYPE: coast of Florida, *s.d., Garber s.n.*

Euphorbia geyeri Engelm. in Engelm. & Gray, Boston J. Nat. Hist. 5: 260. 1845. LECTOTYPE: Beardstown, Illinois, 1842, *C. A. Geyer s.n.*

Euphorbia glyptosperma Engelm. in Torr., Bot. Mex. Bound. Surv. 187. 1859. LECTOTYPE: Fort Kearney, Nebraska, 1856, *H. Engelmann s.n.*

Euphorbia glyptosperma Engelm. var. *tenerrima* Engelm. in Torr., Bot. Mex. Bound. Surv. 187. 1859. LECTOTYPE: Nueces River, Texas, 1851, *C. Wright 1853.* = *E. glyptosperma* Engelm.

Euphorbia grisea Engelm. ex Boiss. in DC., Prod. 15(2): 41. 1862. LECTOTYPE: Cerralro, Nuevo Leon, Mexico, 1847, *J. Gregg 837.*

Euphorbia hirtula Engelm. in Watson, Bot. Calif. 2: 74. 1880. LECTOTYPE: southern California, 1880, *E. Palmer 140.*

Euphorbia humistrata Engelm. ex Gray, Man. Bot. 2: 386. 1856. LECTOTYPE: St. Louis, Missouri, 1833, *G. Engelmann 1139.*

Euphorbia lata Engelm. in Torr., Bot. Mex. Bound. Surv. 189. 1859. LECTOTYPE: western Texas, 1851, *C. Wright 1841.* Syntype: the Cimarron to Sand Creek 1847, *A. Fendler s.n.*

Euphorbia leptocera Engelm. ex Torr., Pacif. Rail. Rep. 4: 135. 1857. TYPE MATERIAL: Grass Valley, California, *s.d., J. M. Bigelow s.n.*

Euphorbia lurida Engelm. in Ives, Rep. Colo. River Bot. 4: 26. 1861. LECTOTYPE: Bill Williams Mt., Arizona, 1858, *Newberry s.n.*

Euphorbia marginata Pursh var. *uloleuca* Engelm. & Gray, Boston J. Nat. Hist 5: 261. 1845. LECTOTYPE: prairies in the Colorado bottom, 1844, *F. Lindheimer 303.*

Euphorbia montana Engelm. var. *gracilor* Engelm. in Torr., Bot. Mex. Bound. Surv. 192. 1859. LECTOTYPE: Santa Fe Creek, New Mexico, 1847, *A. Fendler 786.*

Euphorbia multicaulis Engelm. in Torr., Bot. Mex. Bound. Surv. 191. 1859. HOLOTYPE: Las Playas, Sonora, 1851, *G. Thurber 381.*

Euphorbia palmeri Engelm. in Watson, Bot. Calif. 2: 75. 1880. LECTOTYPE: at Tally's, California, 1875, *E. Palmer s.n.*

Euphorbia parryi Engelm., Amer. Naturalist 9: 350. 1875. LECTOTYPE: St. George, Utah, 1874, *C. C. Parry 247.*

Euphorbia pediculifera Engelm. in Torr., Bot. Mex. Bound. Surv. 186. 1859. LECTOTYPE: Sonoita Creek, Arizona, 1851, *C. Wright 1848.*

Euphorbia peplidion Engelm. in Torr., Bot. Mex. Bound. Surv. 191. 1859. HOLOTYPE: San Pedro, Texas, 1851, *C. Wright 1823.*

Euphorbia petaloidea Engelm. in Torr., Bot. Mex. Bound. Surv. 185. 1859. LECTOTYPE: Platte River, Nebraska Territory, 1858, *H. Engelmann s.n.* = *E. missurica* Raf. var. *intermedia* (Engelm.) L. C. Wheeler.

Euphorbia petaloidea Engelm. var. *flagelliformis* Engelm. in Torr., Bot. Mex. Bound. Surv. 185. 1859. HOLOTYPE: near Frontera, Texas, 1851, *C. Wright 1826.* = *E. parryi* Engelm.

Euphorbia petaloidea Engelm. var. *intermedia* Engelm. in Torr., Bot. Mex. Bound. Surv. 185. 1859. LECTOTYPE: Ft. Pierre, South Dakota, 1853, *F. V. Hayden s.n.* = *E. missurica* Raf. var. *intermedia* (Engelm.) L. C. Wheeler.

Euphorbia petaloidea Engelm. var. *nicollettii* Engelm. in Torr., Bot. Mex. Bound. Surv. 185. 1859. LECTOTYPE: Powder River, Montana, 1854. *F. V. Hayden s.n.* = *E. missurica* Raf. var. *intermedia* (Engelm.) L. C. Wheeler.

Euphorbia pilulifera L. var. *discolor* Engelm. in Torr., Bot. Mex. Bound. Surv. 188. 1859. LECTOTYPE: Sonoita Creek, Arizona, 1842, *C. Wright s.n.* = *E. hirta* L.

Euphorbia platysperma Engelm. in Watson, Bot. Calif. 2: 482. 1880. LECTOTYPE: mouth of Colorado River, 1869, *E. Palmer s.n.*

Euphorbia pringlei Engelm. in Patterson, Check list 115. 1887. LECTOTYPE: Canyon of Santa Rita, Arizona, 1881. *C. G. Pringle 138.*

Euphorbia pycnanthema Engelm. in Torr., Bot. Mex. Bound. Surv. 188. 1859. HOLOTYPE: Lake Santa Maria, Chihuahua, Mexico, 1852, *C. Wright 186.* = *E. capitellata* Engelm.

Euphorbia revoluta Engelm. in Torr., Bot. Mex. Bound. Surv. 186. 1859. LECTOTYPE: between Santa Fe and Moro River, New Mexico, 1847, *A. Fendler 789.*

Euphorbia schizoloba Engelm. in Ives, Rep. Colorado River Bot. 4: 27. 1861. HOLOTYPE: western Arizona, 1858, *Newberry s.n.*

Euphorbia serrula Engelm. in Torr., Bot. Mex. Bound. Surv. 188. 1859. LECTOTYPE: Guadalupe Pass, Sonora, Mexico, 1851, *C. Wright 1843.*

Euphorbia setiloba Engelm. in Torr., Pacif. Rail. Rep. 5: 364. 1857. ISOTYPE: Fort Yuma, California, *G. H. Thomas s.n.*

Euphorbia stictospora Engelm. in Torr., Bot. Mex. Bound. Surv. 187. 1859. LECTOTYPE: Pawnee River, Kansas, 1847, *A. Fendler 798.*

Euphorbia subpubens Engelm. in Watson, Bot. Calif. 2: 76. 1880. ISOTYPE & FRAGMENT OF HOLOTYPE FROM GH: Prescott, Arizona, 1876, *E. Palmer 512.*

Euphorbia tetrapora Engelm. in Torr., Bot. Mex. Bound. Surv. 191. 1859. SYNTYPE: west of Brazos, Texas, 1839, *F. Lindheimer s.n.*

Euphorbia tomentella Engelm. ex Boiss. in DC., Prod. 15(2): 32. 1862. LECTOTYPE: San Luis Potosi, Mexico, 1827, *Berlandier 1358.*

Euphorbia trachysperma Engelm. in Torr., Bot. Mex. Bound. Surv. 189. 1859. HOLOTYPE: San Pedro River, Arizona, 1851, *C. Wright 1832.*

Euphorbia umbellata Engelm. ex Boiss. in DC., Prod. 15(2): 127. 1862. LECTOTYPE: Guadalahara, Mexico, 1849, *J. Gregg 856.*

Euphorbia villifera Scheele var. *nuda* Engelm. ex Boiss. in DC., Prod. 15(2): 45. 1862. LECTOTYPE: New Braunfels, Texas, 1850, *C. Wright s.n.*

Euphorbia xantii Engelm. ex Boiss. in DC., Prod. 15(2): 62. 1862. LECTOTYPE: Cape St. Lucas, California, 1859–1860, *L. T. Xantus s.n.*

Jatropha macrorhiza Benth. var. *septemfida* Engelm. in Rothr., Bot. Wheeler's Surv. 244. 1878. SYNTYPE: Sulphur Springs, Arizona, 1874, *J. T. Rothrock 546.*

Pilinophytum lindheimeri Engelm. & Gray, Boston J. Nat. Hist. 5: 232. 1845. SYNTYPE: Texas, 1843, *F. Lindheimer 171.*

Stillingia angustifolia Engelm. ex Watson, Proc. Amer. Acad. Arts 18: 154. 1883. HOLOTYPE: Comfort, Texas, 1879, *E. Palmer 1256.* = *S. texana* I. M. Johnston.

Tetracoccus dioicus Engelm. ex Parry, West Am. Sci. 1: 13. 1885. PARATYPE: Table Mountain, Northern Lower California, 1883, *C. C. Parry & H. C. Orcutt 313.*

Tragia brevispica Engelm. & Gray, Boston J. Nat. Hist. 5: 226. 1845. SYNTYPE: Texas, 1848, *F. Lindheimer 307.*

FABACEAE

Amorpha canescens Nutt. var. *leptostachya* Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 31. 1849. HOLOTYPE?: in woods between San Miguel and Vegas, 1847, *A. Fendler 125.*

Amorpha incana Engelm., apparently not published. HOLOTYPE?: Texas, 1842, *F. Lindheimer 153,* annotated "n. sp." by Engelm.

Astragalus lindheimeri Engelm. in Gray, Pl. Wrightiana 1: 52. 1852. LECTOTYPE: Texas, *s.d., F. Lindheimer 746.*

Baptisia sulphurea Engelm. Bot. Gaz. 3: 65. 1878. HOLOTYPE: Oklahoma, 1877, *Butler s.n.* (2 sheets). = *B. lactea* (Raf.) Thieret × *B. sphaerocarpa* Nutt.

Calliandra chamaedrys Engelm. ex Gray, Mem. Amer. Acad. Arts. II. 4: 39. 1849. SYNTYPES: Chihuahua, Mexico, 1847, *J. Gregg 529, A. Wislizenus 251.*

Calliandra herbacea Engelm. ex Gray, Mem. Amer. Acad. Arts. II. 4: 39. 1849. LECTOTYPE: New Mexico, *s.d., A. Fendler 180.*

Cercis reniformis Engelm. ex Gray, Boston J. Nat. Hist. 6: 177. 1850. LECTOTYPE: Guadalupe, Texas, 1845, *F. Lindheimer 366.* = *C. occidentalis* Torr.

Desmodium wislizenii Engelm. ex Gray, Pl. Wrightiana 1: 53. 1852. HOLOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus 183.* = *D. retinens* Schlecht.

Eysenhardtia spinosa Engelm. ex Gray, Boston J. Nat. Hist. 6: 174. 1850. ISOTYPE: Chihuahua, Mexico, 1846, *A. Wislizenus 133.*

Lespedeza leptostachya Engelm. in Gray, Proc. Amer. Acad. Arts 12: 57. 1877. LECTOTYPE: Iowa, 1871, *C. E. Bessey s.n.*

FAGACEAE

Quercus chrysolepis Liebm. var. *palmeri* Engelm., Trans. Acad. Sci. St. Louis 3: 393. 1877. HOLOTYPE: 80 mi. E of San Diego, California, 1875, *E. Palmer 30.* = *Q. palmeri* Engelm.

Quercus dumosa Nutt. var. *bullata* Engelm., Trans. Acad. Sci. St. Louis 3: 393. 1877. SYNTYPES: Santa Lucia Mts., California, *s.d., Brewer 473*; New Idria, California, *s.d., Brewer 776*; Pope Valley, California, 1863, *H. Bolander s.n.* = *Q. durata* Jeps.

Quercus falcata Michx. var. *subintegra* Engelm., Trans. Acad. Sci. St. Louis 3: 543. 1877. LECTOTYPE: South Carolina, 1875, *Mellichamp s.n.* = *Q. subintegra* Trel.

Quercus hypoleuca Engelm., Trans. Acad. Sci. St. Louis 3: 384. 1876. LECTOTYPE: Copper Mines, and Arizona, 1851–1852, *C. Wright 1869.*

Quercus lobata Nee var. *fruticosa* Engelm., Trans. Acad. Sci. St. Louis 3: 389. 1877. SYNTYPES: west of Shasta, California, 1862, *H. Brewer 1336*; near Tuolumne River, California, *Lemmon s.n.* = *Q. oerstediana* R. Br.

Quercus muehlenbergii Engelm., Trans. Acad. Sci. St. Louis 3: 391. 1877. TYPE MATERIAL: St. Louis, Missouri, Sept. 1838, *G. Engelmann s.n.* Annotated *Q. muhlenbergii* by Engelmann, but no annotation date. The only prepublication dated specimen.

Quercus tomentella Engelm., Trans. Acad. Sci. St. Louis 3: 393. 1877. HOLOTYPE: Guadalupe Island, California, *E. Palmer 89.*

Quercus undulata Torr. var. *jamesii* Engelm., Trans. Acad. Sci. St.Louis 3: 382. 1876. TYPE MATERIAL: fragment of "original species ex Hb Torrey," Rocky Mountains, *s.d., James s.n.*

FOUQUIERIACEAE

Fouquieria splendens Engelm. in Wisliz., Mem. Tour. No. Mex. 98. 1848. LECTOTYPE: south of Chihuahua, Mexico, 1847, *A. Wislizenus 261.*

FUMARIACEAE

Corydalis curvisiliqua Engelm. ex Gray., Pl. Wrightiana 2: 10. 1853. TYPE MATERIAL: Texas, Apr. 1848, *F. Lindheimer s.n.*; May 1851, *F. Lindheimer s.n.*

GENTIANACEAE

Erythraea nudicaulis Engelm. in Gray, Proc. Amer. Acad. Arts. 17: 222. 1882. HOLOTYPE: base of Santa Catalina Mountains, Arizona, *C. G. Pringle s.n.*

Geniostemon coulteri Engelm. & Gray, Proc. Amer. Acad. Arts 16: 104. 1881. TYPE MATERIAL: Mexico, *s.d.*, *Coulter, s.n.*, appears to be fragment of holotype from Gray's herbarium.

Geniostemon schafferi Engelm. & Gray, Proc. Amer. Acad. Arts 16: 104. 1881. TYPE MATERIAL: San Luis Potosí, Mexico, 1879, *Schaffer 80.*

Gentiana acuta Michx. var. *nana* Engelm., Trans. Acad. Sci. St. Louis 2: 214. 1862. HOLOTYPE: Colorado Territory, 1861, *C. C. Parry 309.* = *Gentianella amarella* (L.) Borner subsp. *acuta* (Michx.) J. M. Gillett.

Gentiana barbellata Engelm., Trans. Acad. Sci. St. Louis 2: 216. 1862. HOLOTYPE: Snowy Range, Colorado, 1862, *C. C. Parry s.n.* = *Gentianella barbellata* (Engelm.) J. M. Gillett.

Gentiana heterosepala Engelm., Trans. Acad. Sci. St. Louis 2: 215. 1862. HOLOTYPE: Uintah Mts., Utah, 1859, *H. Engelmann s.n.* = *Gentianella amarella* (L.) Borner.

Gentiana oregana Engelm. in Gray, Syn. Fl. N. Am. II. 1: 122. 1884. LECTOTYPE: Blue Mts., Oregon, 1874, *R. D. Nevius s.n.*

Gentiana parryi Engelm., Trans. Acad. Sci. St. Louis 2: 218. 1863. LECTOTYPE: Colorado Territory, 1861, *C. C. Parry 304.* Syntype: "Rocky Mountain Flora," 1862, *E. Hall & J. P. Harbour 470.*

Gentiana prostrata Haenke var. *americana* Engelm., Trans. Acad. Sci. St. Louis 2: 217. 1863. SYNTYPES: Rocky Mountains, 1862, *E. Hall & J. P. Harbour 475*; Snowy Range, *s.d.*, *C. C. Parry 306.*

Gentiana wislizenii Engelm., Trans. Acad. Sci. St. Louis 2: 215. 1863. HOLOTYPE: Llanos, Chihuahua, Mexico, 1846, *A. Wislizenus 206.* = *Gentianella wislizenii* (Engelm.) J. M. Gillett.

GERANIACEAE

Geranium fremontii Torr. ex Gray var. *parryi* Engelm. in Gray, Amer. J. Sci. II. 33: 405. 1862. LECTOTYPE: Clear Creek, Colorado, 1861, *C. C. Parry 113?*

Geranium gracile Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 27. 1849. HOLOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus 173* (2 sheets). = *G. atropurpureum* Heller.

Geranium pentagynum Engelm. in Wisliz., Mem. Tour. No. Mex. 90. 1848. HOLOTYPE: Wolf Creek, New Mexico, 1846, *A. Wislizenus 508* (2 sheets). = *G. richardsonii* Fisch. & Trautv.

HYDROPHYLLACEAE

Eutoca patuliflora Engelm. & Gray. Boston J. Nat. Hist. 5: 253. 1845. ISOTYPE: Texas, *s.d.*, *F. Lindheimer 280.* = *Phacelia patuliflora* (Engelm. & Gray) Gray.

Eutoca strictiflora Engelm. & Gray, Boston J. Nat. Hist. 5: 253. 1845. ISOTYPE: Texas, *s.d.*, *F. Lindheimer 279* (2 sheets). = *Phacelia strictiflora* (Engelm. & Gray) Gray.

ISOETACEAE

Isoetes bolanderi Engelm., Amer. Naturalist 8: 214. 1874. LECTOTYPE: Tuolumne River, California, 1866, *H. Bolander 5091.* Syntypes: Mary's Lake, California, 1870, *H. Bolander 5080*; Mono Trail, California, 1870, *H. Bolander 5093.*

Isoetes butleri Engelm. var. *immaculata* Engelm., Trans. Acad. Sci. St. Louis 4: 388. 1882. HOLOTYPE: near Nashville, Tennessee, 1880, *A. Gattinger 3812.* = *I. butleri* Engelm.

Isoetes cubana Engelm., Trans. Acad. Sci. St. Louis 4: 389.1882. HOLOTYPE: eastern Cuba, 1860, *C. Wright s.n.*

Isoetes echinospora Durieu var. *robusta* Engelm., Trans. Acad. Sci. St. Louis 4: 380. 1882. HOLOTYPE: Lake Champlain, New York?, 1879, *C. G. Pringle s.n.*

Isoetes engelmannii A. Braun var. *georgiana* Engelm., Trans. Acad. Sci. St. Louis 4: 385. 1882. HOLOTYPE: Georgia, 1873, *A. W. Chapman s.n.* = *I. engelmannii* A. Braun.

Isoetes flaccida Shuttlew. ex A. Braun var. *chap-*

manii Engelm., Trans. Acad. Sci. St. Louis 4: 386. 1882. HOLOTYPE: near Mariana, Florida, 1850, *Chapman s.n.* = *I. flaccida* Shuttlew.

Isoetes flaccida Shuttlew. ex A. Braun var. *rigida* Engelm., Trans. Acad. Sci. St. Louis 4: 386. 1882. HOLOTYPE: Lake Flint, Florida, 1878, *A. Garber s.n.* = *I. flaccida* Shuttlew.

Isoetes howellii Engelm., Trans. Acad. Sci. St. Louis 4: 385. 1882. HOLOTYPE: The Dalles, Oregon, *J. & T. J. Howell 1880.*

Isoetes lacustris L. var. *paupercula* Engelm., Trans. Acad. Sci. St. Louis 4: 377. 1882. LECTOTYPE: Middle Park, Colorado, 1881, *G. Engelmann s.n.* = *I. occidentalis* Hend.

Isoetes melanospora Engelm., Trans. Acad. Sci. St. Louis 3: 395. 1877.HOLOTYPE: Stone Mt., Georgia, 1869, *Canby s.n.* (2 sheets).

Isoetes nuda Engelm., Trans. Acad. Sci. St. Louis 4: 385. 1882. HOLOTYPE: The Dalles, Oregon, 1882, *T. Howell 26.* = *I. howellii* Engelm.

Isoetes pygmaea Engelm., Amer. Naturalist 8: 214. 1874. HOLOTYPE: Mono Pass, California, 1866, *H. Bolander 6025* (2 sheets). = *I. bolanderi* Engelm. var. *pygmaea* (Engelm.) Clute.

Isoetes riparia Engelm. in A. Braun, Flora (Regensb. Bot. Zeit.) 29: 178. 1846. HOLOTYPE: Philadelphia, Pennsylvania, 1844, *Zantziger s.n.*

Isoetes riparia Engelm. var. *canadensis* Engelm., Trans. Acad. Sci. St. Louis 4: 383. 1884. TYPE MATERIAL: Crow River, Canada, *s.d.*, *J. Macoun s.n.*

Isoetes saccharata Engelm. in Gray, Man. Bot. 5: 676. 1868. HOLOTYPE?: Salisbury, Maryland, 1866, *Canby s.n.*

JUGLANDACEAE

Juglans rupestris Engelm. in Torr., Bot. Sitgr. Rep. 171. 1853. TYPE MATERIAL: Texas, 1849, *F. Lindheimer 20 (1178)*.

JUNCACEAE

Juncus asper Engelm., Trans. Acad. Sci. St. Louis 2: 478. 1868. SYNTYPES: Quaker Bridge, New Jersey, 1864, 1865, 1866, *Smith s.n.*, 1866, 1867; *C. F. Parker s.n.* (2 sheets).

Juncus balticus Willd. var. *littoralis* Engelm., Trans. Acad. Sci. St. Louis 2: 442. LECTOTYPE & ISOLECTOTYPE: Ipswich, 1842, *Oakes s.n.* = *J. arcticus* Willd. subsp. *littoralis* Engelm.

Juncus balticus Willd. var. *montanus* Engelm., Trans. Acad. Sci. St. Louis 2: 442. LECTOTYPE & ISOLECTOTYPE: Rocky Mountains, 1862, *E. Hall & Harbour 567.* = *J. arcticus* Willd. subsp. *ater* (Rydb.) Hult.

Juncus bolanderi Engelm., Trans. Acad. Sci. St. Louis 2: 470. 1868. HOLOTYPE: Mission Dolore, California, 1865, *H. Bolander s.n.*

Juncus brachycarpus Engelm., Trans. Acad. Sci. St. Louis 2: 467. 1868. SYNTYPES: Charleston, South Carolina, *Beyrich s.n.*; Louisiana, no date, *J. Hale s.n.*; Detroit, Michigan, July 1867, *J. M. Bigelow s.n.*; Michigan, no date, *Folwell s.n.*

Juncus breweri Engelm., Trans. Acad. Sci. St. Louis 2: 440. 1866. HOLOTYPE: Monterey, California, May 1866, *W. H. Brewer 651.* Isotype: Monterey, California, May 1861, *W. H. Brewer 651.* = *J. arcticus* Willd. subsp. *mexicanus* (Willd.) Lint × subsp. *pacificus* (Engelm.) Lint.

Juncus canaliculatus Engelm., Bot. Gaz. 7: 6. 1882. HOLOTYPE: San Bernardino, California, 1881, *S. B. & W. F. Parish 1091.* = *J. macrophyllus* Coville.

Juncus chlorocephalus Engelm., Trans. Acad. Sci. St. Louis 2: 485. 1868. SYNTYPES: Sierras, California, 1866, *Hillebrand 2338* (2 sheets); *W. H. Brewer 1804* (2 sheets); *H. Bolander Cal. St. Surv. 6033.*

Juncus drummondii E. Mey. var. *humilus* Engelm., Trans. Acad. Sci. St. Louis 2: 445. 1868. HOLOTYPE: Mt. Shasta, California, 1862, *Brewer 1383.*

Juncus dubius Engelm., Trans. Acad. Sci. St. Louis 2: 459. 1868. SYNTYPE: Mariposa, California, *s.d.*, *H. Bolander Cal. St. Surv. 6032.*

Juncus hallii Engelm., Trans. Acad. Sci. St. Louis 2: 446. 1868. HOLOTYPE: Lake Ranch, Colorado, 1862, *E. Hall & J. P. Harbour 562.*

Juncus kelloggii Engelm., Trans. Acad. Sci. St. Louis 2: 494. 1868. HOLOTYPE: San Francisco, California, 1866, *A. Kellogg s.n.*

Juncus mertensianus Bong. var. *paniculatus* Engelm., Trans. Acad. Sci. St. Louis 2: 480. 1868. ISOTYPE: Rocky Mts., 1858, *Bourgeau s.n.*

Juncus obtusatus Engelm., Trans. Acad. Sci. St. Louis 2: 495. 1868. HOLOTYPE: Big Tree Grove, Mariposa, California, 1866, *H. Bolander Cal. St. Surv. 6028.*

Juncus oxymeris Engelm., Trans. Acad. Sci. St. Louis 2: 483. 1868. SYNTYPES: Big Tree Grove, Mariposa, California, 1866, *H. Bolander 95* (4 sheets).

Juncus parryi Engelm., Trans. Acad. Sci. St. Louis 2: 446. 1866. HOLOTYPE: Colorado, 1861, *C. C. Parry 360.*

Juncus phaeocephalus Engelm. var. *glomeratus*

Engelm., Trans. Acad. Sci. St. Louis 2: 484. 1868. SYNTYPES: San Francisco, California, 1866, *A. Kellogg 96* (6 sheets).

Juncus phaeocephalus Engelm. var. *gracilis* Engelm., Trans. Acad. Sci. St. Louis 2: 473. 1868. SYNTYPES: Sierra Nevadas, California, 1865, *H. Bolander Cal. St. Surv. 2339* (2 sheets), *H. Bolander 98* (6 sheets); 1865, *Brewer 1709.* = *J. mertensianus* Bong.

Juncus phaeocephalus Engelm. var. *paniculatus* Engelm., Trans. Acad. Sci. St. Louis 2: 484. 1868. SYNTYPES: Napa Valley, California, *s.d.*, *J. M. Bigelow s.n.*; San Francisco, California, *A. Kellogg 97* (4 sheets).

Juncus rugulosis Engelm. in Coult., Bot. Gaz. 6: 224: 1881. HOLOTYPE: San Bernardino Mountains, California, 9 Nov. 1880, *W. G. Wright s.n.*

Juncus smithii Engelm., Trans. Acad. Sci. St. Louis 2: 444. 1868. HOLOTYPE: Broad Mt., Pottsville, Pennsylvania, 1865, *C. E. Smith s.n.*

Juncus supiniformis Engelm., Trans. Acad. Sci. St. Louis 2: 461. 1868. HOLOTYPE: Mendocino, California, 1866, *H. Bolander Cal. St. Surv. 4767.*

Juncus triformis Engelm., Trans. Acad. Sci. St. Louis 2: 492. 1868. LECTOTYPE: De Long's Ranch, Yosemite Valley, California, 1866, *H. Bolander 30.*

Juncus triformis Engelm. var. *brachystylus* Engelm., Trans. Acad. Sci. St. Louis 2: 492. 1868. ISOLECTOTYPE: Ukiah, California, 1866, *H. Bolander 31* (3 sheets) & *Cal. St. Surv. 8457.* Syntype: Ukiah, California, 1866, *H. Bolander s.n.*

Juncus triformis Engelm. var. *stylosus* Engelm., Trans. Acad. Sci. St. Louis 2: 492. 1868. ISOLECTOTYPE: Yosemite Valley, California, 1866, *H. Bolander 30.* = *J. triformis* Engelm.

Juncus triformis Engelm. var. *uniflorus* Engelm., Trans. Acad. Sci. St. Louis 2: 493. 1868. SYNTYPES: Sierra Nevada, California, 1866, *Hillebrand Cal. St. Surv. 2333*; Long Valley, California, 1866, *H. Bolander 32 (Cal. St. Surv. 4691)* (2 sheets). = *J. hemiendytus* F. J. Herman.

Juncus vaseyi Engelm., Trans. Acad. Sci. St. Louis 2: 448. 1868. SYNTYPES: Saskatchewan, Canada, 1852 and 1858, *E. Bourgeau s.n.*; Colorado, 1862, *E. Hall s.n.*

LAMIACEAE

Brazoria scutellarioides Engelm. & Gray, Boston J. Nat. Hist. 5: 257. 1845. PARATYPES: on paths and slopes of the prairie, in heavy soil, Texas, *F. Lindheimer 286, 287.*

Monarda lindheimeri Engelm. & Gray, Boston J. Nat. Hist. 5: 228. 1845. SYNTYPE: Houston, Texas, 1843, *F. Lindheimer 151* (2 sheets).

Scutellaria cardiophylla Engelm. & Gray, Boston J. Nat. Hist. 5: 227. 1845. ISOTYPES: Texas, 1843, *F. Lindheimer 144* (2 sheets).

LINACEAE

Linum aristatum Engelm. in Wisliz., Mem. Tour. No. Mex. 101. 1848. HOLOTYPE: near Carizal, south of El Paso, Mexico, 1846, *A. Wislizenus 101.*

Linum greggii Engelm. ex Gray, Pl. Wrightiana 26. 1852. HOLOTYPE: San Antonio near Saltillo, Mexico, 31 Aug. 1848, *J. Gregg s.n.*

Linum rigidum Pursh var. *puberulum* Engelm. ex Gray, Pl. Wrightiana 25. 1852. ISOTYPE: New Mexico, 1847, *A. Fendler 85.* = *L. puberulum* (Engelm.) Heller.

Linum rupestre Engelm. in Gray, Boston J. Nat. Hist. 6: 232. 1850. ISOTYPE: New Braunfels, Texas, 1846, *F. Lindheimer 337.*

Linum rupestre Engelm. var. *cymulosum* Engelm. in Gray, Pl. Wrightiana 26. 1852. HOLOTYPE: battlefield of Buena Vista, Mexico, 1848, *J. Gregg s.n.*

LOASACEAE

Mentzelia chrysantha Engelm. ex Brandegee, Fl. S. W. Col. 237. 1878. HOLOTYPE: Cañon City, Colorado, 1874. *G. Engelmann s.n.*

LORANTHACEAE

Arceuthobium abietinum Engelm. in Gray, Proc. Amer. Acad. Arts 8: 401. 1872. TYPE MATERIAL: Oregon, 1871, *E. Hall 457 & 458* (2 sheets each); California, 1875, *J. Muir 7654.*

Arceuthobium campylopodium Engelm. in Gray, Boston J. Nat. Hist. 6: 214. 1845. ISOTYPE: Oregon, label says Rocky Mountains, ex herb Hooker, 1843, *C. A. Geyer 577* (2 sheets).

Arceuthobium campylopodium Engelm. var. *macrarthron* Engelm. in Gray, Boston J. Nat. Hist. 6: 214. 1845. SYNTYPES: Santa Fe, New Mexico, *A. Fendler 282* (2 sheets); California, 1848, *Douglas s.n.*; 1848, *C. A. Geyer s.n.*

Arceuthobium cryptopodum Engelm., in Gray, Boston J. Nat. Hist. 6: 214. 1850. HOLOTYPE: Santa Fe, New Mexico, 1847, *A. Fendler 283.* = *A. vaginata* (Willd.) Presl. subsp.

cryptopodum (Engelm.) Hawksworth & Wiens.

Arceuthobium divaricatum Engelm. in Rothr., Bot. Wheeler's Surv. 253. 1878. LECTOTYPE: Salt River Valley, Arizona, 1873, *Gilbert 116.* Syntype: Camp Apache, Arizona, 1874, *J. B. Girard s.n.*

Arceuthobium douglasii Engelm. in Rothr., Bot. Wheeler's Surv. 253. 1878. LECTOTYPE: Santa Fe River, New Mexico, 1874, *J. T. Rothrock 69.* Syntype: Camp Apache, Arizona, 1873, *G. K. Gilbert 109.*

Arceuthobium douglasii Engelm. var. *abietinum* Engelm. in Watson, Bot. Calif. 2: 106. 1880. LECTOTYPE: Sierra Valley, California, 1875, *Lemmon s.n.*. = *A. abietinum* Engelm.

Arceuthobium occidentale Engelm. in Rothr., Bot. Wheeler's Surv. 375. 1878. LECTOTYPE: Walker's Basin, California, 1875, *J. T. Rothrock 429.*

Arceuthobium robustum Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 59. 1849. SYNTYPE: Camp Apache, Arizona, 1873, *G. Gilbert 108.* = *A. vaginatum* (Weins) Presl. subsp. *cryptopodum* (Engelm.) Hawksworth & Weins.

Arceuthobium verticilliflorum Engelm. in Watson, Bot. Calif. 2: 107. 1880. HOLOTYPE: Sierra Madre, Durango, Mexico, 1852, *Seeman 2138* (2 sheets).

Phoradendron flavescens Nutt. var. *macrophyllum* Engelm. in Rothr., Bot. Wheeler's Surv. 252. 1878. SYNTYPES: Gila River, Arizona, 1873, *Gilbert 104*; Camp Grant, 1874, *J. T. Rothrock 362.*

Phoradendron juniperinum Engelm. ex Gray, Mem. Amer. Acad. Arts. II. 4: 58. 1849. HOLOTYPE: Santa Fe, New Mexico, 1847, *A. Fendler 281.*

Phoradendron lanceolatum Engelm. ex Gray, Mem. Amer. Acad. Arts. II. 4: 59. 1849. HOLOTYPE: Rinconada, Mexico, 1847, *J. Gregg 255.*

Phoradendron orbiculatum Engelm. in Gray, Mem. Amer. Acad. Arts. II. 4: 59. 1849. LECTOTYPE: Little Rock, Arkansas, 1837, *G. Engelmann 707.* Syntype: same data but *G. Engelmann s.n.* = *P. flavescens* Nutt. var. *orbiculatum* Engelm.

LYTHRACEAE

Lythrum ovalifolium Engelm. ex Gray, Boston J. Nat. Hist. 6: 187. 1850. SYNTYPE: Pierdenales, Texas, 1845, *F. Lindheimer 450.*

MALVACEAE

Sida heterocarpa Engelm. ex Gray, Boston J. Nat. Hist. 6: 163. 1850. TYPE MATERIAL: Industry, Texas, 1844, *F. Lindheimer 189.* = *S. spinosa* L.

MARSILEACEAE

Marsilea macropoda Engelm. in A. Braun, Amer. J. Sci. II. 3: 56. 1847. HOLOTYPE: Matagorda Bay, Texas, 1845, *F. Lindheimer s.n.*

Marsilea tenuifolia Engelm. in A. Braun, Amer. J. Sci. II. 6: 89. 1848. HOLOTYPE: Guadalupe River, Texas, 1837, *F. Lindheimer s.n.*

MARTYNIACEAE

Martynia arenaria Engelm. in Wisliz., Mem. Tour. No. Mex. 100. 1848. HOLOTYPE: sandhills below El Paso, 1846, *A. Wislizenus 92.* = *Proboscidea altheaefolia* (Benth.) Dcne.

Martynia violacea Engelm. in Wisliz., Mem. Tour. No. Mex. 111. 1848. SYNTYPE: Lake Encinilla, north of Chihuahua, Mexico, 1846, *A. Wislizenus 145.* = *Proboscidea louisianica* (Mill.) Thell subsp. *fragrans* (Lindl.) Bretting.

NYMPHAEACEAE

Nuphar polysepalum Engelm. var. *pictum* Engelm., Trans. Acad. Sci. St. Louis 2: 282. 1866. LECTOTYPE: Colorado Territory, 1864, *C. C. Parry s.n.*

OLEACEAE

Menodora scoparia Engelm. ex Gray, Bot. Calif. 1: 471. 1876. SYNTYPES: Saltillo, Mexico, 1848, *J. Gregg 498 & 527.*

ONAGRACEAE

Gaura lindheimeri Engelm. & Gray, Boston J. Nat. History 5: 217. 1845. TYPE MATERIAL: prairie near Houston, Texas, 1843, *F. Lindheimer s.n.*

Gaura suffulta Engelm. in Gray, Boston J. Nat. Hist. 6: 190. 1850. ISOTYPE: New Braunfels, Texas, 1847, *F. Lindheimer 611* (4 sheets).

PAPAVERACEAE

Corydalis aurea Willd. var. *micrantha* Engelm. in Gray, Man. Bot. 5: 62. 1868. TYPE MATERIAL: "459" no additional collection information but label has complete description probably used in publication. = *C. micrantha* (Engelm.) Gray.

Corydalis crystallina Engelm. in Gray, Man. Bot. 5: 62. 1868. TYPE MATERIAL: Washington City, Arkansas, 1835, no collector.

Corydalis montana Engelm. in Gray, Man. Bot. 5: 62. 1868. TYPE MATERIAL: Santa Fe, New Mexico, 1847, *A. Fendler 17*. = *C. aurea* Willd.

Dicentra ochroleuca Engelm. in Coult., Bot. Gaz. 6: 233. 1881. HOLOTYPE: Santa Monica, California, 1880, *G. Engelmann s.n.* (2 sheets).

PASSIFLORACEAE

Passiflora affinis Engelm. ex Gray, Boston J. Nat. Hist. 6: 233. 1850. SYNTYPE: Texas, 1849, *F. Lindheimer 817*.

Passiflora tenuiloba Engelm. in Gray, Boston J. Nat. Hist. 6: 192. 1850. SYNTYPE: on the Liano, 1848 and 1849, *F. Lindheimer s.n.* (2 sheets).

PINACEAE

Abies grandis Lindl. var. *densiflora* Engelm., Trans. Acad. Sci. St. Louis 3: 599. 1878. TYPE MATERIAL: Mt. Hood, Oregon, 1871, *E. Hall s.n.*; British North America, 1862, *D. Lyall s.n.*; British Columbia, Canada, *s.d.*, *D. Lyall s.n.* = *A. amabilis* (Dougl.) Forbes.

Picea pungens Engelm., Gard. Chron. 11: 334. 1879. TYPE MATERIAL: upper Arkansas, Colorado, 1878, *M. E. Jones 364*; Lake County, Colorado, 1876, *G. Vasey s.n.* Both specimens prepublication date and annotated by Engelmann.

Pinus aristata Engelm., Trans. Acad. Sci. St. Louis 2: 205. 1863. TYPE MATERIAL: Rocky Mountains, 1862, *C. C. Parry s.n.*; Rocky Mountains, *s.d.*, *C. C. Parry s.n.* (2 sheets); the latter two specimens probably used for illustrations in publication.

Pinus arizonica Engelm. in Rothr., Bot. Wheeler's Surv. 260. 1878. HOLOTYPE: Santa Rita Mts., Arizona, 1874, *J. T. Rothrock 652*.

Pinus brachyptera Engelm. in Rothr., Bot. Wheeler's Surv. 89. 1878. LECTOTYPE: Rock Creek to Santa Fe, 1846, *A. Wislizenus 534* (2 sheets). = *P. ponderosa* Dougl. ex P. & C. Lawson.

Pinus chihuahuana Engelm. in Rothr., Bot. Wheeler's Surv. 103. 1878. HOLOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus 232* (2 sheets).

Pinus edulis Engelm. in Rothr., Bot. Wheeler's Surv. 88. 1878. SYNTYPES: Cimarron to Santa Fe, 1846, *A. Wislizenus s.n.* & *535* (2 sheets); New Mexico, 1846, *J. Gregg s.n.*

Pinus elliottii Engelm., Trans. Acad. Sci. St. Louis 4: 186. 1880. SYNTYPES: South Carolina, 1871 (2 sheets), 1872, 1873, *Mellichamp s.n.* = *P. cubensis* Griseb.

Pinus flexilis James var. *macrocarpa* Engelm. in Rothr., Bot. Wheeler's Surv. 258. 1878. HOLOTYPE: San Francisco Mts., Arizona, 1871, *F. Bishoff s.n.*

Pinus flexilis James var. *reflexa* Engelm. in Rothr., Bot. Wheeler's Surv. 258. 1878. SYNTYPES: southern Arizona, *s.d.*, *J. T. Rothrock 654* & *1001*.

Pinus flexilis James var. *serrulata* Engelm. in Rothr., Bot. Wheeler's Surv. 258. 1878. HOLOTYPE: Mt. Graham, Arizona, 1874, *J. T. Rothrock 783*.

Pinus greggii Engelm. ex Parl. in DC., Prod. 16(2): 396. 1868. HOLOTYPE: Saltillo, Mexico, 1848, *J. Gregg 402*.

Pinus latisquama Engelm., Gard. Chron. 18: 712. 1882. HOLOTYPE: south of Saltillo, Mexico, 1880, *E. Palmer 1299*. = *P. pinaceana* Gord.

Pinus macrophylla Engelm. in Wisliz., Mem. Tour. No. Mex. 103. 1848. HOLOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus 233* (2 sheets & 1 cone box). = *P. engelmannii* Carr.

Pinus osteosperma Engelm. in Wisliz., Mem. Tour. No. Mex. 89. 1848. LECTOTYPE: Buena Vista, Mexico, 1847, *J. Gregg 321* (2 sheets). = *P. cembroides* Zucc.

Pinus parryana Engelm., Amer. J. Sci. II. 34: 332.1862. HOLOTYPE: southeast of San Diego, California, in Mexico, 1850, *C. C. Parry s.n.* (2 sheets). = *P. quadrifolia* Parry.

Pinus strobiformis Engelm. in Wisliz., Mem. Tour. No. Mex. 102. 1848. LECTOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus 231* (2 sheets & 1 cone box). Syntype: Cosihuiriachi, Mexico, 1846, *A. Wislizenus 155*. = *P. ayacahuite* Ehrenb. ex Schlecht.

Pinus wrightii Engelm., Trans. Acad. Sci. St. Louis 4: 185. 1880. SYNTYPES: eastern Cuba, 1860–1864, *C. Wright 3190* & *1462b* (1 sheet & 1 cone box); 1859, *C. Wright 1462 (a?)*.

Tsuga caroliniana Engelm. in Coult., Bot. Gaz. 6: 223. 1881. SYNTYPES: South Carolina, 1851, *L. R. Gibbs s.n.*, *A. H. Curtiss s.n.*; North Carolina, 1841, *A. Gray & Carey s.n.*

PLANTAGINACEAE

Plantago pusilla Nutt. var. *major* Engelm., Bot. Gaz. 8: 175. 1883. HOLOTYPE: Indian Territory, 1874, *G. D. Butler s.n.* = *P. elongata* Pursh.

POACEAE

Aristida basiramea Engelm. ex Vasey, Coult. Bot. Gaz. 9: 76. 1884. SYNTYPE: Minneapolis, Minnesota, 1883, *W. Upham s.n.*

Aristida ramosissima Engelm. ex Gray, Man. Bot. 5: 618. 1868. TYPE MATERIAL: east of Belleville, Illinois, Aug. 1845, *G. Engelmann s.n.*; St. Clair County, Illinois, Aug. 1858, *G. Engelmann s.n.*; southern Illinois, 1861, *G. Engelmann s.n.*

Monanthochloe littoralis Engelm., Trans. Acad. Sci. St. Louis 1: 436. 1859. SYNTYPES: Mantamoras, *s.d.*, *Berlandier 3227* (2 sheets); Texas, 1841, 1842, 1843, *F. Lindheimer s.n.* (5 sheets).

Spartina junciformis Engelm. & Gray, Boston J. Nat. Hist. 5: 238. 1845. SYNTYPE: Galveston, Texas, 1843, *F. Lindheimer 207* (3 sheets).

POLYGONACEAE

Eriogonum alpinum Engelm., Bot. Gaz. 7: 6. 1882. HOLOTYPE: Scotts Mt., California, 1880, *G. Engelmann s.n.*

Eriogonum atrorubens Engelm. in Wisliz., Mem. Tour. No. Mex. 108. 1848. HOLOTYPE & ISOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus 172* (2 sheets).

Polygonum cristatum Engelm. & Gray, Boston J. Nat. Hist. 5: 259. 1845. HOLOTYPE: Texas, 1844, *F. Lindheimer 237 (exsiccatae no. 296)*, "n. sp." added by Engelm.

PORTULACACEAE

Lewisia brachycalyx Engelm. ex Gray, Proc. Amer. Acad. Arts 7: 400. 1868. SYNTYPES: Fort Whipple, Arizona, 1865, *E. Coues & E. Palmer 211* (2 sheets); Utah, 1859, *Brewer s.n.*

Portulaca lanceolata Engelm. in Gray, Boston J. Nat. Hist. 6: 154. 1850. SYNTYPE: Liano, Texas, 1848, *F. Lindheimer s.n.* = *P. umbraticola* H.B.K.

Portulaca retusa Engelm., Boston J. Nat. Hist. 6: 154. 1850. HOLOTYPE: "ex sem. texanis cult. St. Louis," from Llano in western Texas, Aug. 1849, *G. Engelmann s.n.*

Portulaca suffrutescens Engelm., Bot. Gaz. 6: 236. 1881. SYNTYPES: Copper Mines, 1851, *C. Wright 874*; Fort Whipple, Arizona, 1865, *E. Coues & E. Palmer 547*; Santa Rita Mts., Arizona, 1880, *G. Engelmann s.n.*

Talinum aurantiacum Engelm. in Gray, Boston J. Nat. Hist. 6: 153. 1850. SYNTYPES: on the Llano, Texas, 1848, *F. Lindheimer 579*; on the Sabinas, Texas, 1847, *F. Lindheimer s.n.*

Talinum calycium Engelm. in Wisliz., Mem. Tour. No. Mex. 88. 1848. HOLOTYPE: on the Cimarron, 1846, *A. Wislizenus 475* (2 sheets); one is annotated "n. sp." by Engelm.

Talinum sarmentosum Engelm. in Gray, Boston J. Nat. Hist. 6: 153. 1850. SYNTYPE: Texas, 1847, *F. Lindheimer 580.*

Talinum spathulatum Engelm. in Gray, Pl. Wrightiana 14. 1852. LECTOTYPE: western Texas to El Paso, Texas, 1849, *C. Wright 35.* = *T. paniculatum* (Jacq.) Gaertn.

POTAMOGETONACEAE

Potamogeton diversifolius Raf. var. *spicatus* Engelm., Amer. J. Sci. 46: 102. 1843. HOLOTYPE: Cosihuiriachi, Mexico, 1846–1847, *A. Wislizenus 159.*

RANUNCULACEAE

Ranunculus texensis Engelm. in Engelm. & Gray, Boston J. Nat. Hist. 5: 210. 1845. SYNTYPE: near Houston, Texas, 1843, *F. Lindheimer 1.* = *R. oblongifolius* Ell.

Ranunculus trachyspermus Engelm. in Engelm. & Gray, Boston J. Nat. Hist. 5: 211. 1845. SYNTYPE: Texas, 1843, *F. Lindheimer 2.* = *R. pusillus* Poir. var. *angustifolius* (Engelm.) L. Benson.

Ranunculus trachyspermus Engelm. var. *angustifolius* Engelm. in Engelm. & Gray, Boston J. Nat. Hist. 5: 211. 1845. SYNTYPE: Galveston Island, Texas, 1843, *F. Lindheimer 3.* = *R. pusillus* Poir. var. *angustifolius* (Engelm.) L. Benson.

Ranunculus trachyspermus Engelm. var. *lindheimeri* Engelm. in Engelm. & Gray, Boston J. Nat. Hist. 5: 211. 1845. SYNTYPE: Galveston, Texas, 1843, *F. Lindheimer s.n.*

Thalictrum fendleri Engelm. ex Gray, Mem. Amer. Acad. Arts. II. 4: 5. 1849. ISOTYPE: Santa Fe, New Mexico, 1847, *A. Fendler 13* (2 sheets).

ROSACEAE

Greggia rupestris Engelm. in Wisliz., Mem. Tour. No. Mex. 114. 1848. SYNTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus 228* (2 sheets); Saltillo, Mexico, *A. Wislizenus s.n.*; Buena Vista, Mexico, 1847, *A. Wislizenus 324*. = *Cowania mexicana* D. Don.

Prunus gracilis Engelm. & Gray, Boston J. Nat. Hist. 5: 243. 1845. ISOTYPES: west of the Brazos, Texas, March, 1844, *F. Lindheimer 237*; "Post Oak Plum . . . ," Texas, March, 1844, *F. Lindheimer s.n.*

Prunus minutiflora Engelm. in Gray, Boston J. Nat. Hist. 6: 185. 1850. LECTOTYPE: between San Antonio and New Braunfels, Texas, *s.d.*, *F. Lindheimer 388*.

Rosa minutifolia Engelm., Bull. Torrey Bot. Club 9: 97. 1882. HOLOTYPE: All Saint's Bay, California, 1882, *C. C. Parry & M. E. Jones s.n.*

Rosa spithamea A. Gray var. *subinermis* Engelm., Bot. Gaz. 6: 236. 1881. HOLOTYPE: Big Trees, Sierra Nevada, California, 1880, *G. Engelmann s.n.*

RUBIACEAE

Bouvardia glaberrima Engelm. in Wisliz., Mem. Tour. No. Mex. 107. 1848. LECTOTYPE: Cosihuiriachi, Mexico, 1846, *A. Wislizenus 161* (2 sheets).

SAXIFRAGACEAE

Fendlera rupicola A. Gray var. *lindheimeri* Engelm. & Gray in Gray, Pl. Wrightiana 1: 77. 1852. HOLOTYPE?: Texas, 1850, *F. Lindheimer 792* (2 sheets).

Heuchera sanguinea Engelm. in Wisliz., Mem. Tour. No. Mex. 107. 1848. HOLOTYPE: Llanos, 1846, *A. Wislizenus 210* (2 sheets).

Saxifraga debilis Engelm. ex Gray, Proc. Amer. Acad. Arts 15: 62. 1863. HOLOTYPE OR ISOTYPE: Colorado, 1861, *C. C. Parry 167*.

SCROPHULARIACEAE

Castilleja indivisia Engelm. in Engelm. & Gray, Boston J. Nat. Hist. 5: 47. 1845. SYNTYPE: from Houston to the Colorado, 1844 & 1846, *F. Lindheimer 284* (3 sheets).

Maurandya wislizenii Engelm. ex Gray in Torr., Bot. Mex. Bound. Surv. 111. 1859. LECTOTYPE: near Val Verde, New Mexico, 1846, *A. Wislizenus 45*.

Penstemon coccineus Engelm. in Wisliz., Mem. Tour. No. Mex. 107. 1848. HOLOTYPE: Llanos, 1846, *A. Wislizenus 207*. = *P. wislizenii* (Gray) Straw.

SPARGANIACEAE

Sparganium eurycarpum Engelm. in Gray, Man. Bot. 5: 481. 1868. TYPE MATERIAL: American Bottom, 13 Aug. 1860, *G. Engelmann s.n.* No specimens cited but collected prior to publication date.

Sparganium simplex Huds. var. *androcladum* Engelm. in Gray, Man. Bot. 5: 481. 1868. LECTOTYPE: near Boston, 1856, *G. Engelmann s.n.* Syntypes: American Bottom, near St. Louis, Missouri, 1860, *G. Engelmann s.n.*; St. Clair County, 1854, *G. Engelmann s.n.*; St. Louis, Missouri, *s.d.*, *G. Engelmann s.n.*, annotated "n. sp." by Engelm. = *S. androcladum* (Engelm.) Morong.

STYRACACEAE

Styrax platanifolia Engelm. ex Torr., Smithsonian Contrib. Knowl. 6: 4. 1854. SYNTYPE: Texas, 1851, *F. Lindheimer s.n.*

VALERIANACEAE

Fedia stenocarpa Engelm. ex Gray, Boston J. Nat. Hist. 6: 216. 1850. TYPE MATERIAL: New Braunfels, Texas, 1848, *F. Lindheimer 407*. = *Valerianella stenocarpa* (Engelm. ex Gray) Krok.

VITACEAE

Vitis arizonica Engelm., Amer. Naturalist 2: 321. 1869. SYNTYPES: Santa Cruz, Sonora, Mexico, *C. Wright 919*; New Mexico, *s.d.*, *C. Wright s.n.*; Sonora, Mexico, 1851, *G. Thurber 703*; Rio Verde, Arizona, 1865, *E. Coues & C. C. Parry 551 & 553*; southern Arizona, 1866, *C. C. Parry s.n.* = *V. monticola* Buckley subsp. *arizonica* (Engelm.) Rogers.

Vitis candicans Engelm. in Gray, Boston J. Nat. Hist. 6: 166. 1850. SYNTYPE: Texas, 1844, *F. Lindheimer s.n.*

ZYGOPHYLLACEAE

Guaiacum angustifolium Engelm. in Wisliz., Mem. Tour. No. Mex. 113. 1848. LECTOTYPE: about Parras and Saltillo, Mexico, 1847, *A. Wislizenus 293*. = *Porlieria angustifolia* A. Gray.

Larrea glutinosa Engelm. in Wisliz., Mem. Tour. No. Mex. 93. 1848. HOLOTYPE: Saltillo, Mexico, 1846, *J. Gregg 10*, annotated "n. sp." by Engelm. Syntype: Saltillo, Mexico, 1847, *J. Gregg 369*.

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SYNOPSIS OF *DICHANTHELIUM* (POACEAE) IN FLORIDA[1]

Bruce F. Hansen and Richard P. Wunderlin[2]

ABSTRACT

Twenty-five taxa of Dichanthelium *are recognized for Florida, with synonymy and typification compiled. Keys to species and varieties and an index to names is provided. The new combinations* D. ensifolium *var.* breve, D. ensifolium *var.* unciphyllum, *and* D. portoricense *are proposed.*

Recent papers concerning *Dichanthelium* that have dealt with either the southeastern United States (Gould & Clark, 1978; Lelong, 1984, 1986) or with only a small part of the genus (Freckmann, 1981a) have been very influential in redefining the limits of the taxa. The present paper expands on the treatment of the Florida species in Wunderlin (1982) and Clewell (1985) in order to modernize the concepts and to rectify some errors. At the same time, it is an attempt to classify the Florida specimens better, recognizing that the taxa accepted here might well be inadequately separable in other geographic areas, which seems the rule for this genus. However, we feel that practicality alone would mandate such a classification for this very difficult genus to facilitate assignment of names to specimens. In *Dichanthelium,* reticulate evolution caused by hybridization and autogamy is extremely common (Spellenberg, 1975a, b; Lelong, 1984, 1986). Thus, no claim is made here that a "natural" classification has been constructed.

The merits of accepting the segregate genus *Dichanthelium* versus the inclusive *Panicum* will not be argued here except to point out that *Dichanthelium* is as "good" a grass genus as many others (e.g., *Brachiaria, Sacciolepis,* and many more in different tribes). We will not detail here which authors accept one or the other genus; those that wish to use *Panicum* will not be swayed by our arguments. Gould & Clark (1978) provided 24 characteristics separating *Dichanthelium* from *Panicum*; none of these alone separates the genera, but the total we believe defines *Dichanthelium* as a natural segregate from the large and variable *Panicum.* It is our belief that the acceptance of *Dichanthelium* provides a more consistent generic classification of the grasses of Florida.

The species and varietal concepts used are roughly those of Gould & Clark (1978) as modified by Lelong (1984, 1986). Because the synonymy is so extensive and in many cases confusing, all known synonyms are compiled and included in the hope that future workers will find it easier to follow the nomenclature. The types are listed where known, but it must be emphasized that little original research in typification is involved here; the citation of types is mostly from published material, principally Hitchcock & Chase (1910), Gould & Clark (1978), and Lelong (1984). It seems inevitable that several new combinations are necessary, this in a group already overburdened with surplus names.

The key fairly reflects the variation in *Dichanthelium* species, such that many taxa will key out in two or more places. When a character falls between an overlapping lead, either choice should lead to the correct species.

KEY TO THE FLORIDA SPECIES OF *DICHANTHELIUM*

1a. Leaves at base of plant numerous, relatively long and soft, similar to and only slightly shorter, if at all, than the soft, yellowish green lower culm blades; plants branching only at base; blades mostly 4–10 mm wide.

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ANN. MISSOURI BOT. GARD. 75: 1637–1657. 1988.

2a. Sheaths retrorsely pilose; uppermost culm blade at least ¾ as long as those of basal tuft .... *D. laxiflorum*
2b. Sheaths glabrous or ascending pilose; uppermost culm blade less than ¾ as long as those of basal tuft .... *D. strigosum*
1b. Leaves at base of plant typically forming a basal rosette of short, relatively broad blades, these usually conspicuously shorter than the culm blades; plants normally branching above the base, especially in the autumnal phase; blades 3–25 mm wide or wider.
3a. Spikelets 0.8–3.2 mm long.
4a. Spikelets 0.8–2 mm long.
5a. Ligule hairs, at least some, 2–5 mm long .... *D. acuminatum*
5b. Ligule hairs under 1.5 mm long or absent.
6a. Lower culm internodes (and usually sheaths) pubescent, puberulent, strigose, or villous.
7a. Blades of midculm leaves mostly 2–5 mm wide; plants usually at least 10 cm tall .... *D. aciculare*
7b. Blades of midculm leaves less than 2 mm wide; plants less than 10 cm tall .... *D. ensifolium* (var. *breve*)
6b. Lower culm internodes (and usually sheaths) glabrous.
8a. Blades of midculm leaves (vernal phase) 5–15 cm long, mostly 2–5 mm wide .... *D. aciculare*
8b. Blades of midculm leaves less than 6 cm long, or if longer, then wider than 6 mm.
9a. Bases of lower culm leaves cordate or subcordate; blades 7–30 mm wide.
10a. Spikelets 1–1.1 mm long .... *D. erectifolium*
10b. Spikelets 1.4–2.2 mm long .... *D. sphaerocarpon*
9b. Bases of lower culm leaves other than cordate or subcordate; blades usually less than 7 mm wide.
11a. Spikelets 1.6–2.5 mm long; plants usually diffuse .... *D. dichotomum*
11b. Spikelets 0.8–1.5 mm long; plants usually cushion-forming .... *D. ensifolium*
4b. Spikelets 2.1–3.2 mm long.
12a. Blades of primary culms, at least some, (10–)13–25 mm wide.
13a. Culm nodes conspicuously bearded, the lower internodes with long, spreading hairs .... *D. scoparium*
13b. Culm nodes glabrous or slightly hairy, the internodes typically glabrous.
14a. Ligule a fringed or entire membrane.
15a. Plants less than 75 cm tall; leaf bases cordate .... *D. commutatum*
15b. Plants mostly more than 75 cm tall; leaf bases rounded .... *D. scabriusculum*
14b. Ligule a ring of hairs or absent.
16a. Spikelets 1.4–2.2 mm long, broadly elliptic to suborbicular .... *D. sphaerocarpon*
16b. Spikelets 2.4–3.5 mm long, narrowly ovate or elliptic .... *D. clandestinum*
12b. Blades of primary culms up to 12 mm wide.
17a. Leaf bases cordate or subcordate.
18a. Spikelets 1.4–2.2 mm long, broadly elliptic to ovate .... *D. sphaerocarpon*
18b. Spikelets 2.4–3.2 mm long, elliptic to narrowly ovate .... *D. commutatum*
17b. Leaf bases other than cordate or subcordate.
19a. Ligule hairs, at least some, 2–5 mm long.
20a. Nerves of the upper glume and lemma of the lower floret broad, distinct; sheaths glabrous or pubescent with short hairs .... *D. oligosanthes*
20b. Nerves of the upper glume and lemma of the lower floret narrow, relatively indistinct; sheaths spreading pubescent with long hairs.
21a. Spikelets 2.2–3.1 mm long; ligules usually with a distinct ring of short hairs in front of long hairs .... *D. ovale*
21b. Spikelets 1.4–2 mm long; ligules lacking a distinct ring of shorter hairs .... *D. acuminatum*
19b. Ligule hairs less than 2 mm long.
22a. Culm nodes, at least lower ones, conspicuously bearded.
23a. Glabrous-glandular band present just below the nodes; leaves usually velvety-pubescent below .... *D. scoparium*
23b. Glabrous-glandular band not present; leaves glabrous or variously pubescent below, not velvety.
24a. Culm internodes, at least lower ones, strigose or villous; blades pubescent below .... *D. ovale*
24b. Culm internodes glabrous; blade surfaces glabrous .... *D. dichotomum*
22b. Culm nodes not bearded, lower ones sometimes sparsely hairy or puberulent.
25a. Ligule membranous; plants typically 75–150 cm tall .... *D. scabriusculum*
25b. Ligule a ring of hairs or absent; plants mostly less than 70 cm tall.

26a. Blades of midculm leaves (vernal phase) linear and stiff, often becoming involute, mostly 2–5 mm wide, 6–15 cm long .... *D. aciculare*
26b. Blades of midculm leaves lanceolate, usually soft, remaining flattened, mostly more than 5 mm wide when 8 cm long or longer.
  27a. Upper glume and lemma of the lower floret with broad, rounded nerves; spikelets rounded at the apex .... *D. oligosanthes*
  27b. Upper glume and lemma of the lower floret with narrow, faint or relatively indistinct nerves; spikelets usually pointed at the apex.
    28a. Lower culm internodes pubescent .... *D. portoricense*
    28b. Lower culm internodes glabrous .... *D. dichotomum*
3b. Spikelets 3.3–5.2 mm long.
  29a. Blades of at least some culm leaves 13–35 mm wide.
    30a. Spikelets broadly elliptic to obovate, usually with broad, heavy nerves .... *D. oligosanthes*
    30b. Spikelets narrowly elliptic to obovate, not strongly nerved.
      31a. Culm nodes glabrous or slightly pubescent; spikelets 3.3–3.8 mm long .... *D. clandestinum*
      31b. Culm nodes bearded; spikelets 3.8–5.2 mm long.
        32a. Ligules 2.5–4 mm long; leaf blades usually puberulent-tomentose on one or both sufaces .... *D. ravenelii*
        32b. Ligules 1.5 mm long; leaf blades glabrous to puberulent .... *D. boscii*
  29b. Blades of culm leaves up to 12 mm wide.
    33a. Midculm blades narrow, stiffly ascending, often becoming involute, mostly 6–15 cm long, less than 5 mm wide .... *D. aciculare*
    33b. Midculm blades broader, spreading, 3–8 cm long, 3–8 mm wide .... *D. portoricense*

Dichanthelium aciculare (Desvaux ex Poiret) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1116. 1978. *Panicum aciculare* Desvaux ex Poiret in Lamarck, Encycl. Suppl. 4: 274. July 1816. TYPE: United States. *Desvaux Herb. s.n.* (holotype, P; isotype, US, fragm.). Although the protologue gives the locality as "Habitat in india orientale," Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 166. 1910) stated that the type collection "is without doubt from the southeastern United States."

Panicum angustifolium Elliott, Sketch Bot. S. Carolina 1: 129. Dec 1816. *Panicum nitidum* Lamarck var. *angustifolium* (Elliott) A. Gray, N. Amer. Gram. 2: 112. 1835. *Chasea angustifolia* (Elliott) Nieuwland, Amer. Midl. Naturalist 2: 64. 1911. *Dichanthelium angustifolium* (Elliott) Gould, Brittonia 26: 59. 1974. TYPE: United States. South Carolina: *Elliott s.n.* (holotype, CHARL; isotype, US?).

Panicum setaceum Muhlenberg, Descr. Gram. 99. 1817. TYPE: United States. Georgia: *Muhlenberg Herb. s.n.* (lectotype, PH-M). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 166. 1910).

Panicum subuniflorum Bosc ex Sprengel, Syst. Veg. 1: 312. 1825. TYPE: United States. "Carolina": *Bosc s.n.* (lectotype, B-W; isotype, G). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 166. 1910).

Panicum curtisii Steudel, Syn. Pl. Glumac. 1: 66. 1853. TYPE: United States. South Carolina: *Curtis s.n.* (holotype, P).

Panicum neuranthum Grisebach, Cat. Pl. Cub. 232. 1866. TYPE: Cuba. Oriente: 1860, *Wright 3453* (lectotype, GOET). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 175. 1910).

Panicum neuranthum Grisebach var. *ramosum* Grisebach, Cat. Pl. Cub. 232. 1866. *Panicum fusiforme* A. Hitchcock, Contr. U.S. Natl. Herb. 12: 222. 1909. TYPE: Cuba. 1863, *Wright 3454* (holotype, GOET).

Panicum nemopanthum Ashe, J. Elisha Mitchell Sci. Soc. 15: 42. 1898. TYPE: United States. North Carolina: Wake Co., Penitentiary Woods, Raleigh, Apr. 1895, *Ashe s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 177. 1910).

Panicum arenicola Ashe, J. Elisha Mitchell Sci. Soc. 15: 56. 1898. TYPE: United States. North Carolina: Orange Co., Chapel Hill, June 1898, *Ashe s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 166. 1910).

Panicum ovinum Lamson-Scribner & J. G. Smith, U.S.D.A. Div. Agrost. Circ. 16: 3. 1899. *Panicum aciculare* Desvaux ex Poiret var. *ovinum* (Lamson-Scribner & J. G. Smith) Beetle, Phytologia 48: 192. 1981. TYPE: United States. Texas: Waller Co., 25 May 1898, *Thurow s.n.* (holotype, US).

Panicum arenicoloides Ashe, J. Elisha Mitchell Sci. Soc. 16: 89. Feb. 1900. *Panicum aciculare* Desvaux ex Poiret var. *arenicoloides* (Ashe) Beetle, Phytologia 48: 192. 1981. TYPE: United States. North Carolina: New Hanover Co., near Wilmington, 7 June 1899, *Ashe s.n.* (holotype, NCU?; isotype, US, fragm.). Specimen at NCU not located.

Panicum filirameum Ashe, J. Elisha Mitchell Sci. Soc. 16: 88. Feb. 1900. TYPE: United States. North Carolina: New Hanover Co., June 1899, *Ashe s.n.* (holotype, NCU; isotype, US).

Panicum orthophyllum Ashe, J. Elisha Mitchell Sci. Soc.

16: 90. Feb. 1900. TYPE: United States. North Carolina: New Hanover Co., June 1899, *Ashe s.n.* (holotype, NCU?; isotype, US, fragm.). Specimen at NCU not located.

Panicum delawarense Ashe, North Carolina Agric. Exp. Sta. Bull. 175: 116. Aug 1900. TYPE: United States. Delaware: Newcastle Co., near Centerville, 6 July 1878, *Commons s.n.* (holotype, NCU).

Panicum pinetorum Swallen, Proc. Biol. Soc. Wash. 55: 93. July 1942. TYPE: United States. Florida: Lee Co., near Bonita Springs, 14 Oct. 1940, *Silveus 6604* (holotype, NA).

Panicum bennettense W. Brown, Bull. Torrey Bot. Club 69: 539, f. 1. Oct. 1942. TYPE: United States. North Carolina: Durham Co., Bennett Memorial, 5 mi. W of Durham, *Brown 2492* (holotype, DUKE).

The vernal phase is easily recognized by the long, narrow, rather stiff upright leaves. In the autumnal phase, *D. aciculare* can be confused with several other species, making determinations very difficult.

This species usually occurs in drier sites throughout Florida.

Dichanthelium acuminatum (Swartz) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1123. 1978. *Panicum acuminatum* Swartz, Prodr. 23. 1788. TYPE: Jamaica: *Swartz s.n.* (holotype, S; isotype, US, fragm.).

As treated here, specimens with long ligule hairs define the *Dichanthelium acuminatum* complex, which consists of three species characterized by spikelet length: *D. leucothrix* (0.8–1.2 mm), *D. acuminatum* (1.4–2 mm), and *D. ovale* (2.2–3 mm). *Dichanthelium ovale* was separated from *D. acuminatum* by Gould & Clark (1978) by its supposedly doubled ligule, which forced specimens with midsized spikelets into *D. ovale.* While it can at times be quite pronounced, this character is often difficult to see and actually becomes undetectable on many specimens. When segregated by spikelet length, however, formerly confusing taxa such as *D. ovale* var. *addisonii* (Gould & Clark, 1978) and *D. ovale* vars. *villosum* and *pseudopubescens* (Lelong, 1984, 1986) fall readily into *D. acuminatum.*

Within *D. acuminatum,* many of the pubescence and habit phases have received varietal or specific status in the past. Lelong (1984, 1986) recognized six varieties. His varieties *acuminatum,* "*unciphyllum,*" and *columbianum* rely on whether the culm and sheath pubescence is appressed or spreading or both; this completely intergrades in a large suite of specimens. His variety *fasciculatum* is based on larger leaves, again a completely intergrading character. On the other hand, in the glabrous varieties *lindheimeri* and *densiflorum*, the lack of pubescence seems to be correlated with smaller spikelet size and generally robust habit for the former, and with an elongate inflorescence for the latter. Therefore, we are recognizing only three varieties in Florida:

1a. Culms and sheaths pubescent .... var. *acuminatum*
1b. Culms and sheaths glabrous or nearly so.
  2a. Panicle narrow, commonly 8–12 cm long; leaves dark green .... var. *densiflorum*
  2b. Panicle broad, 5–8 cm long; leaves yellow green .... var. *lindheimeri*

Dichanthelium acuminatum var. acuminatum

Panicum lanuginosum Elliott, Sketch Bot. S. Carolina 1: 123. 1816. *Dichanthelium lanuginosum* (Elliott) Gould, Brittonia 20: 60. 1974. TYPE: United States. Georgia: *Baldwin s.n.* (holotype, CHARL; isotype, US, fragm.).

Panicum dichotomum Linnaeus var. *fasciculatum* Torrey, Fl. N. Middle United States 145. 1824. *Panicum huachucae* Ashe var. *fasciculatum* (Torrey) F. Hubbard, Rhodora 14: 171. 1912. *Panicum lindheimeri* Nash var. *fasciculatum* (Torrey) Fernald, Rhodora 23: 228. 1922 ("1921"). *Panicum lanuginosum* Elliott var. *fasciculatum* (Torrey) Fernald, Rhodora 36: 77. 1934. *Dichanthelium lanuginosum* (Elliott) Gould var. *fasciculatum* (Torrey) Spellenberg, Madroño 23: 145. 1975. *Dichanthelium acuminatum* (Swartz) Gould & Clark var. *fasciculatum* (Torrey) Freckmann, Phytologia 48: 108. 1981. *Panicum acuminatum* Swartz var. *fasciculatum* (Torrey) Lelong, Brittonia 36: 169. 1984. TYPE: United States. New Jersey: *Torrey s.n.* (holotype, NY).

Panicum nitidum Lamarck var. *ciliatum* Torrey, Fl. N. Middle United States 146. 1824. TYPE: United States. New Jersey: *Torrey s.n.* (holotype, NY; isotype, US, fragm.).

Panicum nitidum Lamarck var. *pilosum* Torrey, Fl. N. Middle United States 146. 1824. TYPE: United States. New York: *Torrey s.n.* (holotype, NY; isotype, US, fragm.).

Panicum nitidum Lamarck var. *villosum* A. Gray, N. Amer. Gram. 2: 111. 1835. *Dichanthelium acuminatum* (Swartz) Gould & Clark var. *villosum* (A. Gray) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1124. 1978. *Panicum acuminatum* Swartz var. *villosum* (A. Gray) Beetle, Phytologia 48: 192. 1981. *Panicum ovale* Elliott var. *villosum* (A. Gray) Lelong, Brittonia 36: 272. 1984. TYPE: United States. New York: Ontario Co., *Sartwell? s.n.* (holotype, GH?).

Panicum dichotomum Linnaeus var. *villosum* Vasey, U.S.D.A. Div. Agrost. Bull. 8: 31. 1889. TYPE: United States. District of Columbia: near Pierce's Mill, Rock Creek, 1 July 1883, *Vasey s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 233. 1910).

Panicum villosissimum Nash, Bull. Torrey Bot. Club 23: 149. 1896. *Dichanthelium lanuginosum* (Elliott) Gould var. *villosissimum* (Nash) Gould, Brittonia 26: 60. 1974. *Dichanthelium villosissimum* (Nash) Freckmann, Phytologia 39: 270. 1978. TYPE: United

States. Georgia: Bibb Co., Ocmulgee River swamp below Macon, 18–24 May 1895, *Small s.n.* (holotype, NY; isotypes, NY, US).

Panicum atlanticum Nash, Bull. Torrey Bot. Club 24: 346. 1897. TYPE: United States. New York: Bronx, New York Botanical Garden, 24 June 1897, *Nash s.n.* (holotype, NY; isotypes, NY, US).

Panicum commonsianum Ashe, J. Elisha Mitchell Sci. Soc. 15: 55. Feb. 1898. *Panicum columbianum* Lamson-Scribner var. *commonsianum* (Ashe) Dore in McNeill & Dore, Naturaliste Canad. 103: 562. 1976. *Dichanthelium commonsianum* (Ashe) Freckmann, Phytologia 39: 271. 1978. TYPE: United States. New Jersey: Cape May Co., Cape May, June 1898, *Commons 341* (holotype, NCU; isotypes, NY, US).

Panicum filiculme Ashe, J. Elisha Mitchell Sci. Soc. 15: 59. Feb. 1898, non Hackel 1895. TYPE: United States. Georgia: DeKalb Co., Stone Mountain, Aug. 1895, *Ashe s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 210. 1910).

Panicum haemacarpon Ashe, J. Elisha Mitchell Sci. Soc. 15: 55. Feb. 1898. TYPE: United States. District of Columbia: 1897, *Kearney s.n.* (lectotype, NCU; isolectotypes, NY, US). Lectotypified by Hichcock and Chase (Contr. U.S. Natl. Herb. 15: 233. 1910). Although Lelong (1984) cited NY as the location of the lectotype, Hitchcock & Chase (1910) clearly stated that the type is in Ashe's herbarium, which is now at NCU.

Panicum huachucae Ashe, J. Elisha Mitchell Sci. Soc. 15: 51. Feb. 1898. *Panicum lanuginosum* Elliott var. *huachucae* (Ashe) A. Hitchcock, Rhodora 8: 208. 1906. TYPE: United States. Arizona: Huachuca Mountains, 1882, *Lemmon s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 215. 1910).

Panicum meridionale Ashe, J. Elisha Mitchell Sci. Soc. 15: 59. Feb. 1898. *Panicum unciphyllum* Trinius var. *meridionale* (Ashe) Lamson-Scribner & Merrill, Rhodora 3: 123. 1901. *Panicum lindheimeri* Nash subvar. *meridionale* (Ashe) Farwell, Amer. Midl. Naturalist 11: 45. 1928. *Panicum lanuginosum* Elliott subvar. *meridionale* (Ashe) Farwell, Pap. Michigan Acad. Sci. 26: 5. 1941. *Dichanthelium meridionale* (Ashe) Freckmann, Phytologia 39: 270. 1978. TYPE: United States. North Carolina: Burke Co., Jonas Ridge, June 1893, *Ashe s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 210. 1910).

Panicum microphyllum Ashe, J. Elisha Mitchell Sci. Soc. 15: 61. Feb. 1898. TYPE: United States. North Carolina: Orange Co., Chapel Hill, June 1898, *Ashe s.n.* (holotype, not located). Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 210. 1910) relegated this name to the synonymy of *Panicum meridionale* based on the description only.

Panicum scoparioides Ashe, J. Elisha Mitchell Sci. Soc. 15: 53. Feb. 1898. *Panicum villosissimum* Nash var. *scoparioides* (Ashe) Fernald, Rhodora 36: 79. 1934. TYPE: United States. Delaware: Newcastle Co., Centreville, 25 June 1873, *Commons 283* (lectotype, US; isotype, NY). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 238. 1910).

Panicum tennesseense Ashe, J. Elisha Mitchell Sci. Soc. 15: 52. Feb. 1898. *Panicum lindheimeri* Nash var. *tennesseense* (Ashe) Farwell, Amer. Midl. Naturalist 11: 45. 1928. TYPE: United States. Tennessee: La Vergne Co., 7 Aug. 1897, *Biltmore Herb. 7087* (holotype, US).

Panicum addisonii Nash, Bull. Torrey Bot. Club 25: 83. 12 Feb. 1898. *Panicum commonsianum* Ashe subsp. *addisonii* (Nash) W. Stone, New Jersey State Mus. Annual Rep. 1910: 205. 1911. *Panicum commonsianum* Ashe var. *addisonii* (Nash) R. Pohl, Amer. Midl. Naturalist 38: 582. 1947. *Dichanthelium ovale* (Elliott) Gould & Clark var. *addisonii* (Nash) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1115. 1978. TYPE: United States. New Jersey: Cape May Co., Wildwood, 30–31 May 1897, *Bicknell s.n.* (holotype, NY; isotype, US, fragm.).

Panicum implicatum Lamson-Scribner in Britton & Brown, Ill. Fl. N. U.S. 3: 498. 20 June 1898. *Panicum unciphyllum* Trinius var. *implicatum* (Lamson-Scribner) Lamson-Scribner & Merrill, Rhodora 3: 123. 1901. *Panicum lindheimeri* Nash var. *implicatum* (Lamson-Scribner) Fernald, Rhodora 23: 228. 1922 ("1921"). *Panicum lanuginosum* Elliott var. *implicatum* (Lamson-Scribner) Fernald, Rhodora 36: 77. 1934. *Dichanthelium acuminatum* (Swartz) Gould & Clark var. *implicatum* (Lamson-Scribner) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1126. 1978. *Panicum acuminatum* Swartz var. *implicatum* (Lamson-Scribner) Beetle, Phytologia 48: 192. 1981. TYPE: United States. Maine: Cumberland Co., Cape Elizabeth, 26–27 July 1895, *Lamson-Scribner s.n.* (holotype, US; isotype, NY).

Panicum thurowii Lamson-Scribner & J. G. Smith, U.S.D.A. Div. Agrost. Circ. 16: 5. 1 July 1899. *Dichanthelium acuminatum* (Swartz) Gould & Clark var. *thurowii* (Lamson-Scribner & J. G. Smith) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1125. 1978. TYPE: United States. Texas: Waller Co., 5 June 1898, *Thurow 9* (holotype, US).

Panicum ciliosum Nash, Bull. Torrey Bot. Club 26: 568. Nov. 1899. TYPE: United States. Mississippi: Harrison Co., Biloxi, 1 Sept. 1898, *Tracy 4580* (holotype, NY; isotypes, NCU, US).

Panicum pseudopubescens Nash, Bull. Torrey Bot. Club 26: 577. Nov. 1899. *Panicum villosissimum* Nash var. *pseudopubescens* (Nash) Fernald, Rhodora 36: 79. 1934. *Panicum ovale* Elliott var. *pseudopubescens* (Nash) Lelong, Brittonia 36: 271. 1984. TYPE: United States. Alabama: Lee Co., Auburn, 7 May 1898, *Earle & Baker 1537* (holotype, NY; isotype, US).

Panicum occidentale Lamson-Scribner, Annual Rep. Missouri Bot. Gard. 10: 48. 1899. TYPE: Canada. British Columbia: Vancouver Island, "Hab. in Nootka-Sund," *Haenke s.n.* (holotype, MO; isotypes, PR, US, fragm.). The choice of the PR specimen as lectotype by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 228. 1910) is invalid; Lamson-Scribner worked from the specimen at MO and never saw the PR material.

Panicum orangense Ashe, J. Elisha Mitchell Sci. Soc. 15: 113. 1899. TYPE: United States. North Carolina: Orange Co., Chapel Hill, 29 June 1898, *Ashe s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 220. 1910).

Panicum albemarlense Ashe, J. Elisha Mitchell Sci. Soc. 16: 84. Feb. 1900. *Panicum meridionale* Ashe var. *albemarlense* (Ashe) Fernald, Rhodora 36: 76. 1934. TYPE: United States. North Carolina: Beauford or

Hyde Co., near Scranton, 26 May 1899, *Ashe s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 212. 1910).

Panicum subvillosum Ashe, J. Elisha Mitchell Sci. Soc. 16: 86. Feb. 1900. TYPE: United States. Minnesota: Carlton Co., Carlton, Aug., *Ashe s.n.* (holotype, NCU).

Panicum wilmingtonense Ashe, J. Elisha Mitchell Sci. Soc. 16: 86. Feb. 1900. TYPE: United States. North Carolina: New Hanover Co., near Wilmington, 17 May 1899, *Ashe s.n.* (holotype, NCU; isotype, US).

Panicum alabamense Ashe, North Carolina Agric. Exp. Sta. Bull. 164: 116. Aug. 1900, non Trinius 1854. TYPE: United States. Alabama: Lee Co., Auburn, 7 May 1898, *Alabama Biol. Surv. 1530* (holotype, NCU; isotypes, NY, US).

Panicum auburne Ashe, North Carolina Agric. Exp. Sta. Bull. 175: 115. Aug. 1900. TYPE: United States. Alabama: Lee Co., Auburn, 7 May 1898, *Earle & Baker 1527* (holotype, NCU; isotype, US).

Panicum unciphyllum Trinius forma *pilosum* Lamson-Scribner & Merrill, Rhodora 3: 124. 20 May 1901. TYPE: United States. Maine: Penobscot Co., Orono, 7 July 1891, *Fernald 501* (holotype, GH).

Panicum unciphyllum Trinius forma *prostratum* Lamson-Scribner & Merrill, Rhodora 3: 124. 20 May 1901. *Panicum languidum* A. Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 232. 1910. TYPE: United States. Maine: York Co., South Berwick, 26 Sep. 1897, *Fernald s.n.* (holotype, GH).

Panicum xanthospermum Lamson-Scribner & C. Mohr, in Mohr, Contr. U.S. Natl. Herb. 6: 348. 31 July 1901. TYPE: United States. Alabama: Butler Co., Greenville, 8 May 1898, *Mohr s.n.* (holotype, US).

Panicum comophyllum Nash, Bull. Torrey Bot. Club 30: 380. 10 July 1903. TYPE: Puerto Rico: Santurce, 9 Jan. 1899, *Heller & Heller 12* (holotype, NY).

Panicum chrysopsidifolium Nash in Small, Fl. S.E. U.S. 100, 1327. 22 July 1903. TYPE: United States. Florida: Leon Co., Lake Jackson, 12 May 1886, *Curtiss D* (holotype, NY).

Panicum lanuginosum Elliott var. *siccanum* A. Hitchcock & Chase, Rhodora 8: 207, 1906. TYPE: United States. Illinois: LaSalle Co., Starved Rock, 1 July 1901, *Chase 1602* (holotype, US).

Panicum oricola A. Hitchcock & Chase, Rhodora 8: 208. 1906. *Panicum columbianum* Lamson-Scribner var. *oricola* (A. Hitchcock & Chase) Fernald, Rhodora 36: 79. 1934. TYPE: United States. Delaware: Sussex Co., Lewes, 18 June 1905, *Hitchcock 47* (holotype, US; isotypes, MO, NY).

Panicum praecocius A. Hitchcock & Chase, Rhodora 8: 206. 1906. *Panicum lanuginosum* Elliott var. *praecocius* (A. Hitchcock & Chase) Dore in McNeill & Dore, Naturaliste Canad. 103: 576. 1976. *Dichanthelium villosissimum* (Nash) Freckmann var. *praecocius* (A. Hitchcock & Chase) Freckmann, Phytologia 39: 270. 1978. TYPE: United States. Illinois: Stark Co., near Wady Petra, 30 June 1900, *Chase 649* (holotype, US).

Panicum unciphyllum Trinius var. *thinium* A. Hitchcock & Chase, Rhodora 8: 209. 1906. *Panicum columbianum* Lamson-Scribner var. *thinium* (A. Hitchcock & Chase) A. Hitchcock & Chase in Robinson, Rhodora 10: 64. 1908. *Panicum heterophyllum* Bosc ex C. Nees von Esenbeck var. *thinium* (A. Hitchcock & Chase) F. Hubbard, Rhodora 14: 172. 1912. *Dichanthelium sabulorum* (Lamarck) Gould & Clark var. *thinium* (A. Hitchcock & Chase) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1113. 1978. TYPE: United States. New Jersey: Ocean Co., Toms River, 28 July 1906, *Chase 3577* (holotype, US).

Panicum oweniae Bicknell, Bull. Torrey Bot. Club 35: 185. 29 Apr. 1908. TYPE: United States. Massachusetts: Nantucket Co., W of Nantucket, 20 Sep. 1907, *Bicknell s.n.* (holotype, NY; isotypes, NY, US).

Panicum huachucae Ashe var. *silvicola* A. Hitchcock & Chase in Robinson, Rhodora 10: 64. 16 May 1908. TYPE: United States. District of Columbia: 28 June 1904, *Chase 2400* (holotype, US).

Panicum olivaceum A. Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 225. 1910. TYPE: Guatemala. Alta Verapaz: Coban, Feb. 1888, *Türckheim 428* (holotype, US).

Panicum pacificum A. Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 229. 1910. TYPE: United States. California: Shasta Co., Castle Crag, ¼ mi. E of hotel, 3 Aug. 1908, *Hitchcock 3070* (holotype, US).

Panicum lindheimeri Nash var. *septentrionale* Fernald, Rhodora 23: 227. 1922 ("1921"). *Panicum lanuginosum* Elliott var. *septentrionale* (Fernald) Fernald, Rhodora 36: 77. 1934. TYPE: Canada. New Brunswick: St. John River, Woodstock, 14 July 1916, *Fernald & Long 12527* (holotype, GH).

Panicum deamii A. Hitchcock & Chase in Deam, Indiana Conserv. Dept. Publ. 82: 284, pl. 75(18). 1929. TYPE: United States. Indiana: Lake Co., ¼ mi. S of Pine, 21 June 1926, *Deam 43287* (holotype, US).

Panicum mundum Fernald, Rhodora 38: 392, pl. 443(1–5). 1936. TYPE: United States. Virginia: Sussex Co., 4 mi. NW of Homeville, 25 Aug. 1936, *Fernald & Long 6499* (holotype, GH; isotypes, MO, NY, US).

Panicum brodiei H. Saint John, Fl. S.-e. Washington 51. 1937. TYPE: United States. Washington: Whitman Co., Wawai, Snake River, June 1893, *Brodie s.n.* (holotype, WS).

Panicum lassenianum Schmoll, Madroño 5: 95. 1939. TYPE: United States. California: Plumas Co., Devil's Kitchen, Hot Spring Valley, *Jepson 4082* (holotype, US).

Panicum glutinoscabrum Fernald, Rhodora 49: 122. 1947. TYPE: United States. Virginia: Nansemond Co., ca. ½ mi. W of Kilby, 8–12 Sep. 1946, *Fernald et al. 15186* (holotype, GH; isotype, PH).

This taxon is common in north Florida south to the central peninsula, occurring primarily in pine flatwoods.

Dichanthelium acuminatum (Swartz) Gould & Clark var. **densiflorum** (Rand & Redfield) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1127. 1978. *Panicum nitidum* Lamarck var. *densiflorum* Rand & Redfield, Fl. Mt. Desert 174. 1894. *Panicum acuminatum* Swartz var. *densiflorum* (Rand & Redfield) Lelong, Brittonia 36: 270. 1984. TYPE: United States. Maine: Hancock Co., Mt. Desert, Ripples Pond, 28 July 1892, *Rand s.n.* (holotype, GH).

Panicum spretum Schultes, Mant. 2: 248. 1824. *Dichanthelium spretum* (Schultes) Freckmann, Phytologia 48: 102. 1981. TYPE: United States: "N. Anglica," *Muhlenberg Herb. Panicum no. 37* (holotype, PH).

Panicum eatonii Nash, Bull. Torrey Bot. Club 25: 84. 1898. TYPE: United States. New Hampshire: Rockingham Co., Seabrook, 1897, *Eaton s.n.* (holotype, NY; isotype, US).

Panicum octonodum J. G. Smith, U.S.D.A. Div. Agrost. Bull. 17: 73. 1899. *Panicum nitidum* Lamarck var. *octonodum* (J. G. Smith) Lamson-Scribner & Merrill, U.S.D.A. Div. Agrost. Bull. 24: 34. 1901. TYPE: United States. Texas: Waller Co., 5 May 1898, *Thurow 6* (holotype, US).

Panicum paucipilum Nash, Bull. Torrey Bot. Club 26: 573. Nov. 1899. TYPE: United States. New Jersey: Cape May Co., Wildwood, 30–31 May 1897, *Bicknell s.n.* (holotype, NY; isotypes, NY, US).

This weak variety is apparently rather uncommon in Florida, found only along the northern edge of the state.

Dichanthelium acuminatum var. **lindheimeri** (Nash) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1127. 1978. *Panicum lindheimeri* Nash, Bull. Torrey Bot. Club 24: 196. 1897. *Panicum lindheimeri* Nash var. *typicum* Fernald, Rhodora 23: 227. 1922 ("1921"), nom. inadmiss. *Panicum lanuginosum* Elliott var. *lindheimeri* (Nash) Fernald, Rhodora 36: 77. 1934. *Dichanthelium lindheimeri* (Nash) Gould, Brittonia 26: 60. 1974. *Dichanthelium lanuginosum* (Elliott) Gould var. *lindheimeri* (Nash) Freckmann, Phytologia 39: 270. 1978. *Panicum acuminatum* Swartz var. *lindheimeri* (Nash) Beetle, Phytologia 48: 193. 1981. TYPE: United States. Texas: Comal Co., banks of the Guadelupe River, Near New Braunfels, 1846, *Lindheimer 565* (holotype, NY; isotypes, MO, NY).

Panicum funstonii Lamson-Scribner & Merrill, U.S.D.A. Div. Agrost. Circ. 35: 4. 1901. TYPE: United States. California: Tulare Co., bank of Kaweah River at Three Rivers, 26 July 1891, *Coville & Funston 1286* (holotype, US).

In Florida, this variety is confined to the northern counties. Variety *lindheimeri* represents the more glabrous extremes of *D. acuminatum*.

Dichanthelium boscii (Poiret) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1101. 1978. *Panicum boscii* Poiret in Lamarck, Encycl. Suppl. 4: 278. 1816. TYPE: United States: *Bosc s.n.* (lectotype, P; isotype, US, fragm.). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 317. 1910).

Panicum waltheri Poiret in Lamarck, Encycl. Suppl. 4: 282. 1816. *Panicum porterianum* Nash, Bull. Torrey Bot. Club 22: 420. 1895, nom. illegit. TYPE: United States: "in pratis sylvestris Virginiae Carolinae," *Michaux s.n.* (lectotype, P). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 317. 1910). The application of *Panicum porterianum* can be quite confusing. Nash based his new name on three entities, namely "*Panicum latifolium* Walt. Fl. Car. 73. 1788. Not Linnaeus, 1753. *Panicum Walteri* [*waltheri*] Poir. in Lam. Encycl. Suppl. 4: 282. 1816. Not Pursh, 1814. *Panicum latifolium* var. *molle* Vasey, Bull. Bot. Div., U.S. Dept. Agric. 8: 33 [error for 34]. 1889." If, as interpreted here, *Panicum waltheri* Poir. is not a later homonym of *P. walteri* Pursh 1814, *P. waltheri* Poir. is a valid earlier name cited under *P. porterianum*, which makes the latter name illegitimate and automatically typified by the type of *P. waltheri* Poir. If, on the other hand, *P. waltheri* Poir. is considered a typographic error for *walteri*, and is therefore a later homonym of *P. walteri* Pursh, the lectotype of *P. porterianum* may be chosen from any of the entities cited by Nash. This was effectively done by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 317. 1910), who cited *P. porterianum* as a nomen novum for *P. walt*[*h*]*eri* Poir. Therefore, whether *P. waltheri* Poir. is judged to be valid or not, *P. porterianum* is always disposed as its homotypic synonym.

Panicum latifolium Linnaeus var. *australe* Vasey, U.S.D.A. Div. Agrost. Bull. 8: 34. 1889. TYPE: United States. Alabama: Clark Co., Thomasville, 16 Apr. 1888, *Mohr s.n.* (holotype, US).

Panicum latifolium Linnaeus var. *molle* Vasey, U.S.D.A. Div. Agrost. Bull. 8: 34. 1889. *Panicum waltheri* Poiret var. *molle* (Vasey) Porter, Bull. Torrey Bot. Club 20: 194. 1893. *Panicum boscii* Poiret var. *molle* (Vasey) A. Hitchcock & Chase in Robinson, Rhodora 10: 64. 1908. *Panicum pubifolium* Nash, Bull. Torrey Bot. Club 26: 577. 1899. TYPE: United States. District of Columbia: *Ward s.n.* (holotype, US).

This species is rather uncommon in Florida, occurring in the panhandle and south to Levy County.

Dichanthelium clandestinum (Linnaeus) Gould, Brittonia 26: 59. 1974. *Panicum clandestinum* Linnaeus, Sp. Pl. 58. 1753. *Milium clandestinum* (Linnaeus) Moench, Methodus 204. 1794. *Panicum latifolium* Linnaeus var. *clandestinum* (Linnaeus) Pursh, Fl. Amer. Sept. 1: 68. 1814. *Chasea clandestina* (Linnaeus) Nieuwland, Amer. Midl. Naturalist 2: 64. 1911. TYPE: United States. Pennsylvania: *Kalm s.n.* (lectotype, LINN 80.57). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 312. 1910).

Panicum pedunculatum Torrey, Fl. N. Middle United States 141. 1824. *Panicum clandestinum* Linnaeus var. *pedunculatum* (Torrey) Torrey, Fl. New York

2: 426. 1841. TYPE: United States. New York: "On the island of New-York," Aug., *Torrey s.n.* (holotype, NY; isotype, US, fragm.).

Panicum decoloratum Nash, Bull. Torrey Bot. Club 26: 570. 1899. TYPE: United States. Pennsylvania: Bucks Co., Tullytown, 30 May 1899, *Bicknell s.n.* (holotype, NY; isotype, US).

An uncommon species in Florida, found only in the western panhandle. It occurs in moist to wet sandy soil in woods.

Dichanthelium commutatum (Schultes) Gould, Brittonia 26: 59. 1974. *Panicum nervosum* Muhlenberg ex Elliott, Sketch Bot. S. Carolina 1: 122. 1816, non Lamarck 1797. *Panicum commutatum* Schultes, Mant. 2: 242. 1824. *Panicum polyneuron* Steudel, Syn. Pl. Glumac. 1: 91. 1854, nom. illegit. TYPE: United States. "Car. et Geor.," *Elliott Herb. s.n.* (lectotype, CHARL). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 303. 1910).

Panicum nitidum Lamarck var. *majus* Pursh, Fl. Amer. Sept. 1: 67. 1814. TYPE: United States: *Pursh s.n.* (lectotype, K). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 303. 1910).

Panicum umbrosum LeConte ex Torrey, Cat. Pl. New York 91. 1819, non Retzius 1786. TYPE: United States. New York: Essex Co., Bloomingdale, *LeConte s.n.* (lectotype, NY). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 301. 1910).

Panicum enslinii Trinius, Gram. Panic. 230. 1826. TYPE: United States. "Am. bor.," *Enslin s.n.* (lectotype, LE). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 304. 1910).

Panicum leiophyllum Fournier, Mexic. Pl. 2: 20: 1886, non C. Nees von Esenbeck 1829. TYPE: Mexico. Veracruz: "in valle Cordovensi," Jan., *Bourgeau s.n.* (holotype, P).

Panicum commutatum Schultes var. *minor* Vasey, U.S.D.A. Div. Agrost. Bull. 8: 34. 1889, as "minorus." *Panicum ashei* G. Pearson ex Ashe, J. Elisha Mitchell Sci. Soc. 15: 35. 1898. *Panicum commutatum* Schultes var. *ashei* (G. Pearson ex Ashe) Fernald, Rhodora 36: 83. 1934. TYPE: United States. South Carolina: Aiken Co., Aiken, 1867, *Ravenel s.n.* (lectotype, NY). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 304. 1910). *Panicum ashei* is a new name for Vasey's variety and should be treated as a homotypic synonym, not retypified with another element as did Hitchcock & Chase (1910).

Panicum joorii Vasey, U.S.D.A. Div. Agrost. Bull. 8: 31. 1889. TYPE: United States. Louisiana: East Baton Rouge Par., near Baton Rouge, 1 Oct. 1885, *Joor 39* (holotype, US).

Panicum commutatum Schultes var. *latifolium* Lamson-Scribner in Kearney, Bull. Torrey Bot. Club 20: 476. 1893. TYPE: United States. Kentucky: Harlan Co., Pine Mountain, Aug. 1893, *Kearney 299* [?] (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 304. 1910). The lectotype is a sheet without data; collection data come from the protologue.

Panicum manatense Nash, Bull. Torrey Bot. Club 24: 42. 1897. TYPE: United States. Florida: Manatee Co., NE of Palmetto, 21 Aug. 1895, *Nash 2428a* (holotype, NY).

Panicum equilaterale Lamson-Scribner, U.S.D.A. Div. Agrost. Bull. 11: 42, pl. 2. 30 July 1898. TYPE: United States. Florida: Lake Co., Eustis, Aug. 1894, *Nash 1674* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 310. 1910).

Panicum commelinifolium Ashe, J. Elisha Mitchell Sci. Soc. 15: 29. 1898, non Rudge 1805. *Panicum curranii* Ashe, J. Elisha Mitchell Sci. Soc. 15: 113. 1899. TYPE: United States. Georgia: DeKalb Co., near Stone Mountain, 1–6 Aug. 1895, *Small s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 304. 1910).

Panicum epilifolium Nash, Bull. Torrey Bot. Club 26: 571. 1899. TYPE: United States. Florida: Lake Co., Eustis, 12–31 Mar. 1894, *Nash 45* (lectotype, NY). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 310. 1910).

Panicum subsimplex Ashe, North Carolina Agric. Exp. Sta. Bull. 175: 115. 1900. TYPE: United States. Delaware: Newcastle Co., near Wilmington, 16 Aug. 1897, *Commons s.n.* (holotype, NCU).

Panicum mutabile Lamson-Scribner & J. G. Smith ex Nash in Small, Fl. S.E. U.S. 103, 1327. 1903. TYPE: United States. Mississippi: Harrison Co., Biloxi, 1896, *Tracy 3074* (holotype, NY).

Panicum hintonii Swallen, Contr. U.S. Natl. Herb. 29: 419. 1950. TYPE: Mexico. México: Bejucos, Temascaltepec, 8 Nov. 1932, *Hinton 2527* (holotype, US).

Dichanthelium commutatum is very common throughout Florida. It is found primarily in moist, shaded areas.

Dichanthelium dichotomum (Linnaeus) Gould, Brittonia 26: 59. 1974. *Panicum dichotomum* Linnaeus, Sp. Pl. 58. 1753. TYPE: United States. Virginia: "Habitat in Virginia," *Clayton 458* (lectotype, BM; isotype, US, fragm.). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 190. 1910). Lelong (1984) erred by citing the lectotype at LINN.

Panicum nitidum Lamarck, Tabl. Encycl. 1: 172. 1791. *Panicum dichotomum* Linnaeus var. *nitidum* (Lamarck) Wood, Class-Book Bot., ed. 1861. 786. 1861. TYPE: United States. "E. Carolina," *Fraser s.n.* (holotype, P-LA).

Panicum nodiflorum Lamarck, Encycl. 4: 744. 1798. *Panicum dichotomum* Linnaeus var. *nodiflorum* (Lamarck) Grisebach, Cat. Pl. Cub. 234. 1866. TYPE: United States. "Caroline," *Fraser s.n.* (holotype, P-LA; isotype, US, fragm.).

Panicum barbulatum Michaux, Fl. Bor.-Amer. 1: 49. 1803. *Panicum dichotomum* Linnaeus var. *barbulatum* (Michaux) Alph. Wood, Class-Book Bot., ed. 1861. 786. 1861. *Panicum pubescens* Lamarck var. *barbulatum* (Michaux) Britton, Cat. Pl. New Jersey 280. 1889. *Panicum nitidum* Lamarck var. *barbulatum* (Michaux) Chapman, Fl. South. U.S., ed. 3. 586. 1897. TYPE: Canada: "Hab. in Canada P. capillari affine. Ad ripas amnis: *Riviere* a Jacques Cartier dicti legi," *Michaux s.n.* (lectotype, P-M; isotype, US, fragm.). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 193. 1910).

Panicum microcarpon Muhlenberg ex Elliott, Sketch Bot. S. Carolina 1: 127. 1816. TYPE: United States. Georgia: *Baldwin s.n.* (lectotype, CHARL). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 181. 1910).

Panicum angustifolium LeConte ex Torrey, Cat. Pl. New York 91. 1818, non Elliott 1816. TYPE: unknown.

Panicum tremulum Sprengel, Neue Entd. 2: 103. 1821. TYPE: United States: *Muhlenberg Herb. s.n.* (lectotype, B [destroyed]; isotype, US, fragm.). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 190. 1910).

Panicum nitidum Lamarck var. *barbatum* Torrey, Fl. N. Middle United States 146. 1824. TYPE: unknown.

Panicum nitidum Lamarck var. *ramulosum* Torrey, Fl. N. Middle United States 146. 1824. *Panicum dichotomum* Linnaeus var. *ramulosum* (Torrey) Lelong, Brittonia 36: 265. 1984. TYPE: United States. New Jersey: near Quaker Bridge, June 1818, *Torrey s.n.* (holotype, NY).

Panicum dumus Desvaux, Opusc. Sci. Phys. Nat. 88. 1831. TYPE: United States? "America calidiori," *Desvaux Herb. s.n.* (holotype, P).

Panicum dichotomum Linnaeus var. *divaricatum* Vasey, U.S.D.A. Div. Agrost. Bull. 8: 30. 1889. TYPE: United States. Mississippi: Scott Co., Lake, *Tracy 127* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 191. 1910).

Panicum dichotomum Linnaeus var. *viride* Vasey, U.S.D.A. Div. Agrost. Bull. 8: 30. 1889. *Panicum nitidum* Lamarck var. *viride* (Vasey) Britton, Trans. New York Acad. Sci. 9: 14. 1889. *Panicum ramulosum* Michaux var. *viride* (Vasey) Porter, Bull. Torrey Bot. Club 20: 194. 1893. TYPE: United States. District of Columbia: Woodley Park, 1881, *Ward s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 191. 1910).

Panicum nudicaule Vasey, U.S.D.A. Div. Agrost. Bull. 8: 31. 1889. TYPE: United States. Florida: Santa Rosa Co., May 1886, *Curtiss 3583* (lectotype, US; isotypes, NY, TAES). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 179, 1910).

Panicum dichotomum Linnaeus var. *commune* S. Watson & Coulter in A. Gray, Manual, ed. 6. 633. 1890. TYPE: unknown.

Panicum sphagnicola Nash, Bull. Torrey Bot. Club 22: 422. 1895. TYPE: United States. Florida: Columbia Co., Lake City, 29–31 Aug. 1895, *Nash 2500* (lectotype, NY; isotypes, NY). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 199. 1910).

Panicum annulum Ashe, J. Elisha Mitchell Sci. Soc. 15: 58. 1898. *Panicum bogueanum* Ashe, J. Elisha Mitchell Sci. Soc. 16: 85. 1900, nom. illegit. TYPE: United States. District of Columbia: 1882, *Ward s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 185. 1910).

Panicum lucidum Ashe, J. Elisha Mitchell Sci. Soc. 15: 47. 1898. *Panicum dichotomum* Linnaeus var. *lucidum* (Ashe) Lelong, Brittonia 36: 265. 1984. TYPE: United States. North Carolina: Dare Co., swamps bordering Lake Mattamuskeet, June 1898, *Ashe s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 198. 1910).

Panicum maculatum Ashe, J. Elisha Mitchell Sci. Soc. 15: 44. 1898, non Aublet 1775. *Panicum yadkinense* Ashe, J. Elisha Mitchell Sci. Soc. 16: 85. 1900. *Panicum dichotomum* Linnaeus var. *yadkinense* (Ashe) Lelong, Brittonia 36: 266. 1984. TYPE: United States. North Carolina: Wake Co., Raleigh, May 1895, *Ashe s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 195. 1910).

Panicum mattamuskeetense Ashe, J. Elisha Mitchell Sci. Soc. 15: 45. 1898. *Panicum dichotomum* Linnaeus var. *mattamuskeetense* (Ashe) Lelong, Brittonia 36: 265. 1984. TYPE: United States. North Carolina: Hyde Co., Lake Mattamuskeet, 10 June–6 July 1898, *Ashe s.n.* (lectotype, US; isotype, NY). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 186. 1910).

Panicum roanokense Ashe, J. Elisha Mitchell Sci. Soc. 15: 44. 1898. *Panicum dichotomum* Linnaeus var. *roanokense* (Ashe) Lelong, Brittonia 36: 265. 1984. TYPE: United States. North Carolina: Dare Co., Roanoke Island, June 1898, *Ashe s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 196. 1910).

Panicum clutei Nash, Bull. Torrey Bot. Club 26: 569. 1899. *Panicum mattamuskeetense* Ashe var. *clutei* (Nash) Fernald, Rhodora 39: 386. 1937. TYPE: United States. New Jersey: Tuckerton to Atsion, 3–6 July 1899, *Clute s.n.* (holotype, NY).

Panicum curtivaginum Ashe, J. Elisha Mitchell Sci. Soc. 16: 85. 1900. TYPE: United States. Mississippi: Jackson Co., Petit Bois Island, 8 May 1898, *Tracy 4584* (lectotype, NCU?; isotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 196. 1910). Specimen at NCU not located.

Panicum taxodiorum Ashe, J. Elisha Mitchell Sci. Soc. 16: 91. 1900. TYPE: United States. Louisiana: Calcasieu Par., Lake Charles, Sep. 1898, *Mackenzie 460* (lectotype, NCU; isotype, NY). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 198. 1910). Both Lelong (1984) and Gould & Clark (1978) cited the "holotype" as residing at NY. Hitchcock & Chase, by contrast, stated that the type was in Ashe's herbarium, which is now at NCU.

Panicum multirameum Lamson-Scribner, U.S.D.A. Div. Agrost. Circ. 19: 2. 1900. TYPE: Mexico. Veacruz: Near Jalapa, 1889, *Pringle 7882* (lectotype, US; isotype, MO). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 185. 1910).

Panicum subbarbulatum Lamson-Scribner & Merrill, U.S.D.A. Div. Agrost. Circ. 29: 9. 1901. TYPE: United States: *Elliott Herb. s.n.* (holotype, CHARL).

Panicum gravius A. Hitchcock & Chase, Rhodora 8: 205. 1906. TYPE: United States. Delaware: Newcastle Co., on the old Commons farm, between Centreville and Mt. Cuba, 30 July 1906, *Chase 3620* (holotype, US).

Panicum caerulescens Hackel ex A. Hitchcock, Contr. U.S. Natl. Herb. 12: 219. 1909. TYPE: United States.

Florida: Dade Co., Miami, 3 Apr. 1906, *Hitchcock 706* (holotype, US; isotype, NY).

Panicum lucidum Ashe var. *opacum* Fernald, Rhodora 39: 386. 1937. TYPE: United States. Virginia: Prince George Co., N of Gary Church, 25 Aug. 1936, *Fernald & Long 6484* (holotype, GH; isotypes, MO, NY, PH, US).

Gould & Clark (1978) included the generally cushion-forming plants with small spikelets as varieties of *D. dichotomum.* We agree with Lelong (1984, 1986) that these should be separated from *D. dichotomum,* but instead of two species each with two varieties, as one species with three varieties: *D. ensifolium* vars. *ensifolium, unciphyllum,* and *breve.* This leaves *D. dichotomum* consisting of the larger, more diffuse plants with spikelets longer than 1.5 mm. Lelong (1984, 1986) recognized seven varieties of *P. dichotomum* in this group, based on leaf size and pubescence forms. The Florida material shows too much overlap in these characters for satisfactory separation.

This species is common throughout Florida, occurring in both dry and moist habitats.

Dichanthelium ensifolium (Baldwin ex Elliott) Gould, Brittonia 26: 59. 1974. *Panicum ensifolium* Baldwin ex Elliott, Sketch Bot. S. Carolina 1: 126. 1816. *Panicum nitidum* Lamarck var. *ensifolium* (Baldwin ex Elliott) Vasey, U.S.D.A. Div. Agrost. Bull. 8: 29. 1889. *Dichanthelium dichotomum* (Linnaeus) Gould var. *ensifolium* (Baldwin ex Elliott) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1119. 1978. TYPE: United States. Georgia: *Baldwin s.n.* (holotype, CHARL; isotypes, PH, US, fragm.).

We recognize three varieties of *Dichanthelium ensifolium* in Florida:

1a. Lower internodes strigose; leaves less than 2 mm wide .... var. *breve*
1b. Lower internodes glabrous to slightly puberulent; most leaves wider than 2 mm.
    2a. Spikelets pubescent; leaves often with white margins .... var. *unciphyllum*
    2b. Spikelets glabrous to sparingly pubescent; leaves without white margins ... var. *ensifolium*

Dichanthelium ensifolium (Baldwin ex Elliott) Gould var. **ensifolium**

Panicum chamaelonche Trinius, Gram. Panic. 242. 1826. TYPE: United States. "Am. bor.," *Enslin s.n.* (holotype, LE; isotype, US, fragm.).

Panicum nitidum Lamarck var. *minus* Vasey, Contr. U.S. Natl. Herb. 3: 30. 1892. TYPE: United States. Florida: St. Johns Co., St. Augustine, Apr. 1869, *Canby s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 268. 1910).

Panicum baldwinii Nuttall ex Chapman, Fl. South. U.S., ed. 3. 586. 1897. TYPE: United States. Florida: *Baldwin s.n.* (lectotype, PH). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 168. 1910).

Panicum brittonii Nash, Bull. Torrey Bot. Club 24: 194. 1897. TYPE: United States. New Jersey: Ocean Co., Forked River, 29 May–2 June 1896, *Britton s.n.* (holotype, NY).

Panicum glabrifolium Nash, Bull. Torrey Bot. Club 24: 196. 1897. *Dichanthelium dichotomum* (Linnaeus) Gould var. *glabrifolium* (Nash) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1120. 1978. TYPE: United States. Florida: Hillsborough Co., Tampa, 20 Aug. 1895, *Nash 2415a* (holotype, NY).

Panicum cuthbertii Ashe, J. Elisha Mitchell Sci. Soc. 15: 48. 1898. TYPE: United States. South Carolina: Beaufort Co., St. Helena Island, 1887, *Cuthbert s.n.* (holotype, NCU; isotype, US, fragm.).

Panicum glabrissimum Ashe, J. Elisha Mitchell Sci. Soc. 15: 62. 1898. *Panicum shallotte* Ashe, J. Elisha Mitchell Sci. Soc. 16: 84. 1900, nom. illegit. TYPE: United States. North Carolina: Dare Co., Manteo, June 1898, *Ashe s.n.* (lectotype, US; isotype, NY, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 265. 1910).

Panicum curtifolium Nash, Bull. Torrey Bot. Club 26: 569. 1899. *Panicum ensifolium* Baldwin ex Elliott var. *curtifolium* (Nash) Lelong, Brittonia 36: 266. 1984. TYPE: United States. Mississippi: Jackson Co., Ocean Springs, 2 May 1898, *Nash 4598* (holotype, NY; isotype, US).

Panicum earlei Nash, Bull. Torrey Bot. Club 26: 571. 1899. TYPE: United States. Alabama: Lee Co., Auburn, 7 May 1898, *Earle & Baker 1532* (holotype, NY; isotype, US).

Panicum flavovirens Nash, Bull. Torrey Bot. Club 26: 572. 1899. TYPE: United States. Florida: Lake Co., "along the edge of road leading to the ford near the J.T. & K.W. R.R. bridge across the Wekiva river," near Eustis, 26–30 June 1895, *Nash 2061* (holotype, NY).

Panicum austromontanum Ashe, J. Elisha Mitchell Sci. Soc. 16: 85. 1900. TYPE: United States. Alabama: Jackson Co., Sand Mountain, June 1899, *Ashe s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 267. 1910).

Panicum parvipaniculatum Ashe, J. Elisha Mitchell Sci. Soc. 16: 87. 1900. TYPE: United States. North Carolina: Onslow Co., 10–18 mi. E of Jacksonville, 20 May 1899, *Ashe s.n.* (lectotype, NCU; isotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 265. 1910).

Panicum vernale A. Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 266. 1910. TYPE: United States. Florida: Columbia Co., Lake City, 16 Apr. 1906, *Hitchcock 1020* (holotype, US; isotype, ISC).

This variety is very common throughout Florida, occurring in seeps, bogs, and wet pinelands.

Dichanthelium ensifolium (Baldwin ex Elliott) Gould var. **breve** (A. Hitchcock & Chase) B. F. Hansen & Wunderlin, comb. nov. BASIONYM: *Panicum breve* A. Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 271. 1910. *Dichan-*

thelium dichotomum (Linnaeus) Gould var. *breve* (A. Hitchcock & Chase) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1120. 1978. *Panicum chamaelonche* Trinius var. *breve* (A. Hitchcock & Chase) Lelong, Brittonia 36: 267. 1984. TYPE: United States. Florida: Martin Co., "Jensen," 5 Apr. 1906, *Hitchcock 734* (holotype, US).

This variety is endemic to the white sand scrub vegetation of central Florida.

Dichanthelium ensifolium (Baldwin ex Elliott) Gould var. **unciphyllum** (Trinius) B. F. Hansen & Wunderlin, comb. nov. BASIONYM: *Panicum unciphyllum* Trinius, Gram. Panic. 242. 1826; and the autonym created by *P. unciphyllum* Trinius var. *implicatum* (Lamson-Scribner) Lamson-Scribner & Merrill 1901. *Panicum acuminatum* Swartz var. *unciphyllum* (Trinius) Lelong, Brittonia 36: 269. 1984. TYPE: North America, without data (lectotype, LE). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 259. 1910). For comments concerning the mistypification by Lelong (1984), see under *D. acuminatum* var. *implicatum*.

Panicum tenue Muhlenberg, Descr. Gram. 118. 1817. *Panicum liton* Schultes, Mant. 2: 250. 1824, nom. illegit. *Panicum macrum* Kunth, Révis. Gramin. 1: 40. 1829, nom. illegit. *Dichanthelium dichotomum* (Linnaeus) Gould var. *tenue* (Muhlenberg) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1119. 1978. TYPE: United States: *Muhlenberg Herb. 192* (lectotype, PH-M; isotype, US, fragm.). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 259. 1910).

Panicum albomarginatum Nash, Bull. Torrey Bot. Club 24: 40. 1897. TYPE: United States. Florida: Lake Co., near Eustis, June 1894, *Nash 925* (holotype, NY; isotypes, MO, NY, US).

Panicum trifolium Nash, Bull. Torrey Bot. Club 26: 580. 1899. TYPE: United States. Georgia: Bibb Co., Ocmulgee River Swamp below Macon, 18–24 May 1895, *Small s.n.* (holotype, NY; isotype, US).

Panicum gracilicaule Nash in Small, Fl. S.E. U.S. 98, 1327. 1903, non Rendle 1899. *Panicum concinnius* A. Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 263. 1910. TYPE: United States. Alabama: Jackson Co., Sand Mountain, 1900, *Harbison 2415* (holotype, NY).

Lelong (1984, 1986) applied the epithet *unciphyllum* to a variety of *D. acuminatum*. While *unciphyllum* is certainly the earliest epithet for Lelong's variety, there is a good deal of doubt that it belongs with *D. acuminatum*. Hitchcock & Chase (1910) lectotypified *Panicum unciphyllum* with material now at LE. The LE material apparently has two collections on one sheet. According to Hitchcock & Chase, the collection chosen as lectotype is conspecific with *Panicum tenue*, while the other collection (by Enslin) matches *Panicum columbianum*, neither of which belongs in *D. acuminatum*. Without having seen the specimen, Lelong (1984) cited as holotype (not lectotype) of *Panicum unciphyllum* the Enslin collection at LE, this without explanation of the rejection of the earlier Hitchcock & Chase lectotypification. Without such explanation and barring further discoveries concerning the type, the lectotypification of Hitchcock & Chase must be followed. Therefore, *Panicum unciphyllum* is once again considered conspecific with *Panicum tenue*, which in turn is placed in *Dichanthelium ensifolium*. It is unfortunate that *unciphyllum* also turns out to be the earliest varietal epithet for what has been called *Panicum tenue*, this adding to the confusion.

This variety often approaches *D. dichotomum* in general aspect but is better classified with *D. ensifolium* on the basis of spikelet size. It is common throughout Florida, occurring in wet pinelands and woods.

Dichanthelium erectifolium (Nash) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1105. 1978. *Panicum sphaerocarpon* Elliott var. *floridanum* Vasey, U.S.D.A. Div. Agrost. Bull. 8: 33. 1889. *Panicum erectifolium* Nash, Bull. Torrey Bot. Club 23: 148. 1896. *Panicum floridanum* (Vasey) Chapman, Fl. South. U.S., ed. 3. 585. 1897, non Trinius 1835. TYPE: United States. Florida: "Moist pine barrens, Mosquito Inlet," May 1879, *Curtiss 3599* (lectotype, US; isotype, MO). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 256. 1910).

This species is closely related to *D. sphaerocarpon* but readily separable on the basis of spikelet size. It is quite common throughout most of Florida, except for southern Florida and the Keys, in moist flatwoods and meadows.

Dichanthelium laxiflorum (Lamarck) Gould, Brittonia 26: 60. 1974. *Panicum laxiflorum* Lamarck, Encycl. 4: 748. 1798. *Panicum dichotomum* Linnaeus var. *laxiflorum* (Lamarck) Beal, Grasses N. Amer. 2: 139. 1896. TYPE: United States?: *Lamarck Herb. s.n.* (holotype, P-L).

Panicum xalapense Kunth, in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 1: 103. 1816. TYPE: Mexico. Veracruz: near Jalapa, *Humboldt & Bonpland s.n.* (holotype, P).

Panicum ruprechtii Fournier, Mexic. Pl. 2: 21. 1886, non Fenzl 1854. TYPE: Mexico. Veracruz: Jalapa, *Galeotti 5733* (holotype, BR).

Panicum pyriforme Nash, Bull. Torrey Bot. Club 26: 579. 1899. TYPE: United States. Florida: Lake Co., Orange Bend, 12–31 Mar. 1894, *Nash 239* (holotype, NY; isotypes, MO, NY, US).

Panicum xalapense Kunth var. *strictirameum* A. Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 161. 1910. *Panicum laxiflorum* Lamarck var. *strictirameum* (A. Hitchcock & Chase) Fernald, Rhodora 36: 75. 1934. TYPE: United States. Mississippi: Hinds Co., Jackson, 28 Apr. 1906, *Hitchcock 1311* (holotypes, US).

Dichanthelium laxiflorum is common throughout Florida except for Dade and Monroe counties. It is usually found in moist woods.

Dichanthelium leucothrix (Nash) Freckmann, Phytologia 58: 101. 1981. *Panicum leucothrix* Nash, Bull. Torrey Bot. Club 24: 41. 1897. *Panicum acuminatum* Swartz var. *leucothrix* (Nash) Lelong, Brittonia 36: 271. 1984. TYPE: United States. Florida: Lake Co., near Eustis, July 1894, *Nash 1338* (holotype, NY; isotypes, NCU, NY, TAES, US).

Panicum strictum Bosc ex Roemer & Schultes, Syst. Veg. 2: 447. 1817, non R. Brown 1810. TYPE: United States. "Carolina," *Bosc s.n.* (lectotype, M; isotype, B-W). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 207. 1910).

Panicum minutulum Desvaux, Opusc. Sci. Phys. Nat. 87. 1831, non Gaudichaud-Beaupré 1826. TYPE: United States?: *Desvaux Herb. s.n.* (holotype, P).

Panicum parvispiculum Nash, Bull. Torrey Bot. Club 24: 347. 1897. TYPE: United States. Georgia: McIntosh Co., Darien Junction, 25–27 June 1895, *Small s.n.* (holotype, NY; isotype, US, fragm.).

Panicum wrightianum Lamson-Scribner, U.S.D.A. Div. Agrost. Bull. 11: 44, f. 4. 1898. *Dichanthelium acuminatum* (Swartz) Gould & Clark var. *wrightianum* (Lamson-Scribner) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1126. 1978. *Dichanthelium wrightianum* (Lamson-Scribner) Freckmann, Phytologia 48: 101. 1981. TYPE: Cuba: *Wright 3463* (holotype, US).

Panicum longiligulatum Nash, Bull. Torrey Bot. Club 26: 574. 1899. *Dichanthelium acuminatum* (Swartz) Gould & Clark var. *longiligulatum* (Nash) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1127. 1978. *Dichanthelium longiligulatum* (Nash) Freckmann, Phytologia 48: 102. 1981. *Panicum acuminatum* Swartz var. *longiligulatum* (Nash) Lelong, Brittonia 36: 270. 1984. TYPE: United States. Florida: Franklin Co., Apalachicola, 1892, *Vasey s.n.* (holotype, NY).

Dichanthelium leucothrix is the small-fruited member of the *D. acuminatum* complex. Robust, glabrous specimens may be difficult to separate from *D. acuminatum* var. *lindheimeri*, which has larger, fewer-fruited inflorescences and a more northerly distribution. There may be some justification for the separation of the glabrous (traditionally *Panicum longiligulatum*) and pubescent (*P. leucothrix*) specimens at the varietal level; most previous authors have indeed split this taxon into at least two taxa based on forms of pubescence. The pubescence, however, intergrades completely from the extremes, while otherwise the taxon is quite homogeneous. Therefore, we have chosen not to recognize the segregates.

This species is common throughout Florida, mostly in pine flatwoods.

Dichanthelium oligosanthes (Schultes) Gould, Brittonia 26: 60. 1974. *Panicum pauciflorum* Elliott, Sketch Bot. S. Carolina 1: 120. 1816, non R. Brown 1810. *Panicum oligosanthes* Schultes, Mant. 2: 256. 1824. *Panicum scoparium* Lamarck var. *pauciflorum* Lamson-Scribner, Tennessee Agric. Exp. Sta. Bull. 7: 48. 1894. TYPE: United States. Georgia: *Elliott Herb. s.n.* (lectotype, CHARL: isotype, US, fragm.). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 285. 1910).

Panicum macrocarpon Torrey, Fl. N. Middle United States 143. 1823, non LeConte 1819. TYPE: United States. Massachusetts: Franklin Co., banks of the Connecticut River, near Deerfield, *Cooley s.n.* (holotype, NY).

Panicum scoparium Lamarck var. *angustifolium* Vasey, U.S.D.A. Div. Agrost. Bull. 8: 32. 1889. TYPE: United States. South Carolina: *Ravenel s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 286. 1910).

Panicum scribnerianum Nash, Bull. Torrey Bot. Club 22: 421. 1895. *Panicum oligosanthes* Schultes var. *scribnerianum* (Nash) Fernald, Rhodora 36: 80. 1934. *Dichanthelium oligosanthes* (Schultes) Gould var. *scribnerianum* (Nash) Gould, Brittonia 26: 60. 1974. TYPE: United States. Pennsylvania: Bradford Co., Wysox, July 1836, *Carey s.n.* (lectotype, GH). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 283. 1910). Gould & Clark (1978) erroneously stated that this name is based on *Panicum macrocarpon* Torrey.

Panicum helleri Nash, Bull. Torrey Bot. Club 26: 572. 1899. *Panicum oligosanthes* Schultes var. *helleri* (Nash) Fernald, Rhodora 36: 80. 1934. TYPE: United States. Texas: Kerr Co., Kerrville, 14–21 May 1894, *Heller 1759* (holotype, NY).

Panicum pernervosum Nash, Bull. Torrey Bot. Club 26: 576. 1899. TYPE: United States. Texas: Harris Co., Houston, 16 Apr. 1872, *Hall 830* (holotype, NY).

Most recent authors have followed Fernald in recognizing *P. scribnerianum* at least at the varietal level. The characteristics of pubescence used to separate the taxa, however, are very unreliable and seem not to be correlated with any other concrete evidence that differentiation has occurred in this species. There seems to us little to be gained by the formal recognition of these pubescence phases.

This species is rather uncommon in the northern tier of counties, occurring in dry pine–oak–hickory woods.

Dichanthelium ovale (Elliott) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1115. 1978. *Panicum ovale* Elliott, Sketch Bot. S. Carolina 1: 123. 1816. TYPE: United States. Georgia: Camden Co., St. Marys, *Baldwin s.n.* (holotype, CHARL).

Panicum villosum Elliott, Sketch Bot. S. Carolina 1: 124. 1816, non Lamarck 1791. *Panicum consanguineum* Kunth, Révis. Gramin. 1: 36. 1829. *Panicum commutatum* Schultes var. *consanguineum* (Kunth) Beal, Grasses N. Amer. 2: 141. 1896. *Dichanthelium consanguineum* (Kunth) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1115. 1978. TYPE: United States: *Elliott Herb. s.n.* (holotype, CHARL; isotype, US, fragm.).

Panicum ciliiferum Nash, Bull. Torrey Bot. Club 24: 195. 1897. TYPE: United States. Florida: Lake Co., Eustis, 12–31 Mar. 1894, *Nash 147* (holotype, NY; isotypes, MO, US).

Panicum malacon Nash, Bull. Torrey Bot. Club 24: 197. 1897. TYPE: United States. Florida: Lake Co., Eustis, 1–15 May 1894, *Nash 628* (holotype, NY; isotypes, MO, NY, US).

Panicum georgianum Ashe, J. Elisha Mitchell Sci. Soc. 15: 36. 1898. *Panicum cahoonianum* Ashe, J. Elisha Mitchell Sci. Soc. 15: 113. 1899, nom. illegit. TYPE: United States. Georgia: McIntosh Co., Darien Junction, 27 June 1895, *Small s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 169. 1910).

Panicum strictifolium Nash, Bull. Torrey Bot. Club 26: 579. 1899. TYPE: United States. Florida: Lake Co., Eustis, 3 May 1894, *Nash 603* (holotype, NY; isotypes, NY, US).

Panicum erythrocarpon Ashe, J. Elisha Mitchell Sci. Soc. 16: 90. 1900. TYPE: United States. North Carolina: New Hanover Co., 1 mi. N of Wilmington, 19 May 1899, *Ashe s.n.* (holotype, NCU; isotype, US).

Panicum euchlamydeum Shinners, Amer. Midl. Naturalist 32: 170. 1944. *Panicum commonsianum* Ashe var. *euchlamydeum* (Shinners) R. Pohl, Amer. Midl. Naturalist 38: 507. 1947. *Dichanthelium commonsianum* (Ashe) Freckmann var. *euchlamydeum* (Shinners) Freckmann, Phytologia 39: 271. 1978. TYPE: United States. Wisconsin: Adams Co., 12 mi. SE of Adams, *Shinners & Shaw 4415* (holotype, WIS; isotypes, GH, MIL, MIN, US).

As defined here, *Dichanthelium ovale* consists of the large-fruited specimens of the *D. acuminatum* complex. If smaller-fruited plants are included in this taxon, as in past treatments, problems in naming the many overlapping specimens become insurmountable. By delimiting the species as we have, a more homogeneous and practical system results, one where almost every specimen can be classified.

Gould & Clark (1978) recognized *Dichanthelium consanguineum* as a separate species characterized by pilose upper leaf surfaces. Again, the pubescence character seems insufficient for the separation of species.

Dichanthelium ovale is common in sandhills, pinelands, and disturbed habitats throughout Florida.

Dichanthelium portoricense (Desvaux ex Hamilton) B. F. Hansen & Wunderlin, comb. nov. BASIONYM: *Panicum portoricense* Desvaux ex Hamilton, Prodr. 11. 1825. TYPE: Puerto Rico: *Desvaux Herb. s.n.* (holotype, P).

Panicum lancearium Trinius, Gram. Panic. 223. 1826. TYPE: United States: "Am. bor.," *Enslin s.n.* (holotype, LE; isotype, US, fragm.).

Panicum heterophyllum Bosc. ex C. Nees von Esenbeck in Martius, Fl. Bras. Enum. Pl. 2(1): 227. 1829, non Sprengel 1822. TYPE: United States: *Bosc s.n.* (holotype, B-W).

Panicum webberianum Nash, Bull. Torrey Bot. Club 23: 149. 1896. TYPE: United States. Florida: Lake Co., Eustis, 16–31 May 1894, *Nash 781* (holotype, NY; isotypes, MO, NY, US).

Panicum columbianum Lamson-Scribner, U.S.D.A. Div. Agrost. Bull. 7: 78, f. 60. 1897. *Dichanthelium columbianum* (Lamson-Scribner) Freckmann, Phytologia 39: 270. 1978. *Panicum acuminatum* Swartz var. *columbianum* (Lamson-Scribner) Lelong, Brittonia 36: 270. 1984. TYPE: United States. District of Columbia: Brookland, 14 July 1894, *Lamson-Scribner s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 247. 1910).

Panicum nashianum Lamson-Scribner, U.S.D.A. Div. Agrost. Bull. 7: 79, f. 61. 1897. *Panicum portoricense* Desvaux ex Hamilton var. *nashianum* (Lamson-Scribner) Lelong, Brittonia 36: 267. 1984. TYPE: United States. Florida: Lake Co., vicinity of Eustis, 15–30 Apr. 1894, *Nash 466* (lectotype, US; isotype, MO). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 273. 1910).

Panicum tsugetorum Nash, Bull. Torrey Bot. Club 25: 86. 1898. TYPE: United States. New York: Bronx, New York Botanical Garden, 22 June 1896, *Nash 287* (holotype, NY; isotype, US, fragm.).

Panicum patentifolium Nash, Bull. Torrey Bot. Club 26: 574. 1899. TYPE: United States. Florida: Lake Co., Eustis, 12–31 Mar. 1894, *Nash 72* (holotype, NY; isotypes, MO, NY, US).

Panicum psammophilum Nash, Bull. Torrey Bot. Club 26: 576. Nov. 1899, non Welwitsch July 1899. TYPE: United States. New Jersey: Ocean Co., Tom's River, 25–31 July 1898, *Clute 175* (holotype, NY; isotype, US).

Panicum onslowense Ashe, J. Elisha Mitchell Sci. Soc.

16: 88. Feb. 1900. TYPE: United States. North Carolina: Onslow Co., near Ward's Mill, 11 mi. E of Jacksonville, 19–21 May 1899, *Ashe s.n.* (lectotype, NCU: isotypes, NCU, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 276. 1910). Lelong (1984) cited the lectotype as residing at UNC, but Hitchcock & Chase clearly stated that the type is in Ashe's herbarium, now at NCU.

Panicum pauciciliatum Ashe, J. Elisha Mitchell Sci. Soc. 16: 87. Feb. 1900. TYPE: United States. North Carolina: New Hanover Co., near Wilmington, 20 May 1899, *Ashe s.n.* (lectotype, NCU; isotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 272. 1910). Specimen at NCU not located.

Panicum nashianum Lamson-Scribner var. *patulum* Lamson-Scribner & Merrill, U.S.D.A. Div. Agrost. Circ. 27: 9. Dec. 1900. *Panicum patulum* (Lamson-Scribner & Merrill) A. Hitchcock, Rhodora 8: 209. 1906. *Panicum lancearium* Trinius var. *patulum* (Lamson-Scribner & Merrill) Fernald, Rhodora 36: 80. 1934. *Dichanthelium sabulorum* (Lamarck) Gould & Clark var. *patulum* (Lamson-Scribner & Merrill) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1113. 1978. TYPE: United States. Florida: Manatee Co., Braidentown [Bradenton], 3 Sep. 1898, *Combs 1296* (holotype, US).

As pointed out by Lelong (1984), *Panicum sabulorum* Lamarck, whose type is from Uruguay, is not conspecific with our material, contrary to the treatment by Gould & Clark (1978). This leaves as the earliest name in the taxon *Panicum portoricense* Desvaux ex Hamilton, which unfortunately necessitates a new combination in *Dichanthelium*.

Gould & Clark (1978) and Lelong (1984, 1986) recognized two varieties in this species, based on spikelet length, inflorescence size, and leaf length. In the Florida material, however, spikelet size is but poorly correlated with inflorescence size, both of which seem unrelated to leaf size. Infraspecific taxa have therefore not been applied to this species.

Panicum columbianum was classified by Lelong (1984) as a variety of *P. acuminatum*. According to the description of Hitchcock & Chase (1910), *P. columbianum* and its synonym (fide Lelong) *P. tsugetorum* have ligules up to 1.5 mm long. The short ligules take *P. columbianum* out of the *P. acuminatum* complex.

Dichanthelium portoricense is probably the most commonly collected member of the genus in Florida. It occurs in a variety of habitats throughout the state.

Dichanthelium ravenelii (Lamson-Scribner & Merrill) Gould, Brittonia 26: 60. 1974. *Panicum ravenelii* Lamson-Scribner & Merrill, U.S.D.A. Div. Agrost. Bull. 24: 36. 1901. TYPE: United States. South Carolina: *Elliott s.n.* (lectotype, CHARL). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 287. 1910).

Panicum scoparium Lamarck var. *major* Vasey, U.S.D.A. Div. Agrost. Bull. 8: 32. 1889, as "majus." TYPE: United States. South Carolina: *Ravenel s.n.* (holotype, US).

This large grass, related to *D. scoparium*, is known in Florida only from the panhandle region, occurring in dry hammocks.

Dichanthelium scabriusculum (Elliott) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1110. 1978. *Panicum scabriusculum* Elliott, Sketch Bot. S. Carolina 1: 121. 1816. *Panicum viscidum* Elliott var. *scabriusculum* (Elliott) Beal, Grasses N. Amer. 2: 143. 1896. TYPE: United States. Georgia: Chatham Co., Savannah, *Baldwin s.n.* (holotype, CHARL).

Panicum lanuginosum Bosc ex Sprengel, Syst. Veg. 1: 319. 1825, non Elliott 1816. *Panicum eriophorum* Schultes ex Kunth, Enum. Pl. 1: 128. 1833. TYPE: United States. Georgia: *Bosc s.n.* (holotype, B-W).

Panicum nealleyi Vasey, Bull. Torrey Bot. Club 13: 25. 1886. TYPE: United States. Texas: May 1885, *Nealley s.n.* (holotype, US).

Panicum dichotomum Linnaeus var. *elatum* Vasey, U.S.D.A. Div. Agrost. Bull. 8: 31. 1889. TYPE: United States. Alabama: Mobile Co., 18 June 1888, *Mohr s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 298. 1910).

Panicum cryptanthum Ashe, N. Carolina Agric. Exp. Sta. Bull. 175: 115. 1900. TYPE: United States. North Carolina: Johnston Co., Wilsons Mill, 15 July 1897, *Ashe s.n.* (lectotype, NCU; isotypes, NCU). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 299. 1910).

Panicum aculeatum A. Hitchcock & Chase, Rhodora 8: 209. 1906. TYPE: United States. District of Columbia: Takoma Park, 27 July 1904, *Chase 2520* (holotype, US).

Panicum recognitum Fernald, Rhodora 40: 331, pl. 497–498. 1938. TYPE: United States. New Jersey: Camden Co., headwaters of branch of Timber Creek, Albion, 27 June 1912, *Long 7671* (holotype, GH; isotype, PH). Gould & Clark (1978) erroneously cited the location of the holotype as US.

This species is quite common in northern Florida, ranging southward to Orange County. It is primarily found in bogs, cypress swamps, and wet woods.

Dichanthelium scoparium (Lamarck) Gould, Brittonia 26: 60. 1974. *Panicum scoparium* Lamarck, Encycl. 4: 744. 1798. *Panicum scoparium* Lamarck var. *genuinum* Lamson-

Scribner, Tennessee Agric. Exp. Sta. Bull. 7: 48. 1894, nom. inadmiss. TYPE: United States: "Caroline," *Michaux s.n.* (holotype, P-M). Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 287. 1910) mistypified var. *genuinum* with Elliott's material of *P. ravenelii*. Lamson-Scribner's citation of *P. scoparium* Lamarck necessitates the obvious disposal of this inadmissible varietal epithet here.

Panicum pubescens Lamarck, Encycl. 4: 748. 1798. *Panicum laxiflorum* Lamarck var. *pubescens* (Lamarck) Chapman, Fl. South. U.S., ed. 3. 586. 1897. *Chasea pubescens* (Lamarck) Nieuwland, Amer. Midl. Naturalist 2: 64. 1911. TYPE: United States. South Carolina: *Michaux s.n.* (lectotype, P-M). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 294. 1910).

Panicum viscidum Elliott, Sketch Bot. S. Carolina 1: 123, pl. 7(3). 1816. TYPE: United States: *Elliott Herb. s.n.* (lectotype, CHARL). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 294. 1910).

Panicum nitidum Lamarck var. *velutinum* Döll in Martius, Fl. Bras. 2(2): 247. 1877. TYPE: United States. Texas.

Although this species is usually locally abundant, it is confined in Florida to the northern tier of counties. It occurs in marshes, moist woods, and roadsides.

Dichanthelium sphaerocarpon (Elliott) Gould, Brittonia 26: 60. 1974. *Panicum sphaerocarpon* Elliott, Sketch Bot. S. Carolina 1: 125. 1816. *Panicum dichotomum* Linnaeus var. *sphaerocarpon* (Elliot) Alph. Wood, Class-Book Bot., ed. 1861. 786. 1861. *Panicum microcarpon* Muhlenberg var. *sphaerocarpon* (Elliott) Vasey, Grass. U.S. 12. 1883. TYPE: United States. Georgia: *Baldwin s.n.* (holotype, CHARL).

Panicum kalmii Swartz, Adnot. Bot. 6. 1829. TYPE: United States. Pennsylvania?: *Kalm s.n.* (holotype, S).

Panicum nitidum Lamarck var. *crassifolium* A. Gray ex Döll in Martius, Fl. Bras. 2(2): 247. 1877. TYPE: United States. New Jersey: *Gray? 30* (holotype, KR?; isotype, GH).

Panicum vicarium Fournier, Mexic. Pl. 2: 20. 1886. TYPE: Mexico. Veracruz: Córdoba, s.d., *Schaffner 285* (holotype, P).

Panicum inflatum Lamson-Scribner & J. G. Smith, U.S.D.A. Div. Agrost. Circ. 16: 5. 1899. *Panicum sphaerocarpon* Elliott var. *inflatum* (Lamson-Scribner & J. G. Smith) A. Hitchcock in Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 253. 1910. TYPE: United States. Mississippi: Harrison Co., Biloxi, Oct. 1898, *Tracy 4622* (holotype, US).

Panicum mississippiense Ashe, J. Elisha Mitchell Sci. Soc. 16: 91. 1900. TYPE: United States. Louisiana: Orleans Par., "Banks of the Mississippi River below New Orleans in October," *Ashe s.n.* (holotype, not located).

This species occurs in bogs and seeps in the panhandle area of Florida.

Dichanthelium strigosum (Muhlenberg ex Elliott) Freckman, Brittonia 33: 457. 1981. *Panicum strigosum* Muhlenberg ex Elliott, Sketch Bot. S. Carolina 1: 126. 1816. TYPE: United States. "Hab. in humidis. Car: & Georg:," *Elliott Herb. s.n.* (lectotype, CHARL; isotype, US, fragm.). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 164. 1910).

Freckmann (1981b) recognized that *strigosum* was the earliest specific epithet for this species and made the necessary combinations for the three rather well marked (for this genus) varieties.

KEY TO THE VARIETIES OF *DICHANTHELIUM STRIGOSUM*

1a. Spikelets puberulent or pubescent, 1.5–2.1 mm long .... var. *leucoblepharis*
1b. Spikelets glabrous, 1.1–1.8 mm long.
    2a. Leaf blade surfaces glabrous; spikelets 1.2–1.8 mm long .... var. *glabrescens*
    2b. Leaf blade surfaces pilose; spikelets 1.1–1.5 mm long .... var. *strigosum*

Dichanthelium strigosum (Muhlenberg ex Elliott) Freckmann var. **strigosum**

Panicum laxiflorum Lamarck var. *pubescens* Vasey, Contr. U.S. Natl. Herb. 3: 30. 1892. *Dichanthelium leucoblepharis* (Trinius) Gould & Clark var. *pubescens* (Vasey) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1101. 1978. *Panicum ciliatum* Elliott var. *pubescens* (Vasey) Freckmann ex R. Pohl, Fieldiana, Bot., n.s. 4: 356. 1980. *Panicum leucoblepharis* Trinius var. *pubescens* (Vasey) Beetle, Phytologia 48: 192. 1981. TYPE: United States. Florida: Duval Co., *Curtiss H* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 164. 1910).

Panicum longipedunculatum Lamson-Scribner, Tennessee Agric. Exp. Sta. Bull. 7: 53, pl. 16(61). 1894. TYPE: United States. Tennessee: White Cliff Springs, July 1890, *Lamson-Scribner s.n.* (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 164. 1910).

Uncommon in Florida, this variety ranges from northern Florida south to the central peninsula.

Dichanthelium strigosum (Muhlenberg ex Elliott) Freckmann var. **glabrescens** (Grisebach) Freckmann, Brittonia 33: 457. 1981. *Panicum dichotomum* Linnaeus var. *glabrescens* Grisebach, Fl. Brit. W. I. 553. 1864.

Dichanthelium leucoblepharis (Trinius) Gould & Clark var. *glabrescens* (Grisebach) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1100. 1978. TYPE: Jamaica: *Purdie s.n.* (holotype, K).

Panicum polycaulon Nash, Bull. Torrey Bot. Club 24: 200. 1897. TYPE: United States. Florida: Hillsborough Co., Tampa, 20 Aug. 1895, *Nash 2420a* (holotype, NY; isotype, US, fragm.).

This variety is common throughout Florida in moist pinelands, bogs, and coastal swales.

Dichanthelium strigosum (Muhlenberg ex Elliott) Freckmann var. **leucoblepharis** (Trinius) Freckmann, Brittonia 33: 457. 1981. *Panicum leucoblepharis* Trinius, Clav. Agrostogr. Antiq. 234. 1822. *Dichanthelium leucoblepharis* (Trinius) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1099. 1978. TYPE: United States. "Am. bor.," *Enslin s.n.* (lectotype, LE). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 162. 1910).

Panicum ciliatum Elliott, Sketch Bot. S. Carolina 1: 126. 1816, non Märcklin 1792. *Panicum ciliatifolium* Kunth, Révis. Gramin. 1: 36. 1829. TYPE: United States. *Elliott Herb. s.n.* (holotype, CHARL).

Panicum ciliatifolium Desvaux, Opusc. Sci. Phys. Nat. 88. 1831, non Kunth 1829. TYPE: "America boreali" (specimen unknown).

When making the new combination *Panicum ciliatum* Elliott var. *pubescens* (Vasey) Freckmann ex R. Pohl (1980), based on *P. laxiflorum* var. *pubescens* Vasey (1892), Pohl created the autonym *Panicum ciliatum* Elliott var. *ciliatum*. At first glance, this autonym would seem to be the earliest varietal name for this taxon. However, *Panicum ciliatum* Elliott, 1816, is illegitimate because it is a later homonym of *Panicum ciliatum* Märcklin, 1792, as pointed out by Veldkamp (1976). Since an autonym can only be established on a legitimate name (ICBN Art. 26), as verified by Dan Nicolson (pers. comm.), the next epithet in line, *leucoblepharis*, must be chosen.

This variety is rare in Florida, found only in the northern counties, occurring in pinelands.

EXCLUDED SPECIES

Dichanthelium linearifolium (Lamson-Scribner) Gould

This northern species was reported from the Florida panhandle by Clewell (1985), but no supporting specimens have been found.

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NOTES

PASSIFLORA EGLANDULOSA, A NEW SPECIES IN SECTION *CIECA* (MEDIKUS) DC. FORMERLY INCLUDED WITH *P. TRINIFOLIA* MASTERS

Passiflora trinifolia Masters "is very common in the forests of the Occidente" of Guatemala according to Standley & Williams (1961). Indeed, this name has been applied to a locally abundant apetalous passionflower of the wet montane forests of northern Central America. However, while preparing a revision of *Passiflora* L. section *Cieca* (Medikus) DC., extreme and bimodal variation of vegetative characters was noted among the specimens circulated as *P. trinifolia*. Consequently, closer analysis revealed the existence of two distinct species: the actually very rare *P. trinifolia*, and the more common but previously unnamed species described below.

Passiflora eglandulosa MacDougal, sp. nov. TYPE. Guatemala. San Marcos: wet mountain forest at Aldea Fraternidad, W-facing slope of Sierra Madre between San Rafael Pie de La Cuesta and Palo Gordo [ca. 14°56′N, 91°52′W], 1,800–2,400 m, 10–18 Dec. 1963, *Williams, Molina & Williams 25997* (holotype, F; isotypes, ENCB, G, NY, S, US, W—2 sheets). Figures 1, 2B, 3.

Passiflora ad sectio *Cieca* pertinens, scandens; stipulae ovatae 2.5–9 mm latae; petioli eglandulosi; folia eglandulosa trilobata haud peltata, lobis acuminatis vel caudatis, lobo centrali quam lateralibus longiori, marginibus integris; pedunculi ebracteati; petala nulla; coronae filamenta biseriata, filamentis exterioribus 3–4 mm longis, usque ad 0.2–0.3 mm diametro, filamentis interioribus ad 1.5 mm longis; operculum plicatum; ovarium glabrum; semina reticulato-foveata.

Slender, climbing, perennial herb 2–4 m long, minutely puberulent and sparsely to lightly pubescent with trichomes of 2 size classes: smaller (microscopic) trichomes 0.05–0.10 mm, unicellular, clavate and antrorsely bent or appressed, present throughout; larger trichomes (0.2–)0.4–0.6(–0.8) mm, unicellular, cylindrical and pointed, slightly bent antrorsely. Stem perennial with little secondary growth, terete or subterete but drying strongly obtusely sulcate, glabrescent below, sparsely to lightly pubescent above with trichomes 0.25–0.6 (–0.7) mm, pubescence often restricted to one side of stem; posture of shoot apex straight, negatively geotropic. Stipules (3.5–)5–14(–20) × (2.5–)3–8(–9) mm, ovate, with ca. 5–7 veins departing from stem, the midvein only slightly off center (stipule only slightly oblique), apex acute, often apiculate, margins ciliolate-setose. Petioles (0.6–) 1–3.5(–4.6) cm, eglandular, slightly canaliculate and adaxially pubescent (at least distally) with trichomes (0.2–)0.3–0.5(–0.6) mm, abaxially glabrescent with only microscopic trichomes. Laminas 2.8–10(–12) × 4.0–15(–17) cm at fertile nodes, with 5 primary veins, 3-lobed ca. ¼–½ the distance to the shallowly cordate base, the lobes triangular to deltate or ovate, long-acuminate to caudate, the angle between the lateral lobes (120–)125–160 (–170)°, the central lobe longest, with the ratio of lateral to central lobe lengths (0.68–)0.75–0.90 (–0.95), the ratio of laminar width to length 1.30–1.65(–1.75), adaxially nearly glabrous or glabrescent with a few (0.2–)0.3–0.6(–0.8) mm trichomes restricted to the primary veins, abaxially sparsely to lightly puberulent with microscopic trichomes 0.05–0.06 mm; laminas not variegated (except trace of pericostal whiteness seen on very few leaves at distal flowering nodes of *MacDougal 316*); laminar nectaries absent; seedling and juvenile laminas depressed obovate or narrowly transversely rhombic/elliptic, more shallowly 2–3-lobed, the angle between the long-acuminate lateral lobes 105–120° in seedlings and 160–170° in juveniles, central lobe shortest (or reduced to a cusp), with ratio of lateral to central lobe lengths 1.25–2.8, ratio of laminar width to length 2.0–5.7. Tendrils straight

ANN. MISSOURI BOT. GARD. 75: 1658–1662. 1988.

during development at shoot apex, often suppressed on fertile determinate axillary branches. Prophyll of vegetative ramifying bud 1, narrowly ovate, acute. Peduncles (5–)8–19(–23) mm, geminate or occasionally solitary, uniflorous, ebracteate. Flowers ca. 1.5–2 cm diam.; hypanthium 4–5.5 mm diam. with 5 retrorse spurs 0.4–0.8 mm long between bases of sepals, or sometimes spurs obsolete; stipe (2.0–)3.0–5.0(–8.0) mm; flowers borne between horizontally and erect, pale to light yellow-green except as noted, nearly inodorous; sepals (6.5–)7.5–9.0 × 2.3–3.9 mm, broadly lanceolate, rounded at apex, the 2–3 outermost cucullate and with a (0.5–)0.8–1.2 mm blunt subapical cornus, often abaxially flushed with very deep red to purplish red; petals absent; filamentous corona in 2 series, the outer filaments ca. 29–31, 3.0–4.0 mm long, 0.2–0.3 mm diam., filiform, widest at base, slightly attenuate distally, reflexed above the middle and the tips often slightly incurved, yellowish green at base, light yellow distally; inner series (0.7–)1.0–1.5 mm, capillary to subclavate, suberect; operculum 1.5–2.0 mm, membranous, plicate, sometimes with an inconspicuous narrow purplish band near middle, apex white-papillose; nectary trough without raised annulus; limen (disk) not colored or spotted; staminal filaments connate (2.5–)3.0–3.6(–4.0) mm along androgynophore, the free portions ca. 3 mm, spreading but not perpendicular to androgynophore; anthers 2.2–2.7 mm, oriented perpendicular or nearly so to their filaments at anthesis; ovary 1.5–1.9 × 1.0–1.4 mm, ellipsoid to widely ellipsoid, glabrous; styles ca. 4–5 mm, filiform, typically geniculate above middle; stigma capitellate, 0.7–0.9 mm diam. Fruit 10–13(–16) × 9–13(–14) mm, widely ellipsoid to subglobose or slightly obovoid, pericarp bluish black, glaucous, insipid; arils only half the length of the seed, firm, whitish or grayish, insipid; seeds 4.6–5.0 mm long, (2.9–)3.1–3.5 mm wide, (2.0 –)2.2–2.5 mm thick, reticulate-foveate with (15–)18–21(–24) foveae per side, obovate to widely obovate or subpyriform, the chalazal beak obtuse or obsolete, the micropylar beak obtuse or often somewhat oblong and blunt.

Additional specimens examined. EL SALVADOR. AHUACHAPAN: nebelwald region, Cerro Grande de Apaneca, ca. 1,700 m, 26 Aug. 1958 (fl), *Weberling 2610* (M—2 sheets). SANTA ANA: disturbed cloud forest near top of Cerro Verde, 30 July 1977, *Croat 42222* (MO); cloud forest, Mountain Cerro Verde, 1,800 m, 20 Feb. 1968 (fr), *Molina & Montalvo 21514* (F, NY). HONDURAS. SANTA BÁRBARA: bosque nublado, Cerro Santa Bárbara, cuestas de piedra caliza, 10 km E of Lago Yojoa, 14°55′N, 88°05′W, 1,500–2,000 m, 28–30 Apr. 1973 (fl, fr), *Clewell & Hazlett 3858* (MO, TEFH). GUATEMALA. EL PROGRESO: Montaña Canahuí between Finca San Miguel and summit of mountain, near upper limits of Finca Caieta [ca. 14°59′N, 89°54′W], 1,600–2,300 m, 10 Feb. 1942, *Steyermark 43787* (BR, F). GUATEMALA: Finca Nacional "La Aurora," 1938–1939, *Aguilar 89* (F); cerca encino y *Pinus maximinoi*, Choacorrán, km 20 a San Juan Sacatepéquez, 2,000 m, 17 Sep. 1982 (fl), *J. Castillo et al. 82.347* (F); moist thickets in deep ravines, vicinity of San Andrecillo, 1,700 m, 26 Sep. 1972 (fl, fr), *Molina & Molina 27543* (ENCB, F, US); ravine near Canales, 1,900 m, 25 Jan. 1947 (fr), *Williams & Molina 11822* (F). JALAPA: Volcán Jumay, N of Jalapa, 1,300–2,200 m, 1 Dec. 1939, *Steyermark 32352* (F). QUEZALTENANGO: cultivated at Duke University 1978–1982 from roots collected 2.5 mi. below tunnel at Santa María de Jesús, between Km posts 202–203 on Hwy. 9S, July 1978, *MacDougal 316* (AAU, BM, DUKE, F, HUA, MEXU, MO, USCG); moist forest at and above Aguas Amargas, slopes of Volcán de Zunil, 2,430–2,850 m, 17 Feb. 1939, *Standley 65404* (F); wet hillside forest, Aguas Amargas, western slope of Volcán de Zunil, 2,450 m, 14 Jan. 1941 (fl), *Standley 83336* (F); damp thicket along road above Santa María de Jesús, ca. 1,680 m, 25 Jan. 1941 (fr), *Standley 84846* (F, US); densely forested white sand quebrada, El Pocito, S of San Martín Chile Verde on road to Colomba, 2,200 m, 27 Jan. 1941, *Standley 84997* (F, G—2 sheets); damp dense mixed forest on white sand slopes above Mujuliá, between San Martín Chile Verde and Colomba, 1,800 m, 1 Feb. 1941, *Standley 85571* (F); thickets on slopes and ridges between Quebrada Chicharro and Montaña Chicharro, on SE-facing slopes of Volcán María, 1,300–1,400 m, 18 Jan. 1940 (fl, fr), *Steyermark 34360* (F); western slopes of Volcán Zunil, opposite Santa María de Jesús, 1,500 m, 21 Jan. 1940 (fr), *Steyermark 35094* (F). SAN MARCOS: wet forested quebrada, Barranco Eminencia, road between San Marcos and San Rafael Pie de la Cuesta, in upper part of the barranca between Finca La Lucha and Buena Vista, 2,500–2,700 m, 6 Feb. 1941, *Standley 86368, 86379* (F); thickets in pine woods in flat below cliffs along Río Malacaté, barrancos 6 mi. S & W of town of Tajumulco, NW slopes of Volcán Tajumulco, 2,300–2,380 m, 26 Feb. 1940, *Steyermark 36663* (F, US); montane cloud forest on outer slopes of Tajumulco Volcano, ca. 8–10 km W of San Marcos, ca. 2,300 m, 31 Dec.–1 Jan. 1964 (fl), *Williams et al. 26864* (F, GH, NY). SUCHITEPEQUEZ: Volcán Santa Clara, between Finca El Naranjo and upper slopes, 1,250–2,650 m, 23 May 1942, *Steyermark 46628, 46692* (F, US). ZACAPA: cloud forest in ravine bordering Quebrada Alejandria, summit of Sierra de las Minas, vicinity of Finca Alejandria, 2,500 m, 13 Oct. 1939 (seedling), *Steyermark 29859* (F).

The following common names are recorded from herbarium specimens: "granadilla de culebra" (Guatemala, Guatemala); "Hoja de murciélago," "flor de murciélago," "granadilla" (Quezaltenango, Guatemala).

Specimens of *P. eglandulosa* were not collected until after Killip's 1938 monograph, so the description there of *P. trinifolia* applies strictly to Masters's species. The description of *P. trinifolia* in Standley & Williams (1961), however, is a composite drawn from Killip and their observations of *P. eglandulosa*. *Passiflora eglandulosa* is superficially similar to the poorly known *P. trinifolia* by

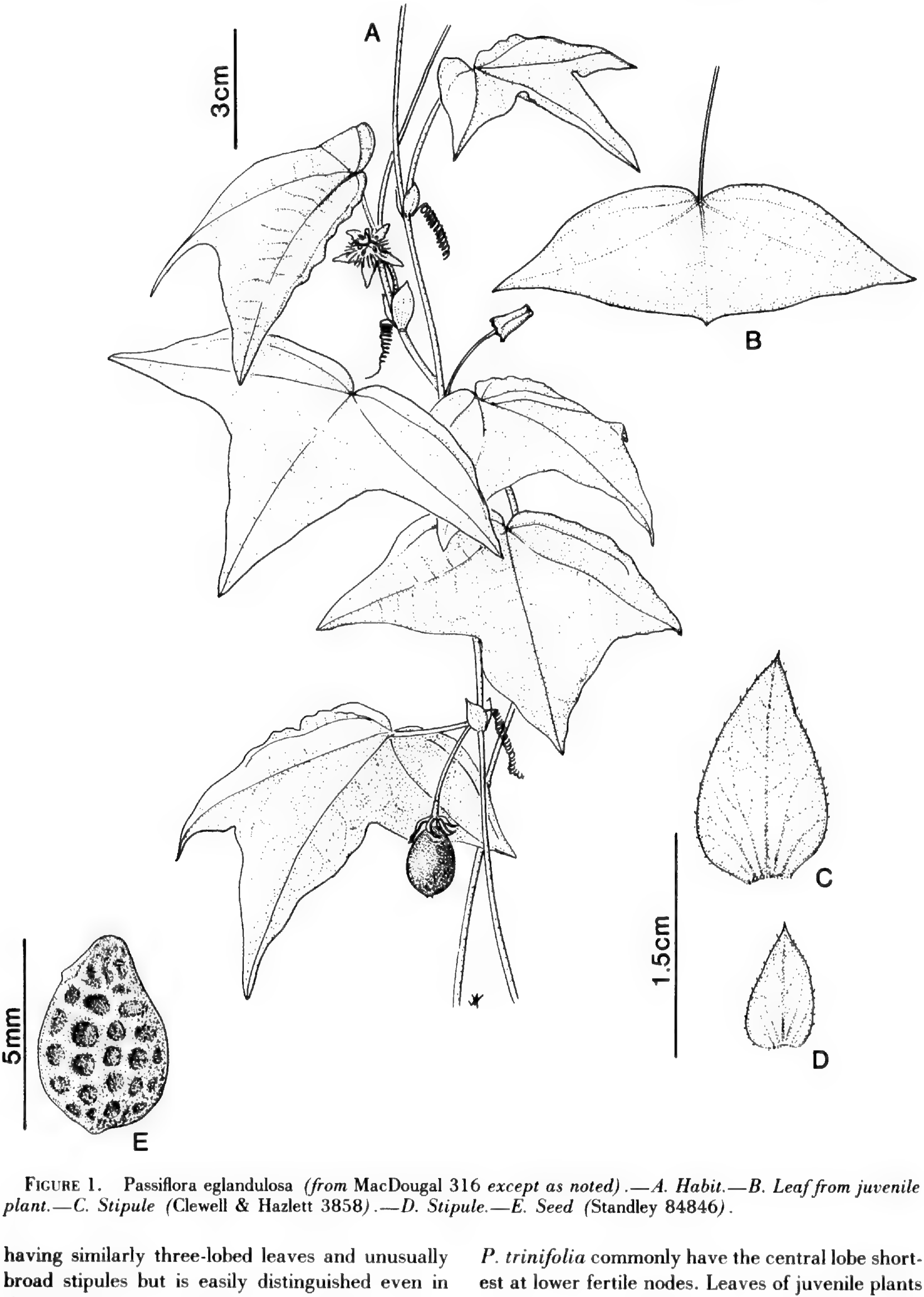

FIGURE 1. Passiflora eglandulosa *(from* MacDougal 316 *except as noted).—A. Habit.—B. Leaf from juvenile plant.—C. Stipule (*Clewell & Hazlett 3858*).—D. Stipule.—E. Seed (*Standley 84846*).*

having similarly three-lobed leaves and unusually broad stipules but is easily distinguished even in the herbarium by the absence of petiolar and laminar nectaries. Additionally, at fertile nodes the leaves of *P. eglandulosa* always have the central lobe longest; the laminas resemble those of the sympatric *Oreopanax sanderianus.* The leaves of *P. trinifolia* commonly have the central lobe shortest at lower fertile nodes. Leaves of juvenile plants are transversely bilobed in both species but are occasionally peltate in *P. trinifolia,* resembling miniature leaves of *P. coriacea* A. L. Juss. The leaves of juveniles are never at all peltate in *P. eglandulosa.*

FIGURE 2. *A. Flower of* Passiflora trinifolia *from type locality* (MacDougal 637GR).—*B. Flower of* Passiflora eglandulosa (MacDougal 316).

Living material of both species was collected in the field by the author and grown at Duke University, allowing detailed comparison of the flowers (Fig. 2). *Passiflora eglandulosa* differs notably in having flowers oriented above rather than near or below the horizontal plane; buds slightly horned at the apex; sepals proportionally narrower; outer coronal filaments much finer and broadest at the base; inner coronal filaments not broadly capitate; limen smaller and unspotted; more gracile androecium and gynoecium; and anthers that present pollen distally to laterally instead of subproximally. This anther orientation is unusual in the section and genus as a whole, and may be associated with a mode of pollination different than that of the other species in the section.

The habits and habitats of the two species are remarkably different, and they are not sympatric (Fig. 3). *Passiflora eglandulosa* climbs to around four meters in shady ravines and at the edges of wet premontane to montane broad-leaved forest on the volcanic cones of southern Guatemala to central Honduras. The chartaceous leaves are bright green adaxially and usually exhibit drip tips. In contrast, *P. trinifolia* is known only from Baja Verapáz, Guatemala, from three stations within 12 km of each other. The habitat is open, strongly seasonally dry pine with oak forest, associated with grasses and agave. Although perennial, the species has annual shoots that are only up to 1 m long, and some fertile shoots may be but 0.25 m long. The leaves are dark green, without drip tips, and are very stiff and rigid.

Passiflora trinifolia is apparently self-incompatible, since 33 attempts to self-pollinate it in the greenhouse failed to yield fruit. Fully mature fruits are unknown in this species. *Passiflora eglandulosa,* on the other hand, proved to be significantly self-compatible but not autogamous in cultivation. No unpollinated flowers set fruit over several years of cultivation, but 10 of 18 self-pollinated flowers produced (1–)3–9 seeds per fruit. The fruits turned purple 40–44 days after pollination. Nine or 10

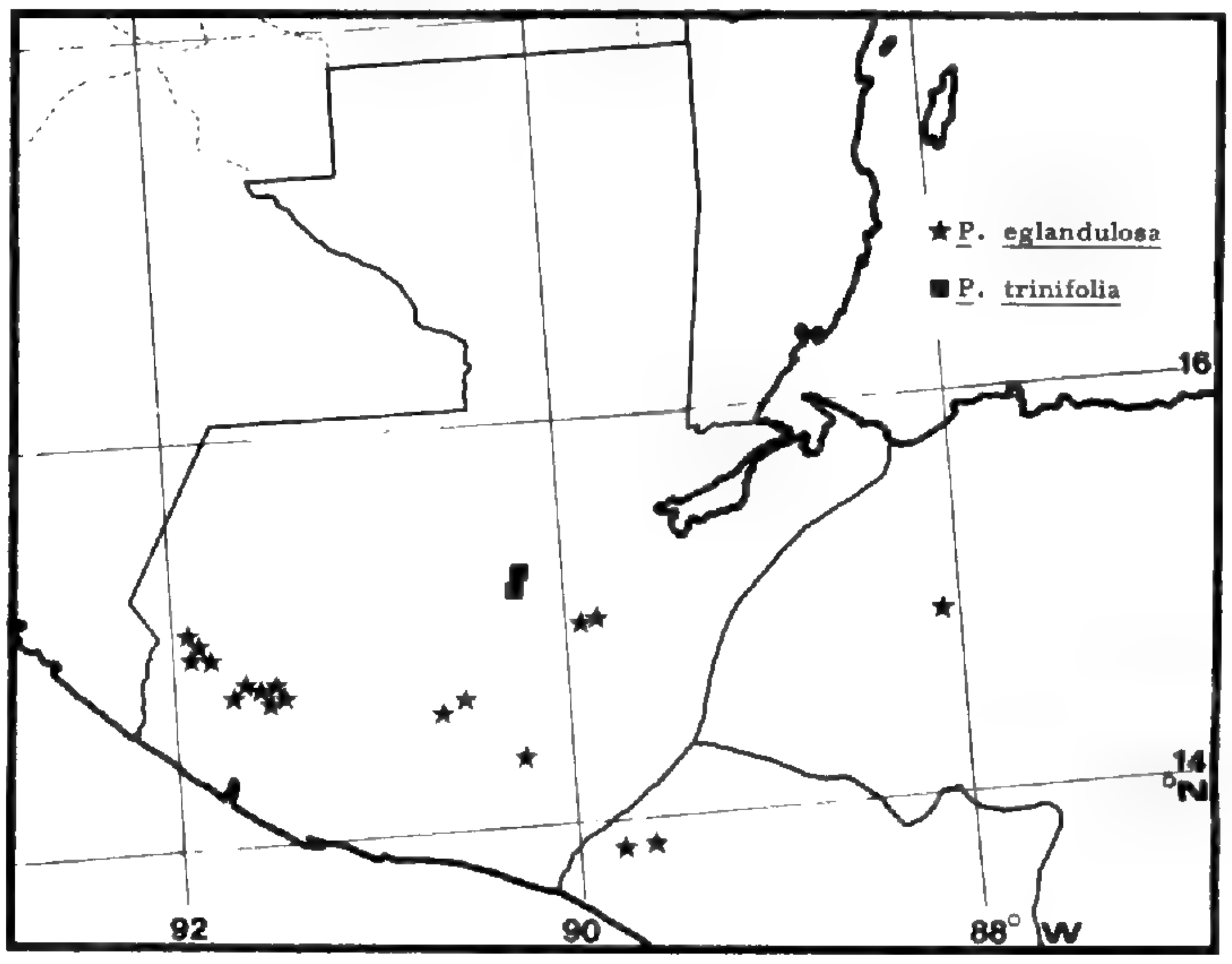

FIGURE 3. *Map of Guatemala and neighboring countries showing distributions of* Passiflora eglandulosa *and* P. trinifolia.

seeds per fruit appears to be the normal maximum for this species, judging from the several fruiting collections examined.

Passiflora eglandulosa (misidentified as *P. trinifolia*) has been included in three other studies of passionflowers. The development and physiology of the floral nectary of a clone of *MacDougal 316* was examined by Durkee et al. (1981), who found it to be similar to the others in their study. Dried leaf samples of *MacDougal 316* were chromatographically screened by McCormick (1982) for flavonoids. Concentrations were so low that no compounds could be verified, but according to McCormick (pers. comm.), traces of 3-*O*-glycosylflavonols but not *C*-glycosylflavones were detected. This is similar to several other species in section *Cieca*. Benson et al. (1975) reported the passionflower butterfly *Heliconius hortense* to be an herbivore of this species, a report that I confirm from field observations (insect voucher identified by J. Mallet).

I am grateful to D. E. Stone of Duke University, who directed the fieldwork and establishment of the living collections. The initial research was accomplished during graduate studies at Duke University under a National Science Foundation Fellowship, further supported by NSF grant DEB-7912607. Postdoctoral support has been generously provided by the Jessie Smith Noyes Foundation. John Myers prepared the drawing.

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MOLLINEDIA (MONIMIACEAE), A NEW GENUS FOR PARAGUAY

Two genera of Monimiaceae have been reported previously for Paraguay—the monotypic *Hennecartia* (*H. omphalandra* Poisson, endemic to Southern Brazil, eastern Paraguay, and northeastern Argentina) and *Siparuna* (*S. guyanensis* Aubl., cited by Hassler, 1917: 19). A third genus, *Mollinedia* (*M. clavigera* Tulasne), has recently been collected in eastern Paraguay. This is a predictable occurrence, since the species grows in the nearby states of São Paulo, Paraná, and Santa Catarina in southern Brazil (Peixoto, 1979).

Paraguayan material of Mollinedia clavigera *examined.* PARAGUAY. CANENDIYU: 15 km SE of Katueté, isolated pond in middle of cultivated field dominated by grasses with zone of agricultural weeds next to soybean field, 24°15'S, 65°40'W, *Hahn 2087*, 15 Feb. 84 (PY).

The three genera of Monimiaceae found in Paraguay can be distinguished as follows:

1a. Drupes free on a flat receptacle. Ovule pendulous. Anthers sessile, longitudinally dehiscent .... *Mollinedia*

1b. Drupes surrounded by a concave receptacle.
  2a. Drupes 1–2. Receptacle opening in segments. Anthers sessile, transversely dehiscent. Ovule pendulous .... *Hennecartia*
  2b. Drupes many. Receptacle not opening. Anthers stipitate, valvately dehiscent. Ovule erect .... *Siparuna*

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A NEW SPECIES OF *RUELLIA* (ACANTHACEAE) FROM WESTERN MEXICO

Ruellia L., of tribe *Ruellieae* Nees emend. Bremekamp (1944), is a tropical and subtropical genus of 200 species (Long, 1964). Its variation is impressive and its taxonomy complex. Lindau's (1895) circumscription is adopted here, and its unifying characters are contorted aestivation of the corolla lobes; didynamous stamens with muticous, equal or nearly equal two-celled anther lobes; and spheroid or ellipsoid, three- or more-porate, reticulate, and spinulose or banded pollen grains.

The primary centers of diversity of the genus are Indo-Malaya, Brazil, Africa, Mexico, and Central America (Long, 1970). In Mexico there are about 40 species of *Ruellia*, many of which occur locally, which suggests evolution by fragmentation (Ramamoorthy & Lorence, 1987). The variation in shape, size, and color of the corolla is very pronounced, indicating strong adaptive radiation to pollen vectors, which has led to definable natural constellations of infrageneric species groups. These deserve sectional ranks, but their recognition awaits revisionary studies (Ramamoorthy, in prep.). Among these is the chiropterophilous group: *Ruellia bourgaei*, *R. coulteri*, *R. palmeri*, *R. pulcherrima*, *R. jaliscana*, and the new species described below. The bats pollinating some of these are *Leptonycteris nivalis* and *Anoura geoffreyi*, both of the subfamily *Glossophaginae*.

Ruellia sarukhaniana Ramamoorthy, sp. nov. TYPE: Mexico. Michoacán: Coalcomán, S of Naranjillo, 1,200 m, in woods, 24 Nov. 1938, *G. Hinton et al. 12659* (holotype, GH). Figure 1.

Ruellia jaliscanae Standley affinis a qua foliis oblanceolatis differt.

Suffrutescent herbs to 1 m high. Stem distinctly 4-angled, with numerous cystoliths; angles reddish brown. The leaves 15–22 cm long, 2–3.8 cm wide, oblanceolate, acuminate at tip, narrowed and decurrent onto the 1-cm-long petiole, sinuately dentate along margin, chartaceous, venation (12–14 pairs) actinodromus, pilose above with short, multicelled, white hairs, pubescent along nerves below, cystoliths numerous. Inflorescence terminal and axillary, cymose-panicles, the peduncle and its branches densely tomentose with white hairs, interspersed with glandular hairs. Leaves subtending inflorescences reduced, bractlike, to 8 cm long, to 0.05 cm wide, oblanceolate. Bracts to 4.2 cm long, narrowly oblanceolate, tomentose with white hairs; bracteoles linear to subulate, glandular hairy. Pedicel to 2 cm long, tomentose glandular hairy. Calyx 3.2 cm long, deeply subequally 5-lobed with 2 lobes longer than the rest, the lobes to 2.2 cm long, 0.3 cm wide, linear, villous with glandular hairs. Corolla to 7 cm long (the tube 3.5 cm long, 4 mm wide), yellowish, the throat 2.5 cm long, 1 cm wide, the lobes 1 cm long, 1 cm wide. Stamens 4 in pairs, the filaments 1.5 cm long; anthers 0.7 cm long. Ovary 6 mm high, glabrous, the nectariferous disc surrounding ovary 2 mm high, fleshy, the style 5.7 cm long, the stigma of 2 flat lobes. Seeds not known.

The species is named after Dr. José Sarukhán Kermez, formerly Director of the Instituto de Biología and currently coordinator of scientific research in the National University of Mexico.

Ruellia sarukhaniana is similar to *R. jaliscana* with which it shares the glandular hairy, linear-lanceolate calyx lobes and its corolla form and branched inflorescence. The new species differs from the broadly ovate leaved *R. jaliscana* by having oblanceolate leaves.

The two are allopatric: *Ruellia jaliscana* is restricted to northwestern parts of the transmexican volcanic chain in the state of Jalisco, and *R. sarukhaniana* is found in the Coalcomán area, the northernmost parts of the Sierra Madre del Sur. Their similarities and affinities suggest a possible common origin for the two species, with allopatry contributing to their differentiation.

I thank Drs. D. Wasshausen (US) and T. Daniel (CAS) for comments on an earlier version of the typescript, and Fernando Chiang (MEXU) for the Latin diagnosis.

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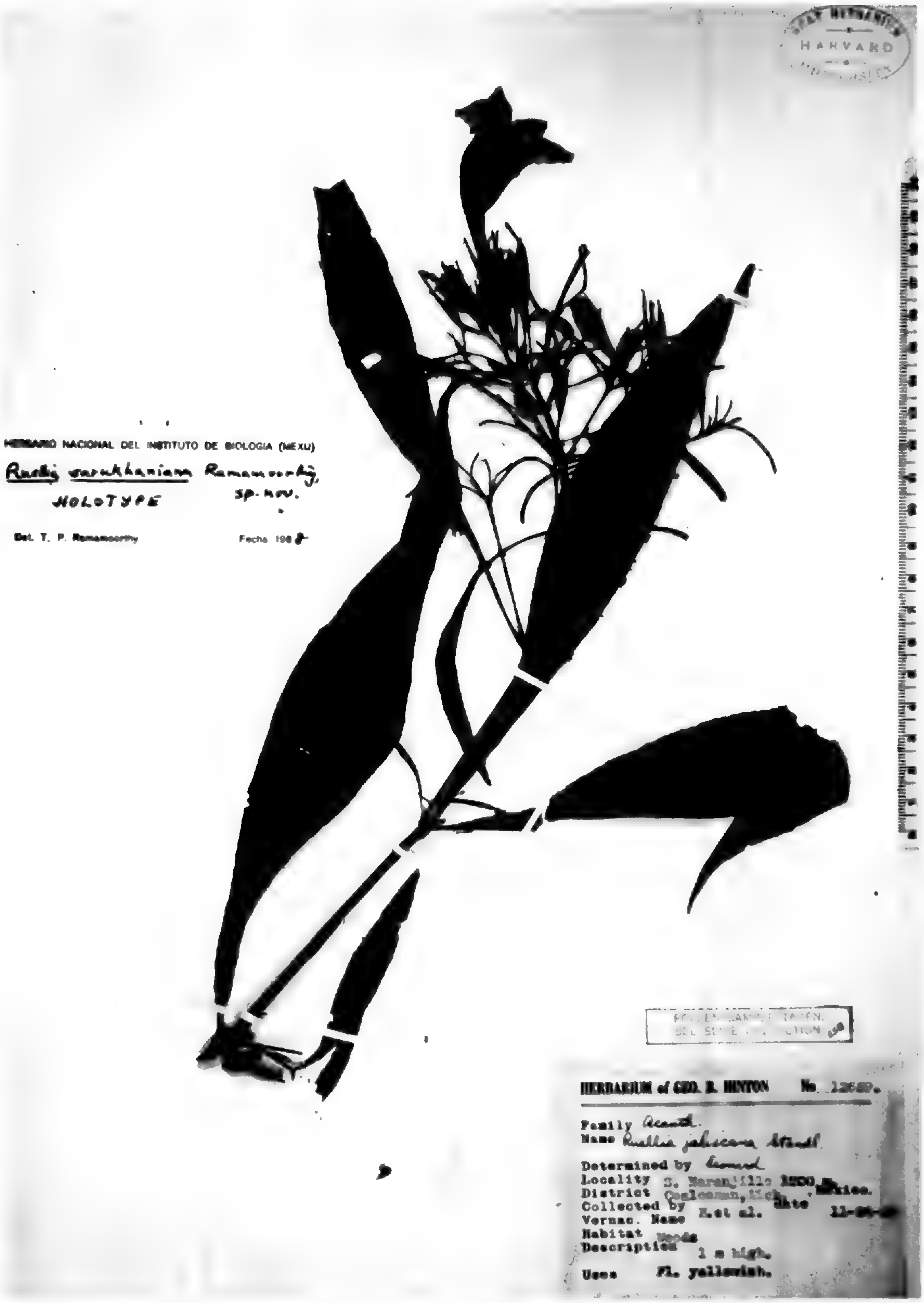

FIGURE 1. Ruellia sarukhaniana. *Photograph of holotype.*

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A NEW SPECIES OF *STILLINGIA* (EUPHORBIACEAE) FROM NORTHERN PERU

The predominantly neotropical genus *Stillingia* Garden ex L. was last revised by Rogers (1951), who recognized 23 American species. He did not treat the three or four paleotropical species that are distributed from Madagascar to Fiji. One additional species has since been described from Minas Gerais, Brazil (*S. argutedentata* Jabl., *Phytologia* 14: 451. 1967). A recently discovered species in northern Peru brings the total of American species to 25.

Stillingia parvifolia Sánchez Vega, Sagást. & Huft, sp. nov. TYPE: Peru. Dept. Cajamarca: Prov. Cajamarca, Distr. Namora, en la quebrada del Río Llallumayo, 2,775 m, 18 June 1984, *I. Sánchez Vega & W. Ruiz Vigo 3618* (holotype, CPUN, F neg. 62127; isotype, HUT). Figure 1.

Frutex glaber plus minusve ramosissimus, ramulis teretibus; folia brevipetiolata, alterna vel in brachyblastis 2–4 mm longis portata, laminae coriaceae, ovato-ellipticae, 6–11(–13) mm longae, margine callosae aequaliter serratae, dentibus glanduliformibus. Inflorescentiae terminales, bisexuales; cymulae masculinae uniflorae, bracteis navicularibus; cymulae femineae 1–3 basi inflorescentiae, sepala 3, orbicularia, navicularia, persistentia; capsulae globosae, profunde trilobae; semina (immatura) laevia, carunculata.

Shrub, glabrous, ± highly branched, the branchlets terete, ± maroon, the bark irregularly sulcate; short shoots 2–4 mm long. *Leaves* alternate or borne on short shoots, short-petiolate; petioles canaliculate, 1–1.5 mm long; blades coriaceous, ovate-elliptic, 6–11(–13) mm long, 5–6 mm wide, 1.25–2.2 times as long as wide, broadly obtuse to rounded at base, obtuse to rounded at apex; margin callose, minutely and remotely serrulate, the teeth glanduliform, 4–19 per side, the base eglandular; midrib conspicuous, prominent below, the secondary veins obscure. *Inflorescences* terminal, 1–2 cm long, bisexual. *Staminate cymules* single-flowered, the bracts obovate, acute, navicular, ca. 1.2 mm long, persistent, biglandular at base, the glands oblong or suborbicular, 0.8–1 mm long, patelliform; calyx 2-lobed, ca. 1 mm long; stamens 2, the filaments 1–1.2 mm long, the anthers 2, ca. 0.8 mm long, longitudinally dehiscent. *Pistillate cymules* 1–3 at base of inflorescence, single-flowered, the bracts as in the staminate cymules; sepals 3, orbicular, navicular, ca. 12 mm long, the apex truncate or obtuse, slightly erose; ovary sessile, 3-carpellate; styles 3, free, 1.5–1.7 mm long, recurved at tip. *Capsule* globose, glabrous, deeply 3-lobed, ca. 5 mm long; lobes of the persistent gynobase 3–4 mm long; seeds (only immature seen) ca. 4 mm long, ca. 1.5 mm wide, smooth, prominently carunculate.

Rogers (1951) distinguished two subgenera in *Stillingia*. Subgenus *Stillingia* is characterized by staminate cymules with 3–13 flowers, pistillate flowers with two or three well-developed sepals, and carunculate seeds, whereas subgenus *Gymnostillingia* (Muell. Arg.) D. Rogers is characterized by staminate cymules with a single flower, pistillate flowers with obsolete or minute and fugacious sepals, and usually ecarunculate seeds. The single-flowered staminate cymules of *S. parvifolia* would seem at first sight to place that species in subg. *Gymnostillingia*, but the ample and persistent sepals of the pistillate flowers and the carunculate seeds argue against an easy accceptance of that disposition. Furthermore, the restriction of subg. *Gymnostillingia* to Mexico and adjacent areas of Guatemala and the United States makes such a conclusion even more unlikely. In addition, *S. parvifolia* is not particularly close morphologically to any of the species that comprise subg. *Gymnostillingia*.

Stillingia parvifolia shares several specialized characters with two South American species of subg. *Stillingia*, *S. peruviana* D. Rogers (the only other species of the genus in Peru), and *S. bodenbenderi* (Kuntze) D. Rogers of Brazil and Argentina. All three species are shrubs, have small short-petiolate leaves that are often borne on small peg-like short-shoots, and leaf margins that are evenly serrate, often callose, and with peculiar glanduliform serrations.

The most reasonable interpretation of *S. par-*

ANN. MISSOURI BOT. GARD. 75: 1666–1668. 1988.

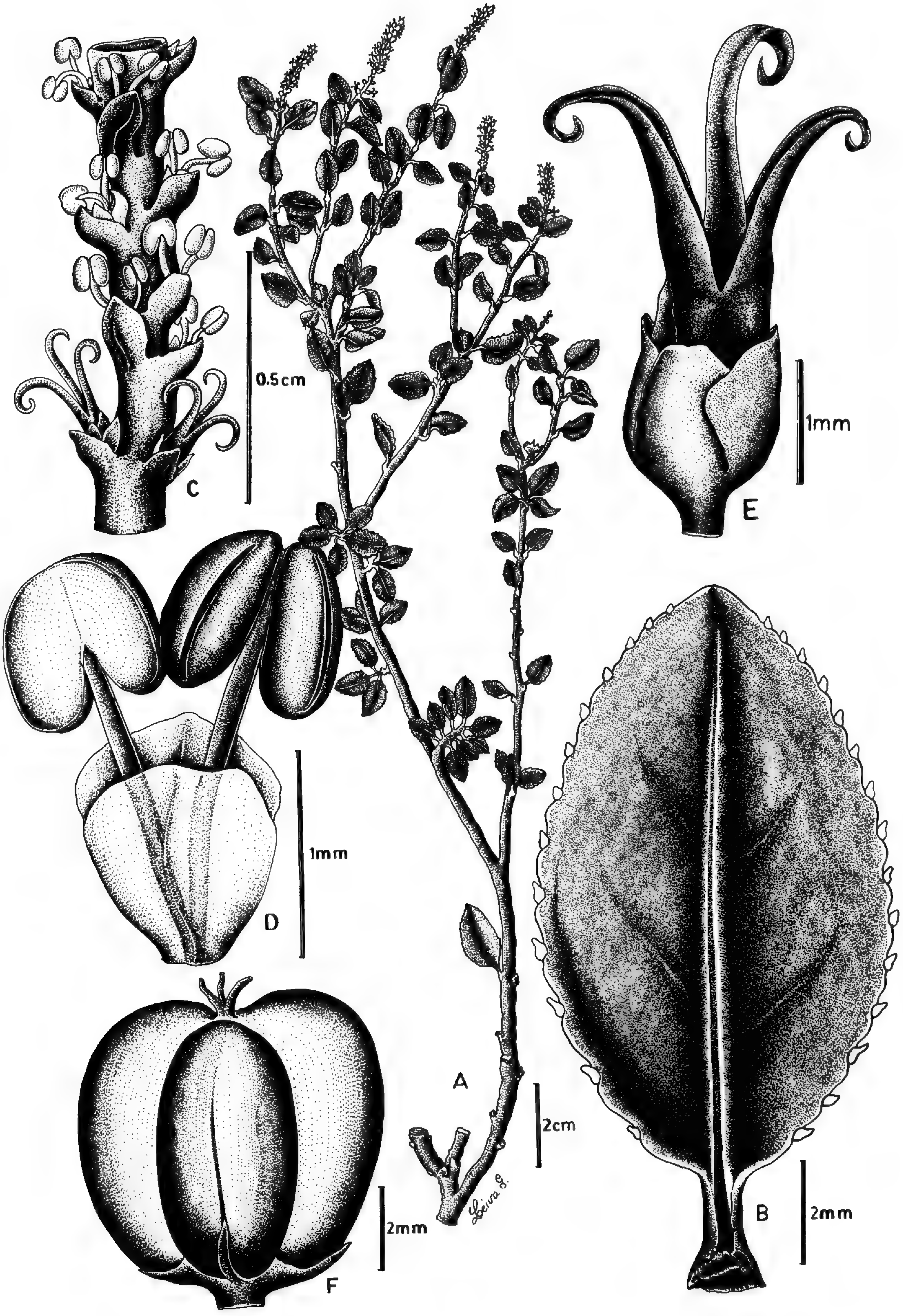

FIGURE 1. Stillingia parvifolia (Sánchez Vega & Ruiz Vigo 3618, *CPUN*).—*A. Flowering branch.—B. Leaf.—C. Lower portion of inflorescence.—D. Staminate flower.—E. Pistillate flower.—F. Capsule.*

vifolia would seem to be that it belongs to subg. *Stillingia*, where it is particularly closely related to *S. bodenbenderi* and *S. peruviana*, and that it has developed a reduced staminate cymule independently from the species in subg. *Gymnostillingia*.

Stillingia parvifolia may be distinguished from its closest relatives by means of the following key:

KEY TO *STILLINGIA PARVIFOLIA* AND RELATIVES

1a. Staminate cymules 5–7(–9)-flowered; branchlets slender, wandlike, 1–1.5 mm thick; petioles 2–3(–7) mm long; blades (0.8–)2–4 cm long, tapering to an acute (rarely rounded) apex; staminate bracts plane.
    2a. Petioles 0–3 mm long; leaf margins prominently callose, the serrations obscurely glanduliform; staminate bracts rounded, not mucronate .... *S. bodenbenderi*
    2b. Petioles 2–7 mm long; leaf margins obscurely callose, the serrations prominently glanduliform; staminate bracts deltate, mucronate .... *S. peruviana*
1b. Staminate cymules 1-flowered; branchlets not wandlike, 2–3 mm thick; petioles 1–1.5 mm long; blades 6–11(–13) mm long, not tapering to apex, this rounded or obtuse; staminate bracts navicular .... *S. parvifolia*

All three species in this group have highly restricted distributions and are poorly known. *Stillingia peruviana* is known from three collections in Huancavelica Province, Peru, while *S. bodenbenderi* is known from only two collections in Córdoba Province, Argentina, and a third from the state of São Paulo, Brazil. The distinctions between *S. bodenbenderi* and *S. peruviana* are not entirely convincing; the relative status of these two species will depend on the future availability of more ample collections.

Stillingia parvifolia is known only from the type collection from dry forest in a rocky ravine with clayey soil, where its associates include the shrubs *Myrica* sp., *Prunus* sp., *Piper* sp., and *Gynoxys* sp.; the herbaceous perennials *Calceolaria phaceliifolia* Edwin and *Dalea* sp.; as well as several annuals.

We are grateful to Segundo Leiva González for preparing the drawing and to Dr. Michael O. Dillon of the Field Museum for facilitating communications between the authors.

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KUBITZKIA VAN DER WERFF, A SUPERFLUOUS NAME OR NOT?

Kostermans (1988) discussed the need for a new generic name to replace *Systemonodaphne* Mez and came to the conclusion that the new name *Kubitzkia* van der Werff (Taxon 35: 164. 1986) is superfluous. Kostermans's argument is that Meissner (1864) cited *Laurus geminiflora* Desv. as the basionym of his *Goeppertia geminiflora* with a question mark; his opinion is that citation of a doubtful synonym in the description of a new taxon rules out this doubtful synonym as the basionym of the new taxon and that, in the case of *Kubitzkia, Laurus geminiflora* Ham. is not the basionym of *Goeppertia geminiflora,* and therefore also not the type species of *Systemonodaphne* Mez. The difficulty is that here one is led to speculate whether Meissner, when he cited *Laurus geminiflora* Ham. as a basionym of his *Goeppertia geminiflora* with a question mark, accepted what he published or published what he did not accept (see Articles 34.1 and 34.2 of the Code). In his particular case, the choice is an easy one for the following reasons: A) Meissner (1864, p. 175), under his description of *Goeppertia* (?) *geminiflora,* cited the earlier references as follows: "*Laurus geminiflora* Desv. in Hamilt. Prodr. Fl. Ind. occ. p. 37. Walp. Ann. 1 p. 578? (non Reinw.)." In Walpers (1848), this species is cited as follows, "*L.* ? *geminiflora* Dsvx. in Hamilt. Prodr. 37 (nec Reinw. mss.)." It seems very likely that Meissner, in citing the Walpers reference, cited him correctly and included Walpers's question mark. This question mark reflected the doubt Walpers expressed about the correct generic placement of *Laurus geminiflora* Ham. and not any doubt from Meissner as to *L. geminiflora* being the basionym of *Goeppertia geminiflora.* B) Meissner (1864) also included lists of excluded species at the end of each genus and gave the generic placement he accepted. On p. 236 he lists "*L. geminiflora* Desv. = *Goeppertia* (?) *geminiflora.*" When Meissner had doubt about the placement of certain species, he clearly expressed this; see p. 239: "*L. surinamensis* Sw. = Species obscura, cfr. *Oreodaphne guianensis* N.," or p. 236: "*L. dubia* Wall. = *Cinnamomum iners* Rw. δ ?" In my opinion, Meissner's treatment of *Goeppertia geminiflora* shows that Meissner accepted without doubt *Laurus geminiflora* Ham. as the basionym for his *Goeppertia geminiflora* and that for reasons explained earlier (van der Werff, 1986), *Kubitzkia* is the valid name for *Systemonodaphne* sensu Mez non sensu typi.

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—*Henk van der Werff, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.*

EDITOR'S NOTE

THANKS

The editors wish to close the year with an expression of gratitude to Dr. John Dwyer and Dr. Henk van der Werff for a year of willing, cheerful, and able help in reviewing and polishing Latin descriptions.

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Keys should be dichotomous, indented, and consistent with descriptions. Couplets should be numbered as 1a, 1b, 2a, and so forth.

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